Assessment of *Bactrocera dorsalis* (Diptera: Tephritidae) Diets on Adult Fecundity and Larval Development: Insights Into Employing the Sterile Insect Technique

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**Abstract**

*Bactrocera dorsalis* (Hendel) is a notorious insect pest that attacks diverse vegetables and fruits worldwide. The sterile insect technique has been developed as an environmentally friendly and effective control method that depends on the mass production of target flies. Because dietary yeast (protein) and sucrose (carbohydrate) are important in adult diets, yeast:sucrose (Y:S) mixtures are crucial for the mass-rearing of *B. dorsalis*. In this study, we found adult diets with different ratios of yeast to sucrose-influenced fecundity, and an extremely high or low Y:S ratios significantly decreased egg production of *B. dorsalis*. Additionally, the maximum oviposition efficiency was realized at dietary yeast to sucrose ratios of 1:1 and 1:3, suggesting their potential use to produce more eggs for the mass production of *B. dorsalis*. Here, new gel diets having different yeast concentrations (g/L water) were also assessed for rearing *B. dorsalis* larvae. Gel diets containing 20 g/L yeast led to a higher pupation, pupal weight and adult eclosion rate, and a shorter developmental time than other yeast concentrations. Moreover, the present gel diet also resulted in greater pupal production and adult emergence rates than previously used liquid and solid artificial diets, revealing that it is suitable for rearing *B. dorsalis* larvae. This research provides a useful reference on artificial diets mixtures for mass rearing *B. dorsalis*, which is critical for employing the sterile insect technique.

**Key words:** *Bactrocera dorsalis*, sterile insect technique, dietary yeast, fecundity, larval development
as reported in Queensland fruit fly (Moadeli et al. 2018a,b). Therefore, to increase the SIT’s efficiency, studies have focused on improving artificial diets (Aquino et al. 2016, Chang 2017, Moadeli et al. 2017). Furthermore, yeast and sucrose are not only the respective source of protein and carbohydrate, but also provide vitamins, lipids, and minerals to support insect development. Therefore, they are the main nutritional ingredients in diets used for the mass-rearing of fruit flies (adult and larval stages; Chan et al. 1990, Ling et al. 2000, Moadeli et al. 2018b). Previous studies showed that the nutritional quality of the diet significantly affected the male reproductive success, female fecundity, and larval development in fruit flies (Blay and Yuval 1997, Kaspi et al. 2002, Mohamed et al. 2016). Females fed with protein source attained high fecundity level, and reducing the amount of protein source in the diet negatively affected fecundity and ovary maturation (Goane et al. 2019). Additionally, the larval diet had a significant effect on adult development and behavior, such as insect egg productions (Telang et al. 2004), female oviposition preference (Matavelli et al. 2015), and flight ability (Moadeli et al. 2017). Interestingly, expensive protein source or nutritious diets do not necessarily translate into a better performance of the resulting flies compared with low-cost diets (Pascacio-Villafán et al. 2015, Goane et al. 2019). The proportion of nutritional composition of artificial diets is important for B. dorsalis (Aluja et al. 2001, Rollifs and Hoffmeister 2005, Ling 2009). Therefore, in the present study, we investigated the impact of adult diets with different yeast:sucrose (Y:S) mixtures on adult fecundity and ovary development, and also of larval gel diets with varied yeast concentrations on the larval growth and pupal performance to determine optimal diets for the mass-rearing of B. dorsalis.

Materials and Methods

Flies

The oriental fruit fly, B. dorsalis, was originally collected from Hainan Province, People’s Republic of China. The newly hatched adult flies were sorted by sex and offered with diets at different yeast ratios, as described above. To confirm the experimental cohorts were of a uniform age, the virgin flies were collected within 24 h after adult emergence. Then, fresh orange pulp was used to collect eggs. After egg hatching, the larvae were reared on gel larval diets having different yeast concentrations, and the third-instar larvae were transferred into a plastic basin containing sand for pupation. All stages of B. dorsalis were reared at 27 ± 1°C and 70% ± 5% relative humidity with a photoperiod cycle of 14 h light/10 h dark.

