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Effects of Diet Composition on the Life-History Traits of *Bactrocera Dorsalis* (Hendel) (Diptera: Tephritidae)

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Abstract

Nutrient acquisition at the larval stage has significant impacts on the development, body weight, and fecundity of fruit flies. In this study, we examined the effects of diet composition on the life-history traits of the oriental fruit fly Bactrocera dorsalis (Hendel) (Diptera: Tephritidae). We reared the flies on four larval diets, namely three artificial diets, which had the main ingredients of sugar, brewer's yeast, and preservatives; and one fruit-based diet, which had the main contents of ground guava, brewer's yeast, and preservatives. The three artificial diets had varied yeast-to-sugar ratios (Y:S) of 5:1 in the protein-rich diet, 1.67:1 in the standard diet, and 1:3 in the sugar-rich diet. Differences in development time, pupal weight, adult weight, and fecundity of *B. dorsalis* were investigated. It was found that the development times of fruit flies on the protein-rich and fruit-based diets were shorter than those on the sugar-rich and standard diets. Pupae and adults in the fruit-based and standard diets were heavier than those from the protein-rich and sugar-rich diets. There was a strong effect of diet on the per-day fecundity whereby the flies in the fruit-based diet had the highest per-day fecundity, while the lowest per-day fecundity was in the sugar-rich diet. The per-day fecundity of the fruit flies on the standard and sugar-rich diets increased gradually from day 1 to day 15, while it decreased in the protein-rich and fruit-based diets.

Keywords

Diet composition, larval, development, body weight, reproduction

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Introduction

The oriental fruit fly *Bactrocera dorsalis* (Diptera: Tephritidae) is a destructive pest that has been recorded in many countries around the world and is especially common in Southeast Asian countries including Vietnam (Clarke *et al.*, 2005; Weems *et al.*, 2012; Zeng *et al.*, 2019). This pest has significant impacts on horticultural and agricultural production, causes great economic losses, and influences exported products (Clarke *et al.* , 2005). Like other species in the *Bactrocera* genus, *B. dorsalis* has high fecundity and longevity as well as superior mobility (Ekesi *et al.*, 2007), which has allowed them to become a highly invasive pest. In Vietnam, *B. dorsalis* has been recorded on a wide range of fruits such as lychee, longan (Bui Minh Hong *et al.*, 2019), star apple (Truong Huynh Ngoc, 2010), mango (Tran Van Hau, 2015; Nguyen Thi Oanh & Ha Danh Duc, 2020), dragon fruit (Le Thi Dieu & Nguyen Van Huynh, 2009; Le Duc Khanh *et al.*, 2016), and guava (Nguyen Van Tuat *et al.*, 2015; Bui Minh Hong & Pham Thi Viet Chinh, 2018). Due to the serious impacts of this pest, control tactics have been developed. However, since the hosts of *B. dorsalis* are mostly fresh products, the use of chemical pesticides is not recommended due to concerns for people's health. To ensure food safety, biological control methods such as releasing parasitoid wasps (Vargas *et al.*, 2007; Gu *et al.*, 2018), introducing pathogenic nematodes (Godjo *et al.*, 2018), and the sterile insect technique (SIT) (Keawchoung *et al.*, 2000; Orankanok *et al.*, 2007) have been applied as part of integrated pest management systems. Among these methods, SIT could potentially be applied in a wide area with high efficiency (Guillén & Sánchez, 2007; Stringer *et al.*, 2017). To enhance the efficiency of this method, it is necessary to produce sterilized flies with good fitness and viability that are able to adapt after being released to the field; and therefore, ecological factors during the mass rearing process such as density, temperature, and especially diet should be considered.

