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Life Table and Demographic Parameters of *Bactrocera dorsalis* Reared on Mango (*Mangifera indica* L.)

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Survivorship from egg to adult emergence and fecundity from three cohorts of Oriental fruit fly, *Batrocera dorsalis* eggs on mango (*Mangifera indica* L.) were studied under laboratory conditions (28 ± 2° C, 70-80% RH and 12:12h photoperiod). The life table showed that the survivorship of *B. dorsalis* falls in Type III with about 22.33% of the eggs successfully reached adult stage. The highest mortality recorded was in the 1st instar larvae (48.59%) with k-value of 0.29 indicated that is the key factor regulating the population size of *B. dorsalis*. The sex ratio (proportion of female to male) was 1.09:1. The maximum life span of female was 50 days and the trend of oviposition showed a peak at about the 26th day of female life span. Age specific fecundity (m_x) showed the earliest egg laying on day 35 and the last female died on day 69. The female laid on average 410.0±61.22 eggs. The intrinsic rate of natural increase (r_m) was 0.06 per female per day with mean generation time (T_c) of 46.39 days. The net reproductive rate (R_o) was 13.68 female offspring per female and the population of doubling time occurred within 12.38 days. This showed that the population of *B. dorsalis* has rapid buildup in short period of time.

Keywords: *Bactrocera dorsalis*, fruit fly, artificial diet, life table

INTRODUCTION

One of the most suitable methods to account for natality and reproduction of a population is through a life table analysis (Begon and Mortimer, 1981; Price, 1997). It is the only solid theory to describe in details the survival, stage differentiation and reproduction of insects such as fruit flies (Huang and Chi, 2012). In addition, the demographic information of the insect can be demonstrated through a life table construction (Maia et al., 2000). Later, the biology of the insect can be understood in order to develop a complete management system for that specific insect mainly a control strategy for particular insect pest species.

An Oriental fruit fly *Bactrocera dorsalis* Hendel (formerly known as *Bactrocera papayae*), is considered the most virulent and serious fruit fly species because it can attack about 209 plant species from 51 different families (Chua, 1991; Drew and Romig, 1997; White and Elson-Harris, 1992). In Peninsular Malaysia, commercial crops such as mango (*Mangifera indica* L.) has been seriously attacked by *B. dorsalis* (Allwood et al., 1999; Wee and Tan, 2005). Studied by Salmah et al. (2017) found that *B. dorsalis* is the predominance species and seriously infested mango in Peninsular Malaysia if not properly

controlled. Therefore, this study provided basic information on the life stages and demographic parameters of *B. dorsalis* conducted on mango larval diet under laboratory conditions. Life table studies on *B. dorsalis* in Malaysia will provide the necessary data for its mass production in a pest management programs.

MATERIALS AND METHODS

Laboratory Cultures and Rearing of *Bactrocera dorsalis*

The adults of *Bactrocera dorsalis* Hendel (Diptera: Tephritidae) used in this experiment were obtained from the established fly colonies cultured (fifth generation) and maintained in the laboratory. Fifty pairs of newly emerged *B. dorsalis* adults from the stock culture were sexed and released into a new adult rearing cage (30 x 30 x 30 cm). The adults were fed with water soaked on sponge and sugar cubes with mixture of yeast extract and sugar at ratio 3:1. The experiment was conducted at the Laboratory of Entomology, Department of Plant Protection, Faculty of Agriculture, Universiti Putra Malaysia. All experiments were maintained in a laboratory room with a temperature of 28 ± 2^{o} C, 70-80% RH and 12:12h photoperiod.

Eggs Collection

The eggs of *B. dorsalis* were collected when the age of adult flies from above cultures reached 3 weeks old. According to Walker et al. (1997), at this age the females of *B. dorsalis* lay eggs at the optimum level. Fruit domes were used as egg collection device by cutting papaya fruit into half. The flesh of papaya was scooped out and leaving as little flesh as possible on the skin and domes were washed and placed in a Petri dish (15 cm diameter). The outer skin of domes was pierced 30-50 times with an entomological pin (#0) as oviposition holes. The papaya domes were placed inside the cage and the flies were allowed to oviposit for 24 hours and then the eggs inside the domes were collected using camel hair fine brush. The collected eggs were placed on moistened filter paper to ensure the eggs remain moist and viable.