Experiment 1: Adult Rearing Media

For the experimental adult fly diets, the diets were varied to the following yeast:sucrose ratios (Y:S): 100:0, 96:1, 48:1, 24:1, 12:1, 6:1, 3:1, 1:1, 1:3, 1:6, 1:12, 1:24, 1:48, 1:96, and 1:100 by altering the amount of yeast extract (Oxoid, Basingstoke, Hampshire, United Kingdom) per 100 g of adult food, and the details of the adult diets used in this experiment are shown in Table 1. Strictly speaking, the flies were given ad libitum access to all diluted yeast diets, and the yeast used here mainly contained protein (62.5%), but also comprised water soluble B-complex vitamins, sodium chloride, lipids, and minerals with a pH (0.5% solution) of 7.0 ± 0.2 at 25°C. In this study, we used the fecundity (egg production and ovary development) as the measured parameters to evaluate the adult-rearing diet (Davies et al. 2005).

Effects of Adult Diets on Egg Production

For each adult diet having different Y:S mixtures (100:0, 96:1, 48:1, 24:1, 12:1, 6:1, 3:1, 1:1, 1:3, 1:6, 1:12, 1:24, 1:48, 1:96, and 1:100), 10 jars (100-mm height; 70-mm diameter) were established to study the fecundity response. Each jar contained five females and five males (n = 50 females for each treatment). Diets and water were provided in two separate small vessels, placed inside the jar, and replaced every 2 d. Then, an oviposition device (2-ml microfuge tubes) that consisted of 1.5-ml orange juice and 16 pinholes on the surface was used to collect eggs and the eggs number was counted from days 5 to 13 after adult emergence.

Effects of Adult Diets on Ovary Development

For each yeast level, 10 cylindrical jars (100 mm in height × 70 mm in diameter) were established to investigate the impact of adult diets with different yeast concentrations on ovary development in B. dorsalis. Each jar included five females and five males, and per treatment we used 50 flies. Diets and water were placed inside the jar and replaced every 2 d. Then, the females were collected and dissected from each diet to observe ovary development. A Leica M205A stereomicroscope (Leica Microsystems, Wetzlar, Germany) was used to capture images of ovaries and to measure the maximum diameter of each ovary.

Experiment 2: Larval Rearing Media

The performances of B. dorsalis flies reared on larval liquid and solid carrot-based diets have been studied (Anato et al. 2017), and the detailed compositions of these two diets are provided in Table 2. Based on the previous liquid diet (Chang et al. 2006), we developed a new gel larval diet for B. dorsalis that contains agar, nipagin, sorbic acid, ascorbic acid, linoelic acid, water, sucrose, and yeast (Oxoid; Table 2). Additionally, the nutritional resources of the wheat germ and corn powders were also added as nutritional supplements for yeast. To determine the appropriate yeast contents, five artificial larval diets differing in yeast concentrations (0, 10, 20, 60, and 100 g/L) were used to manipulate the larval resource availability. To prepare the gel diets for each yeast formulation, the agar was mixed with the water and heated for 4 min in a stove to activate the agar. After heating, the other dry ingredients were added into the agar and mixed using a blender until all the diets were fully homogenous. Then, the diets were cooled to room temperature.

Evaluation of Larval Development Parameters

To evaluate the effects of different concentrations of yeast on the development of B. dorsalis, some parameters, including pupation rate,
pupal weight, development time (egg–pupa), and adult emergence, were measured (Khan et al. 2013). Here, 10 ml of each gel larval diet was placed into a Petri dish (55 mm), and 50 eggs were transferred to the surface of each diet. Then, the Petri dish was incubated in the stable laboratory environment (27 ± 1°C at 70% ± 5% relative humidity), and 10 replicates were conducted per yeast concentration. The pupae generated from each diet were collected from sand to calculate the pupation rate (the number of pupae divided by the initial number of collected eggs), and pupal weight at 3 d postpupal ecdlosion was estimated as the mean weight of collected pupae in the same replicate (it should be noted that weighing pupae with mixed ages is a confounding factor as pupae lose weight with age, here only the same age pupae that at 3 d postpupal ecdlosion were chose for pupa weight). For the assessment of development time (egg–pupal period), the mean numbers of days required for each fly to go from egg to pupa were calculated. For the adult emergence rate, the pupae had higher pupation rates (0.82 ± 0.094 and 0.88 ± 0.037, respectively) which was significantly greater than those of females reared on diets with 10 and 20 g/L yeast diets.

### Results

#### Experiment 1: Egg Production

There was a significant effect of adult diet treatments on fecundity, and the egg numbers laid by per fly per day showed a parabolic shape (Fig. 1; F = 21.50; df = 8, 81; P < 0.001). Specifically, all of the female flies reared on high Y:S ratios, from 100:0 to 24:1, died before egg laying. Although the flies could survive on the extreme low Y:S ratios, 1:96 and 0:100, no eggs were produced. For the Y:S ratios ranging from 12:1 to 1:1, the egg numbers significantly increased as the yeast concentrations decreased in the diets. On the contrary, as the Y:S ratios decreased from 1:1 to 1:48, the number of eggs significantly decreased. The fecundity levels on diets with 1:1 and 1:3 Y:S ratios were higher than those on any other diet regimes.