Regarding the importance of diet, previous research has shown that the nutrient composition acquired during the larval stage greatly contributes to the development, fitness, and reproduction of fruit flies (Matzkin *et al.*, 2011; Güler *et al.*, 2015; Morimoto *et al.*, 2022). For example, larval diet influences the development time of the fruit flies *B. tryoni* (Morimoto *et al.* , 2022) and *Drosophila melanogaster* (Matzkin *et al.* , 2011; Güler *et al.* , 2015). The nutritional content strongly influences the body mass and size of fruit flies, whereby a sugar-rich diet increases body weight through a lipid accumulation process as shown in *D. melanogaster* (Rovenko *et al.*, 2015) and a protein-rich diet positively influences body weight through muscle building as shown in *Ceratitis capitata* Wiedemann (1824) (Diptera: Tephritidae). In addition, the sexual behavior and reproductive outcome of insects are also modulated by larval diet. For instance, a high protein content has been shown to significantly increase female fecundity of the fruit fly *B. tryoni* (Morimoto *et al.* , 2022). A protein-rich diet can shift the nutrient allocation from somatic tissue formation to reproductive tissue, which then influences reproduction (Kaspi *et al.*, 2002). In addition, a high level of sucrose in the diet and supplementary vitamins and minerals also increase fecundity (Geister *et al.*, 2008). Therefore, diet composition has long-lasting implications for the development, fitness, and reproduction of fruit flies. Despite this, there is a lack of knowledge of how larval diet composition, in particular the yeast-to-sugar ratio, influences the life-history traits of the oriental fruit fly *B. dorsalis*. To address this gap, we generated three artificial diets, namely protein-rich, standard, and sugar-rich diets, and one fruit-based (guava) diet, to assess the effects of larval diet composition on developmental time, body weight, and fecundity of *B. dorsalis*. We predicted that (1) flies reared on a sugar-rich diet will have higher body weights than those reared on a protein-diet; (2) flies reared on a protein-rich diet will have a higher fecundity; and (3) flies will develop faster on the fruit-based and standard diets due to the balanced ingredients in the diets.

Materials and Methods

Fly stock

Larvae of *B. dorsalis* flies were collected from 20kg of guava fruits from an orchard at Dong Du commune, Gia Lam district, Hanoi city in early 2020. The larvae were left to develop inside the guava fruits and maintained in a laboratory. The fruits were placed on Petri dishes and then kept in 1-litre boxes containing 100g of sawdust to facilitate pupation. Five days after pupation, pupae were separated from the sawdust by using a sieve and the pupae were then transferred into a mesh cage for adult emergence. Adults were fed on a free-choice of food *ad-libitum* of hydrolysed yeast, sugar, and water. Fifteen days after emergence, a small plastic bottle (100mL) with holes (size 1mm) was placed into the cage to collect eggs (Morimoto *et al.* , 2022). A paint brush was used to transfer the collected eggs to 90mm Petri dishes containing 25mL artificial diet as described by Moadeli *et al.* (2017) to maintain the colony. All stocks were kept in a controlled temperature cabinet at 25 ± 0.5°C and a light cycle of 12h light:12h dark at a laboratory of the Department of Entomology, Vietnam National University of Agriculture.

Diet manipulation

Three artificial diets and one fruit-based (guava) diet were created to test the effects of diet on the life-history traits of the fly *B. dorsalis*. The standard diet was created based on the methods of Moadeli *et al.* (2017) (with a yeast-to-sugar ratio (Y:S) = 1.67:1), and the Y:S ratio was manipulated to create the protein-rich (Y:S = 5:1) and sugar-rich (Y:S = 1:3) diets. The fruit-based diet (guava) was made from ground guava with supplemental brewer's yeast and nipagin as a preservative. All the diets were adjusted to the pH level of 3.7 with citric acid, and 25mL of a diet was poured into 90mm Petri dishes. The diet-filled Petri dishes were left for two hours before eggs were transferred into the dishes for the experiment. The recipes for making the diets are presented in **Table 1**.