Mango Larval Diet Preparation

The larvae of *B. dorsalis* were reared on mango pulp diet instead of the whole mango fruit to facilitate the daily calculation of survival and mortality of larvae in survivorship study. The formula of the larval diet was adopted and modified from Ekesi and Mohamed (2011) as presented in Table 1. All ingredients were thoroughly mixed by using a blender (BRAUN ZK 200, Germany) for 3 minutes. The diet was stored in a plastic container (18x12x5 cm) at 4ºC for 24 hrs prior to use to allow the mixture to gel before decanting excess water.

Table 1: Formula ingredients of mango pulp larval diet

Ingredients	Quantity (%)
Mango pulp	25.00
Torula yeast	8.10
Nipagin	0.20
Sodium benzoate	0.20
Sugar	8.00
Water	58.50
Total	100.00

Survivorship Determination of *B.dorsalis*

Survivorship from egg to adult emergence of *B. dorsalis* were studied with three different cohorts. Each cohort approximately comprising of 100 viable eggs of one-day-old of *B. dorsalis* obtained from fifth generation colonies. The freshly collected eggs were counted under Meiji Techno RZ stereo microscope (Meiji Techno, Japan). For each cohort, the eggs were then divided into 10 groups with 10 eggs per group for survivorship observation. Each group of eggs was placed on 20 g of mango pulp diet (in Petri dish 6 cm in diameter).

To ensure the eggs remain moist, the Petri dish was covered and sealed with parafilm for the first 3 days. After egg hatching, the larval developmental time was measured as time in days within each stage. The eggs and early instar larvae were observed under Meiji Techno RZ stereo microscope (Meiji Techno, Japan) to record egg hatch and the survival of the first instar larvae until they reached the third instar larval.

The third instar larvae which can be identified by their jumping behaviour were transferred from rearing Petri dish using a fine forcep to plastic cups containing 0.5 cm sterilized fine vermiculite as pupation medium. After 3 days of incubation, the pupae were sieved from vermiculite and placed individually in small plastic cups (4.5 cm height, 7 cm diameter) layered with moistened tissue paper for adult emergence. The survival and mortality of eggs, larvae, pupae and adults were observed and recorded daily.

Fecundity Determination of *B.dorsalis*

Five pairs of 1-day old fly adults were selected from adults that emerged in survival and mortality study

and each pair was kept in inverted plastic containers (10.5 cm height, 12 cm diameter). The top of the containers was cut out in the middle and replaced with muslin cloth for ventilation. The adults were fed with granulated sugar and water (soaked in a piece of cotton wool) in a vial cap (2 cm in diameter), and yeast extract mixture (plastered on a small filter paper) was provided at 5-days old.

At day 12 of adult's age (which at this age the females of *B. dorsalis* will start to oviposit their eggs based on the preliminary study), a fresh slice of papaya (2x2 cm) which the flesh was scooped out and the outer skin of papaya was pierced several times with an entomological pin (#0) as oviposition holes was provided as oviposition egging device. The papaya slice was exposed to females in each plastic containers for 24 hrs. After 24 hrs of exposure, the papaya slices were removed from containers and eggs were counted daily under Meiji Techno RZ stereo microscope (Meiji Techno, Japan). The new fresh slice of papaya was supplied every day for oviposition. Eggs laid by each female were counted and recorded daily until the death of all individuals. The pre-oviposition periods, oviposition periods and fecundity of females and adult longevity of females and males of *B. dorsalis* adults were recorded.

Data Analysis

The experiment design was based on Completely Randomized Design (CRD) with three cohorts per diet for survivorship study and five replications for fecundity and other biological parameters. Comparison of male and female longevity was subjected to independent sample t-test at 0.05 level of significance. All the analysis were done using MINITAB 18 software.