Life history experiment

Eggs were collected from the stock and a group of 50 eggs was transferred into each 90mm Petri dish containing the corresponding diet. There were ten replicates *per* diet and a total sample size of 40 (N= 40). The Petri dishes were kept in a controlled temperature cabinet at 25±0.5°C and a light cycle of 12-hour light:12-hour dark, and were monitored daily to measure the egg hatching time. On day six after hatching, the lids of the Petri dishes were discarded, and the remained portions were transferred individually into 1L plastic boxes containing 50g of sawdust to facilitate pupation. The time it took for the first larva to jump out from the diet in each box was recorded as the pupation time. On day six after pupation, pupae were sieved from the sawdust and ten pupae were randomly selected and weighed on a microbalance (Ahaus PA214). Ten pupae were then placed into 90 mm Petri dishes and transferred into plastic cages (20x15x15cm) for emergence. Time of the first emergence and the total number of females in each cage were measured on day three after emergence. The egg-to-adult development time was calculated as the period from egg seeding to the first emergence. Ten newly emerged adults (5 males and 5 females) per replicate were randomly selected and temporarily frozen in a -5°C freezer for 5m and then were weighed on a

Table 1. Sugar-rich, standard, protein-rich, and fruit-based diet recipes

Ingredients	Artificial diets			Fruit-based diet
	Sugar-rich	Protein-rich	Standard	
Brewer's yeast (g)	81.45	271.50	204	10
Sucrose (g)	244.35	54.30	121.80	3
Guava (g)	-	-	-	86
Nipagin (g)	2	2	2	1
Sodium Benzoate (g)	2	2	2	-
Wheat germ oil (mL)	2	2	2	-
Agar (g)	10	10	10	2
Water (mL)	1000	1000	1000	50

microbalance to measure the fresh weight of the adults. Ten adults (5 males and 5 females) were transferred into small plastic cages (10x10x15cm) and were fed on sugar, brewer's yeast, and water *ad libitum* for the fecundity assay. On day 15 post-emergence, a 35mm Petri dish containing 1mL apple juice and covered with a Parafilm layer with 1mm holes was placed in each cage to collect eggs. Eggs in each cage were collected every 24 hours for 15 continuous days and the number of eggs was counted as a proxy of fecundity. We also measured the number of living females every day which enabled us to calculate per-day fecundity.

Statistical analysis

Generalized linear models (GLM) were used for testing the statistical significances of pupal weight, adult weight, and per-day fecundity. *P*-values were obtained from ANOVA with F-statistics for all the GLM models. The Student-Newman-Keuls (SNK) post hoc test was used to compare the statistical significances among the larval diets in all the GLM models. The normality of data was examined by using histogram plots and the Shapiro-Wilk test, and model fit was assessed by using diagnostic plots (Q-Q plot and residuals plot). All data analyses were performed in R (R Development Core Team, 2017) version 3.6.1 and R Studio version 1.2.1335, and plots were created by using the ggplot2 package (Wickham, 2009).

Results

Developmental time

There were significant effects of the larval diet on developmental time at the larval ($F_{3,36} = 3.1836$, $p = 0.035$), pupal ($F_{3,36} = 8.5135$, $p = 0.00021$), and pre-oviposition stages ($F_{3,36} = 7.4651$, $P = 0.0005$), and the life cycle of *B. dorsalis* ($F_{3,36} = 15.4286$, $P < 0.0001$), but there was no effect of larval diet on egg hatching time ($F_{3,36} = 0.428$, $P = 0.734$). The life cycle of *B. dorsalis* was elongated when larvae fed on the sugar-rich diet (32.8 days), while it was significantly shorter in the fruit-based diet (30.7 days) and the protein-rich diet (30.2 days). In particular, flies from the sugar-rich diet had longer pupal and pre-oviposition periods before starting egg laying. In contrast, flies from the protein-rich diet had shorter larval and pre-oviposition periods, and therefore, had shorter life cycles (**Table 2**).

Pupal weight

Larval diet composition significantly influenced the pupal weight of *B. dorsalis* ($F_{3,196} = 20.737$, $P < 0.0001$) (**Figure 1**). The pupae reared on the fruit-based and standard diets had higher pupal weights (0.0167g and 0.0145g, respectively) than the pupae from the protein-rich and sugar-rich diets (0.0131g and 0.0132g, respectively).

Adult weight

There was a significant interaction between the larval diet and fly sex on the adult weight of flies ($F_{3,192} = 20.3490$, $P < 0.0001$). Females were significantly heavier than males ($F_{3,195} = 142.79$, $P < 0.0001$), however, the difference between sexes was more accentuated in the protein-rich diet (**Figure 2**). Nonetheless, there was no significant difference in the adult weight between the two sexes in the sugar -rich diet ($F_{1,48} = 0.0241$, $P = 0.877$). The diets were shown to significantly influence the adult weight of the flies ($F_{3,196} = 7.890$, $P < 0.0001$). The adult weights of flies from the fruit-based diet were higher than the flies on the sugar-rich and protein-rich diets, however, there was no significant difference in adult weight between the fruit-based and standard diets (**Figure 2** and **Figure 3**).

Fecundity

There was a significant interaction between the diet and the per-day fecundity of the flies ($F_{3,292} = 11.632$, $P < 0.0001$). In specific, the number of eggs per female in the standard and sugar-rich diets increased substantially from day 1 to day 15, while this number decreased gradually in the fruit-based and protein-rich diets. Regarding single effects, diet significantly influenced the per-day fecundity ($F_{3,296} = 3.6017$, $P = 0.0139$) whereby the number of eggs in the fruit-based diet (19.94 ± 6.302) was higher than in the sugar-rich diet (17.368 ± 3.373) (**Figure**

Table 2. Developmental time of *B. dorsalis*

Development stages	Developmental time (days) (Means ± SD)			
	Protein-rich	*Standard*	*Sugar-rich*	*Fruit-based diet*
Egg	1.40 ± 0.52[a]	1.30 ± 0.48[a]	1.20 ± 0.42[a]	1.20 ± 0.42[a]
Larval	7.80 ± 0.42[b]	8.50 ± 0.53[a]	8.30 ± 0.67[ab]	8.20 ± 0.42[ab]
Pupal	8.80 ± 0.42[b]	8.90 ± 0.74[b]	9.70 ± 0.48[a]	8.50 ± 0.53[b]
Pre-oviposition	12.20 ± 0.42[c]	13.20 ± 0.79[ab]	13.60 ± 0.97[a]	12.80 ± 0.42[bc]
Life cycle	30.20 ± 0.63[c]	31.90 ± 0.99[b]	32.80 ± 1.23[a]	30.70 ± 0.82[c]

Note: The different lowercase letters in the same row indicate significant differences in development time among the diets, which were assessed by the SNK post hoc test at P <0.05.