Standard life table parameters and population age structures were calculated from daily records of survival, mortality and fecundity of each cohort. The parameters were following the procedures outlined by Carey (1993) and Southwood (1978) as shown in Table 2.

Table 2: Definitions for life table and demographic parameters of *B. dorsalis*

Parameter	Definition
x	Age interval in days/developmental stage
l_x	Proportion of individuals surviving to start of the age interval. The number of individuals alive, during a given age interval class as a fraction
L_x	Number of individuals alive between age x and x+1
d_x	Number dying during age interval x
100_{qx}	Percent apparent mortality
S_x	Survival stage rate within stage
T_x	Total number of living individuals at age x and beyond the age x
e_x	Life expectancy for individuals of age x
m_x	Number of female eggs laid by average female at age x
Pre-oviposition period	Amount of time prior to eggs being laid
Gross reproduction rate (GRR)	Theoretical natality rate during lifetime of organism
Daily reproduction	Average number of eggs produced per day in terms of entire female lifespan
Female longevity	Life-span of female
Male longevity	Life-span of male
R_o	Net reproductive rate
r_m	Intrinsic rate of natural increase
T_c	Cohort generation time (in days)
T	Corrected generation time
λ	Finite rate of increase, the number of female off-springs female^{-1} day $^{-1}$
DT	Doubling time, the number of days required by a population to double
GRR	Gross reproduction rate

RESULTS

Age-specific Survival Life Table for *B. dorsalis*

The patterns of survivorship of three cohorts of *B. dorsalis* reared on mango diet are shown in Figure

1. Overall, the survivorship in all cohorts showed similar pattern which a sharp drop of survivorship occurred on day three and lasted until day six with high mortalities were recorded during 1st instar larvae. Percentage of eggs hatchability of *B. dorsalis* recorded was 92%, 97% and 95% on Cohort 1, Cohort 2 and Cohort 3, respectively. However only 18%, 29% and 20% of individuals were survived until adult's stage for respective Cohort 1, Cohort 2 and Cohort 3. The first emerging adults recorded was on day 21 for all cohorts and the last adult died was on day 63 (Cohort 1), 68 (Cohort 2) and 66 (Cohort 3).

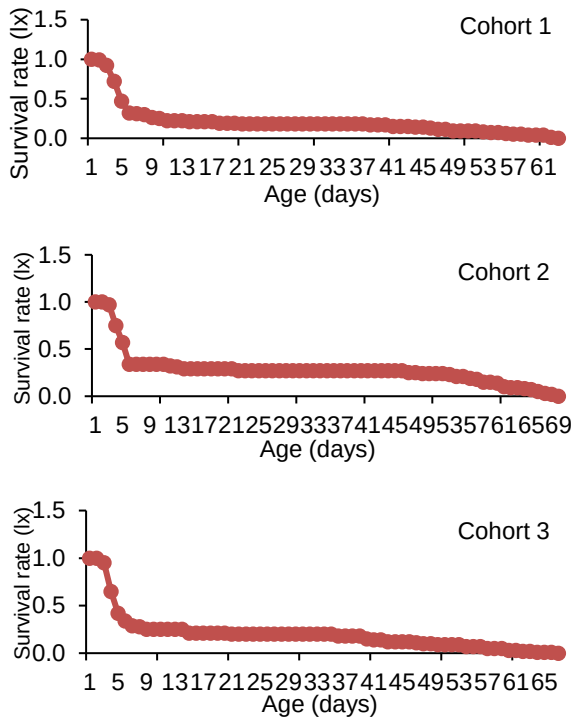

Figure 1: Patterns of survivorship curve (l_x) of *B. dorsalis* for three cohorts.

The pooled life table of *B. dorsalis* for the three cohorts was showed in Table 3. All larvae underwent three larval moults before transforming into pupae. The fruit fly pupa gradually changed from pale yellow to dark brown before adult emergence. From the total of 300 eggs of *B. dorsalis*, only 22.33% of individuals successfully reached the adult stage with an average sex ratio of female to male was 1.09:1. The highest mortality recorded was in the 1st instar larvae (48.59%) with K-value of 0.29 followed by mortality in the 2nd instar larvae (36.99%) with K-value of 0.20, 3rd instar larvae (15.21%) with K-value of 0.07 and pupa (14.10%) with K-value of 0.07 (Table 3).