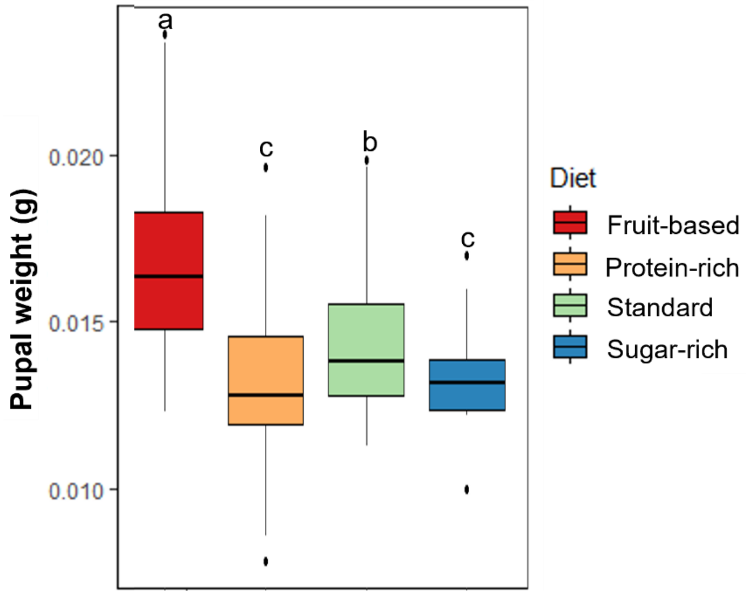

Figure 1. Effects of larval diet on the pupal weight of B. dorsalis. The figure shows the differences in pupal weights, which were measured in the four diets: protein-rich diet (high P:C), standard diet (balanced), sugar-rich diet (low Y:S), and fruit-based diet made from guava. Different letters in the figure indicate significant differences in the pupal weights among the larval diet treatments, which were assessed by the SNK post hoc test at *P* <0.05.

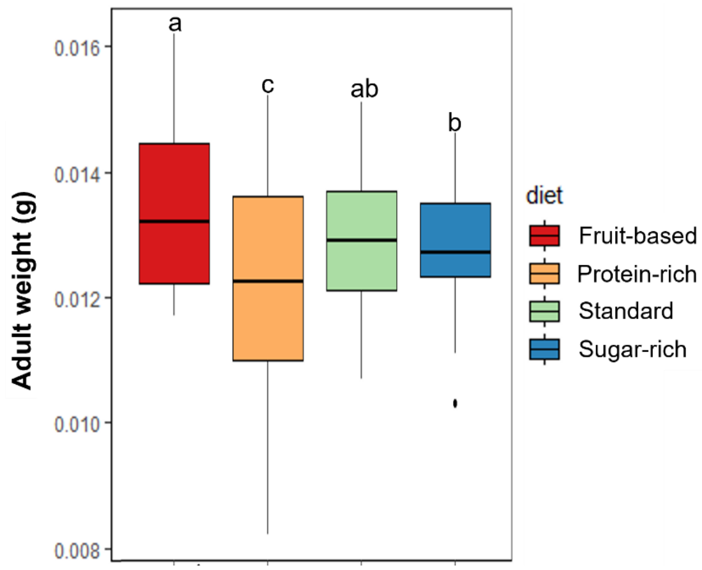

Figure 2. Effects of larval diet on the adult weight of *B. dorsalis*. The figure shows the differences in adult weight, which were measured in the four diets: protein-rich diet (high P:C), standard diet (balanced), sugar-rich diet (low Y:S), and fruit-based diet made from guava. Different letters in the figure indicate significant differences in adult weights among the larval diet treatments, which were assessed by the SNK post hoc test at *P <0.05*.

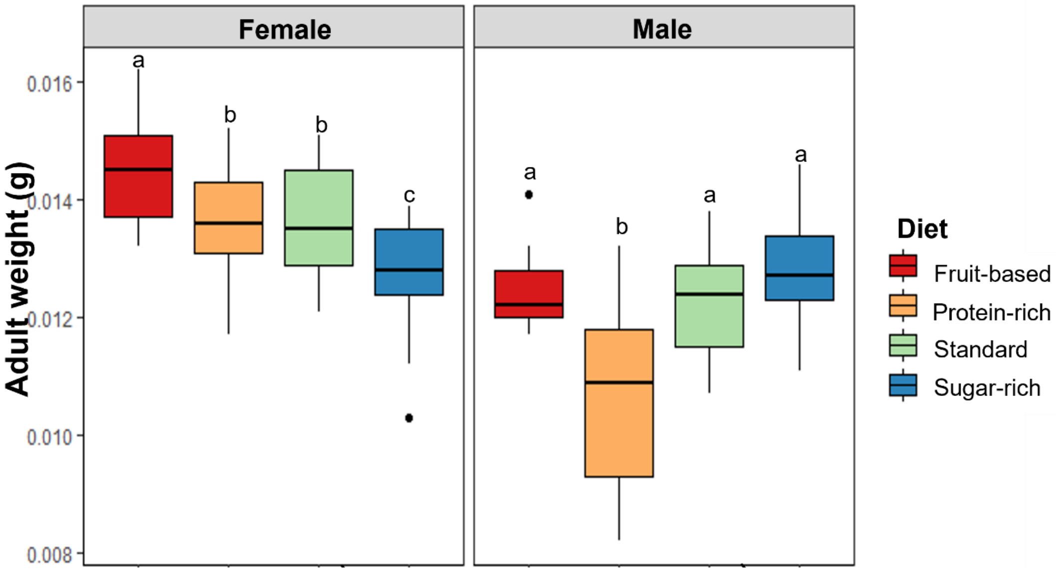

Figure 3. Effects of larval diet on adult weight in males and females of *B. dorsalis*. The figure shows the differences in the adult weights of males and females, which were measured in the four diets: protein-rich diet (high P:C), standard diet (balanced), sugar-rich diet (low Y:S), and fruit-based diet made from guava. Different letters in the figure indicate significant differences in adult weights among the larval diet treatments, which were assessed by the SNK post hoc test at $P < 0.05$.

4a). There was also a significant effect of day on the per-day fecundity of *B. dorsalis* ($F_{1,295} = 13.1502$, $P < 0.001$) whereby flies from the sugar-rich and standard diets laid more eggs on day 15 than on day 1 of egg collection.

Discussion

In the current study, we investigated how larval diet compositions shape important life-history traits, namely developmental time, pupal weight, adult weight, and per-day fecundity, of *B. dorsalis*. The results showed that the protein-rich and fruit-based diets shortened the development time of *B. dorsalis*, whereas the sugar-rich diet delayed development (**Table 2**). The results of the study showed the delayed effects of a high carbohydrate diet on development, which supports prediction 1, and are consistent with previous research on flies and other insect species (Roeder & Behmer, 2014; Cammack & Tomberlin, 2017; Young *et al.*, 2018; Kim *et al.*, 2020). A sugar-rich diet may not provide enough of the yeast *S. cerevisiae*, which contains essential amino acids (Abdel-Hafez *et al.*, 1977) that are important for the growth and development of flies. Importantly, a sugar-rich diet might not contain the required amino acids for the activation of the target of rapamycin (TOR), an important signalling integrator of nutrient and growth factors that modulates cell growth in animals (Fingar & Blenis, 2004; Bar-Peled & Sabatini, 2014; Zhai *et al.*, 2015). It has been suggested that the TOR pathway influences the development of the prothoracic gland, which is a source of the molting hormone ecdysone, and therefore it can modulate developmental time (Kemirembe *et al.*, 2012).

We found significant effects of diet composition on the body weight of *B. dorsalis*. In both the pupal and adult stages, the body weights of flies on the fruit-based and sugar-rich diets were higher than the other diets. This result supports our prediction 2, and is also in accordance with previous studies that have shown that a high carbohydrate diet positively influences body weight in insects (Kaufmann *et al.*, 2013; Wills *et al.*, 2015; Morimoto *et al.* , 2022). In particular, sugar intake from the insect's diet can be converted to lipids and stored in the insect's body as energy reserves, and a sugar-rich diet increases lipid storage in the insect body (Kaufmann *et al.* , 2013; Wills *et al.* , 2015; Morimoto *et al.* , 2022) and therefore increases total body weight. There are also studies showing the positive effects of yeast on