Table 3: Stage-specific pooled life table of *B. dorsalis*

x	l_x	d_x	T_x	e_x	K-value
Egg	300	16	780.5	780.5	0.02
Larval					
1st instar	284	138	488.5	515.8	0.29
2nd instar	146	54	276.5	567.8	0.20
3rd instar	92	14	157.5	513.0	0.07
Pupa	78	11	72.5	278.9	0.07
Adult	67		0		

*Adult sex ratio (Female: Male) = 1.09:1
x=developmental stage in days, l_x=proportion of number entering stage, d_x=number of dying in stage x, T_x=total number of age x beyond the age, e_x=life expectancy

Age-specific Fecundity Life Table for *B. dorsalis*

Figure 2 shows the survivorship (l_x) and fecundity (m_x) curve of *B. dorsalis*. It was noted that the first female emerged was on day 21 and first oviposition began after 14 days of emergence (on day 35). The reproduction period of *B. dorsalis* lasted as long as 44 days after first adult emergence. The number of eggs deposited per surviving individual was varied and range from as low as 0.333 eggs (on day 64) to a very high value of 10.476 (on day 52). The eggs was actively produced when the female adults reached at age 14 to 41 days (from day 35 until day 61). The fecundity showed decreasing trend after day 61 and the females remained alive for a maximum of 50 days.

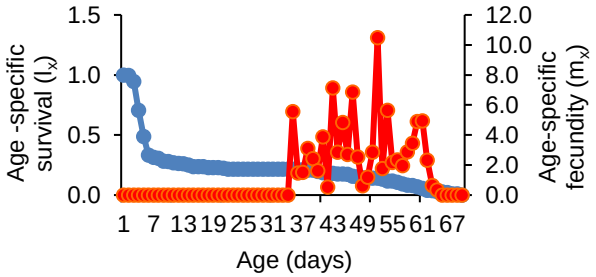

Figure 2: Daily age-specific survival (l_x) and fecundity (m_x) of female *B. dorsalis*.

Population and Reproductive of *B. dorsalis*

Table 4 summarized the population and reproductive parameters of *B. dorsalis*. The intrinsic rate of natural increase (r_m) of *B. dorsalis* on mango was 0.06 per female per day and the daily finite rate of increase (λ) was 1.06 female

progenies per female per day with mean generation time (T_c) of 46.39 days. The gross reproduction rate (GRR) and net reproductive rate (R_o) of female were 95.60 and 13.68, respectively. Population of *B. dorsalis* required about 12.38 days to double its number.

Table 4: Life table parameters of *B. dorsalis*

Parameter	Formula	Values
Gross reproduction rate (GRR)	$\sum m_x$	95.60
Net reproduction rate (R_o)	$\sum l_x m_x$	13.68
Mean generation time (T_c), in days	$\sum (x l_x m_x) / \sum l_x m_x$	46.39
Intrinsic rate of natural increase (r_m)	$\ln R_o / T_c$	0.06
Finite rate of increase (λ)	e^r	1.06
Doubling time (DT), in days	$\ln 2 / r_m$	12.38

Adult Longevity, Pre-oviposition Period, Oviposition Period and Reproduction of *B. dorsalis*

The results in Table 5 shows that the adult longevity of *B. dorsalis* male was not significantly different (P>0.05) with female longevity but the male longevity (42.0 ± 4.5 days) was slightly longer than female (39.9 ± 4.8 days). The pre-oviposition and oviposition period of *B. dorsalis* females were recorded as 14.3 ± 0.3 days and 19.0 ± 3.2 days, respectively. Results showed that the daily eggs produced by a *B. dorsalis* female was recorded as 93.18 ± 17.2 eggs whilst female fecundity was about 410.0 ± 61.2 eggs (Table 5).