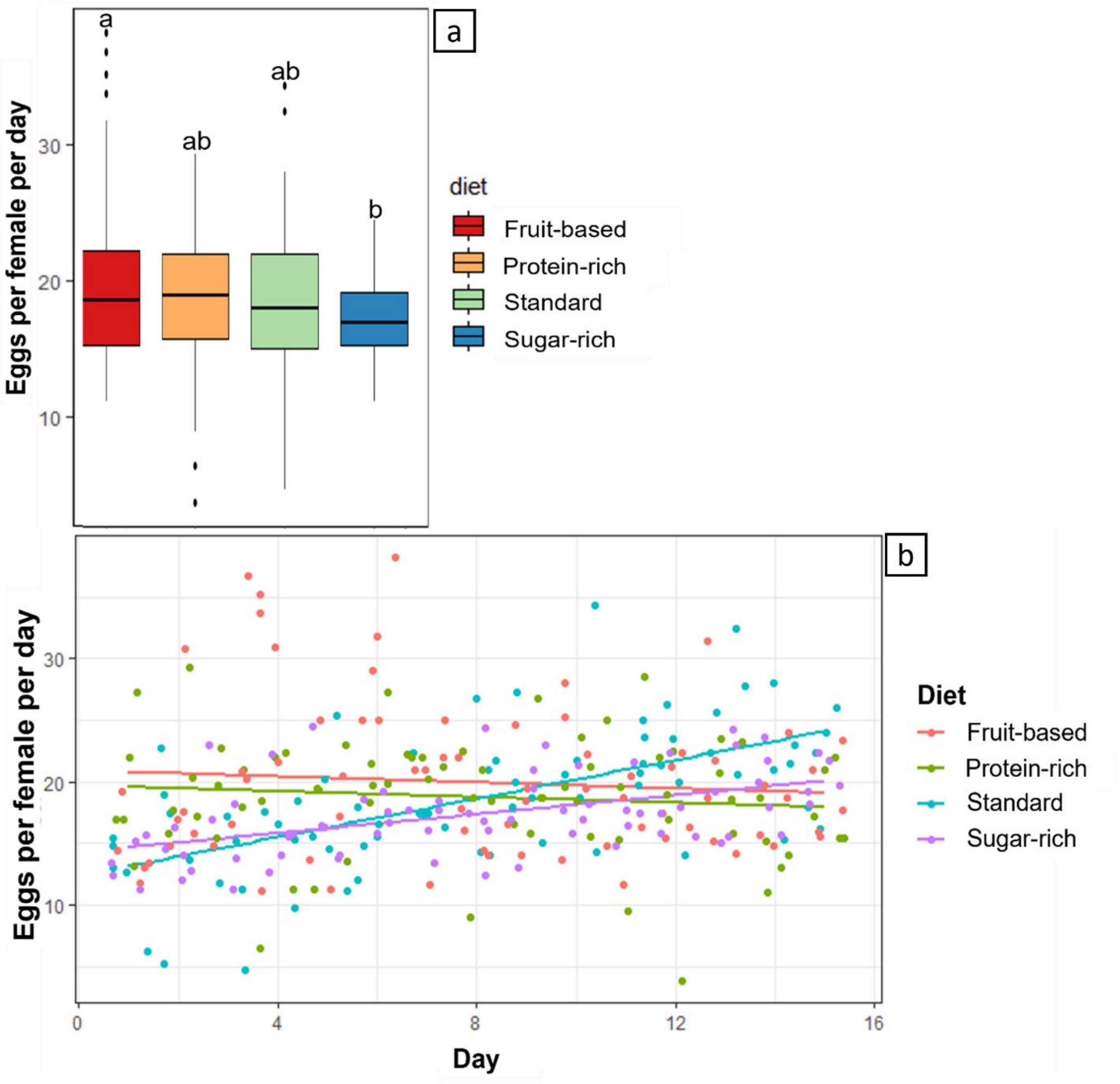

Figure 4. Effects of larval diet on the per-day fecundity of *B. dorsalis*. Figure 4a shows the differences in per-day fecundity, which were measured in the four diets: protein-rich diet (high P:C), standard diet (balanced), sugar-rich diet (low Y:S), and fruit-based diet made from guava. Different letters in the figure indicate significant differences in per-day fecundity among the larval diet treatments, which were assessed by the SNK test at *P <0.05*. Figure 4b shows the number of eggs laid by one female per day from the four diets over the 15 day period.