Table 5: Adult longevity and reproductive parameters of *B. dorsalis*

Parameter	Mean ± SE
Male longevity (days)	42.0 ± 4.5 a
Female longevity (days)	39.9 ± 4.8 a
Pre-oviposition period (days)	14.3 ± 0.3
Oviposition period (days)	19.0 ± 3.2
Daily eggs (eggs/day)	93.2 ± 17.2
Fecundity (eggs/female)	410.0 ± 61.2

DISCUSSION

The survivorship curves (l_x) of *B. dorsalis* observed in the three cohorts as shown in Figure 1 recorded high mortalities during early instar larvae stage and low mortality during later life stages, indicated that it falls in Type III as classified by Schowalter (2016). According to Schowalter (2016), Type III survivorship among insects must have very high rates of mortality at the early stages of development but low on late stages as to ensure that it can reach ages of maturity to produce eggs for their next generation.

The number of emerged females and males showed that the sex ratio (proportion of female to male) at 1:1.06.was similar with Mohd Noor et al. (2011) but they reared it on guava. Huang and Chi (2012) recorded that the sex ratio of *B. curcubitae* was close to 1:1 in cucumber, carrot and sponge gourd media. Equality of *Bactrocera* sex ratio (around 1:1) facilitates the way to control fruit flies populations in the field through pheromone traps such as cure lure and methyl eugenol that attracts male flies (Kumar et al., 2011). On the other hand, sex ratio approaches 50:50 in insect species generally indicates equally important roles of males and females given that selection would minimize the less-productive sex and in the same time maximizes genetic heterogeneity (Schowalter, 2016). This is very important in optimizing production flies in the fruit flies mass-rearing program.

In this study, results showed that the highest mortality recorded was in the 1st instar larvae with K-value of 0.29. The highest K-value recorded during the 1st instar larvae indicated that it was the main factor regulating the population size of *B. dorsalis* on mango and suggested that it is the most suitable stage to control *B. dorsalis* population. According to Kakde et al. (2014), the increasing or decreasing of number from one generation to another is showed by a key factor known as 'K-value' and it was computed as difference between successive values for log 'l_x' but the total generation mortality was calculated by adding 'K' values of different development stages which are indicated as 'K'. However, this high mortality in the early instar larvae stages may be also due to the ventilation in the laboratory was not sufficient enough as ventilation is important for efficient gas and heat exchange (Walket et al., 1997). Furthermore, intraspecific competition between larvae on diet provided may be occurred. Thus, the process of checking and counting the number of larvae that live and die every day may cause injury to the larvae and this also may contribute to the high mortality of the larvae. Nonetheless, Chang et al. (2007) stated that high mortalities of early instar larvae before reaching the third instar stage may be due to the microbial infestation of the eggs. For

example, Mohd Noor et al. (2011) reported that from 96.03% of *B. dorsalis* eggs hatched only 26.39% of the larvae reached the third instar stage due to microbial infections on the guava pulp when the pulp is changed and exposed to the environmental laboratory.

Results also showed that the lowest mortality was recorded in eggs stage (5.33%) with K-value of 0.024 (Table 3). This may be due to eggs are an immobile stage and were inserted underneath the diet which safely concealed. The scenario is similar in the field which the eggs were inserted beneath the skin of host fruits and make it more survival and hard to control. On the contrary, Mohd Noor et al. (2011) found that about 4% of *B. dorsalis* eggs failed to hatch. They suggested that this phenomenon might be due to the temperature fluctuated in the laboratory which may affect the viability of the eggs. According to Walker et al. (1997), the *Bactrocera* eggs must always remain moist to ensure a high percentage of hatchability which should be around 75-95%.