body weight, such as in *Drosophila melanogaster* (Anagnostou *et al.*, 2010), however, in the current study, flies from the protein-rich diet had a lower body weight than in the other diets. This may be a result of the shorter larval developmental time in the protein-rich diet. The larval stage is the main feeding stage of flies, and a shorter larval stage may result in lower food consumption and weight gain. More importantly, flies on a protein-rich diet often spend more nutritional resources on reproductive purposes to roduce more eggs and therefore have less nutrient reserves in their bodies than those on a sugar-rich or balanced diet (Kaspi *et al.* , 2002). For example, moths that emerge from a protein-rich diet invested more nutrients in formulating reproductive tissue than somatic tissue, while the flies on a high sugar diet allocated more to somatic tissue and thus had larger body weights (Colasurdo *et al.*, 2009). Interestingly, body weights were highest in the fruit-based and standard diets, and this might have been because of the balanced ratio of carbohydrates and protein in these two diets.

The results showed that diet composition had a significant effect on the fecundity of *B. dorsalis*. Flies from the fruit-based diet laid more eggs than flies on the sugar-rich diet, but not more than the number of eggs laid by flies from the standard and protein-rich diets. This result did not match our expectation that the higher protein level (yeast) in the protein-rich diet would significantly increase fecundity. Dietary yeast is important for reproduction in flies and other insects, as has been shown in previous research (Kaspi *et al.* , 2002). For instance, a protein-rich diet influenced the allocation of nutrients for reproductive and somatic tissue formation as shown in the moth *Malacosoma disstria* Hübner (Colasurdo *et al.* , 2009), which therefore influences reproductive success. A protein diet has also been shown to modulate the sexual activity of male flies through pheromone emission to modulate reproductive outcomes (Kaspi *et al.*, 2000). Protein-fed males were more likely to emit pheromones compared to protein-deprived male flies and therefore male mating efforts increased in the protein-fed flies. In **Figure 3b**, the number of eggs laid by flies from the protein-rich diet in the first ten days was higher than that of the sugar-rich diet. This can be explained in that the protein-rich diet made the male flies more sexually active, which helped female flies copulate sooner (Kaspi *et al.* , 2002), and therefore, flies from the protein-rich diet had a higher fecundity in the first ten days. However, the negative effects of a high level of protein in the diet are lower energetic reserves (Kaufmann *et al.* , 2013; Wills *et al.* , 2015) and a shorter lifespan than flies on a sugar-rich diet, and this can lead to a decrease in the number of eggs per day in the last five days (**Figure 4b**). In contrast, the sugar-rich diet helped the flies store more lipids, which then increased the average reproductive period and lifespan of the flies (Winkler *et al.*, 2006). More importantly, there is also research indicating the beneficial effects of sugar on fecundity, for example, a high sucrose diet with supplementary vitamins and minerals significantly increased the fecundity of female *B. anynana* flies (Geister *et al.* , 2008), and this can explain why there was no significant difference in the per-day fecundity of flies between the sugar-rich and protein-rich diets. The fruit-based diet had the greater per-day fecundity, and we suggest that this was a result of the balanced sugar content in the guava with an appropriate amount of supplementary yeast. The number of eggs laid by flies from the standard diet increased substantially and we expect that this diet composition would support the flies to have the highest fecundity if we had counted eggs over a longer period. Nonetheless, there were inconsistent effects of diet composition on the fecundity of insects, thus the question of how diet composition influences fecundity will require future research to investigate the underlying mechanisms of this phenomenon.

Conclusions

Diet composition had a strong effect on the development time, pupal weight, adult weight, and fecundity of *B. dorsalis.* The fruit-based and standard diets supported the development of *B. dorsalis* and had positive effects on fitness (body weight) and fecundity, and we can conclude that these two diets are suitable for the mass-rearing of the fruit fly *B. dorsalis.* However, since the fruit-based diet was made from guava, whose quality is strongly affected by the crop season, we suggest using the standard diet for mass rearing *B. dorsalis* in the lab to enable flies to be continuously reared. This diet will sustain the fitness and reproduction of fruit flies in the lab for developing SIT control techniques for this destructive pest.

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