It was observed that the eggs were actively produced by female within age 14 to 41 days which closed to that obtained by Huang and Chi (2014). Tthey recorded that higher age-specific daily fecundities of *B. dorsalis* females on mango were observed during ages 25-45 days. On the contrary, *B. dorsalis* females deposited the maximum number of eggs on mango was between the 11th and the 28th day after emergence (Gomina et al., 2014). Hence, Walker et al. (1997) stated that the optimum reproduction age of *Bactrocera* fruit flies is when the female flies are about 3 to 7 weeks old. In addition, the ability of *B. dorsalis* females to live and reproduce in longer time make it suitable for use in mass rearing program particularly on production and maintenance the insect culture in laboratory as intended to produce high quality flies mainly for sterile insect technique (SIT), evaluation of attractants, host for natural enemies and other basic biological studies.

Meanwhile, the characteristic life patterns and population growth of particular species was provided by useful keys in life table parameters such as r_m, T_c, DT, GRR and R_o. In general, short developmental time and high reproduction rate are presumed reflect the adaptability of the species. In this study, the life table results displayed that this particular *B. dorsalis* species shows high net reproductive rate (R_o) and finite rate of increase (λ) with lower doubling time (DT). This showed that the population of *B. dorsalis* has rapid buildup in short period of time. Therefore, suitable management strategies for controlling *B. dorsalis* should be properly evaluated in order to prevent the fruit flies infestation particularly through IPM program such as fruit bagging and biopesticides application.

The findings also showed that the longevity of female and male was not significantly difference but the male's longevity was slightly longer than a female. The slightly differences of *B. dorsalis* adult longevities observed in this study would be linked to the larval diet used. As stated by Papadopoulos et al. (2002), the suitability of a host for larval development was determined by the nutritional elements, texture of the fruit pulp and chemical composition. Moreover, Vargas et al. (2000) stated that the growth of fruit flies and longevity of the adult's tephritids depends on the diet consumed either natural, semi-natural or artificially diet. Nevertheless, the larval diet is not the only factors influenced the adult longevity. According to Wang et al. (2009), adequate protein source in adult's diet will prolong their longevities but the flies will died earlier if the source is provided early as they will utilize and reproduce faster. In addition, female longevity of fruit flies was significantly influenced by mating activities which the mating and remating process can decreased their longevity (Wei et al., 2015).

Next, the results showed that the pre-oviposition, oviposition period, daily eggs and fecundity of *B. dorsalis* reared on mango pulp were different with previous studies (Huang and Chi, 2014; Vargas et al. 2000). According to Gomina et al. (2014), the differences of fecundity observed in *Bactrocera* species mainly affected by the diet provided to the larval besides the host variety and quality, the methodology used in the follow up of egg hatching as well as the experimental conditions could also affect the fecundity. For example, the fecundity of *B. dorsalis* larvae fed with the whole mango was recorded at 252.3 eggs but higher fecundity was observed when the larvae fed with the artificial diet (1122 eggs) (Huang and Chi, 2014).

CONCLUSION

In this study, it was observed that only 22.33% of *B. dorsalis* eggs successfully reached adult stage indicated that the survivorship of *B. dorsalis* was classified as Type III. The results also showed that high mortality occurred during the early immature stages of *B. dorsalis,* especially in 1st instar larvae.

This high mortalities recorded may be regarded as the key factor regulating the population size of *B. dorsalis*. It is very useful to know when a pest population suffers high mortality because at this time is usually when it is the most vulnerable stages. Therefore, by knowing such vulnerable stages from a life table study, a time-based application of suitable management control methods for the insect pests can be prepared as well as to conserve the natural enemies and to reduce the negative impact on the environment. In addition, the life table results displayed that this particular species shows high net reproductive rate (R_o) and finite rate of increase (λ) with lower doubling time (DT). This showed that the population of *B. dorsalis* has rapid buildup in short period of time. The demographic parameters of *B. dorsalis* of mango in Malaysia will provide the necessary data for its mass production and strategy in IPM programs for the pest.

CONFLICT OF INTEREST

The authors declared that present study was performed in absence of any conflict of interest.

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AUTHOR CONTRIBUTIONS

SM designed and performleed the experiments, data collection and analysis, and also wrote the manuscript. MR help with the data analysis. NAA is the project leader and supervisor of this research, and reviewed the manuscript. HMS reviewed the manuscript. All authors read and approved the final version.

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