#### Ovary Development

Consistent with egg production, a significant effect of adult diet regimes was found on ovary development (F = 56.79; df = 8, 81; P < 0.001), and the ovaries of flies reared on diets with 1:1 and 1:3 Y:S ratios developed better than on any other B. dorsalis diet treatments (Fig. 2A). Namely, the ovary size (the diameter of the entire ovary per fly) of the female adults reared on diets with 1:1 and 1:3 Y:S ratios was significantly greater than those of females reared on diets with other yeast ratios (Fig. 2B).

#### Experiment 2: Pupation Rate

There was a significant impact of yeast concentrations on the pupation rate; Bactrocera dorsalis fed on the 10 and 20 g/L yeast diets had higher pupation rates (0.82 ± 0.094 and 0.88 ± 0.037, respectively) than the other two diet regimes (60 g/L, 0.43 ± 0.044 and 100 g/L, 0.17 ± 0.034; F = 36.13; df = 3, 36; P < 0.001). Bactrocera dorsalis could not survive on the 0 g/L yeast diet (Fig. 3A), and there was no significant difference in the pupation rates between the 10- and 20-g/L yeast diets.

#### Pupal Weight

The pupal weights from each larval diet were 12.93 ± 0.73 mg (10 g/L), 16.77 ± 0.23 mg (20 g/L), 15.31 ± 0.27 mg (60 g/L), and 11.64 ± 0.50 mg (100 g/L; Fig. 3B). Pupae from larvae reared on the 20- and 60-g/L yeast diet had greater pupal weights than those reared on the other two concentrations (F = 23.57; df = 3, 36; P < 0.001). There was no significant difference in the pupal weight between the 20- and 60-g/L yeast diets.

### Statistical Analyses

For the experiment 1 with the adult rearing media, the predictor variables were Y:S ratios, and the response variables included egg production and ovary development in B. dorsalis. In the experiment 2 with the larval rearing media, the yeast concentrations in the gel diets were the predictor variables, and the larval development parameters, pupation rate, pupal weight, development time (egg–pupa), and adult emergence were considered as the response variables. For the measurement scales of these variables, the Y:S ratios and yeast concentrations were considered as categorical data, and the egg production (the number of eggs) was considered as the discrete data (count data), and the ovary development (the maximum diameter of ovary), pupation rate, pupal weight, development time (egg–pupa), and adult emergence were considered as continuous data. In the present study, the SPSS 16.0 for Windows (IBM, Chicago, IL) was used for the statistical analyses. The normality and homoscedasticity analysis showed that these variables were normally distributed with the constant variance, and thus, one-way analysis of variance (ANOVA) was the appropriate analysis for those specific variables. Means were separated using Tukey’s Honestly Significant Difference test (P < 0.05). Additionally, percentage values have been transformed by using arcsin square-root before subjected to ANOVA. The values of count data (egg production) have also been log-transformed for the subsequent ANOVA analysis.

### Table 2. Composition of the previous (Anato et al. 2017) liquid, solid, and the present gel diets for rearing larvae of Bactrocera dorsalis

| Ingredients          | Anato-2017 Carrot-based liquid diet (% solid) | Anato-2017 Liquid diet (per 1 L water) | The present gel diet (per 1 L water) |
|----------------------|---------------------------------------------|---------------------------------------|--------------------------------------|
| Agar                 | –                                           | –                                     | 6 g/L                                |
| Wheat germ powder    | –                                           | –                                     | 25 g/L                               |
| Corn powder          | –                                           | –                                     | 60 g/L                               |
| nipagen              | –                                           | 1.1 g/L                               | 1.4 g/L                              |
| Sorbic acid          | –                                           | –                                     | 0.7 g/L                              |
| Ascorbic acid        | –                                           | –                                     | 1 g/L                                |
| Linoleic acid        | –                                           | –                                     | 0.2 mL/L                             |
| Potassium            | 0.40%                                       | –                                     | –                                    |
| sodium benzoate      | –                                           | 1.1 g/L                               | –                                    |
| Citric acid          | 0.60%                                       | 15.5 g/L                              | –                                    |
| Dehydrated carrot paste | 74.70%                                     | –                                     | –                                    |
| Water                | 16.20%                                      | 73.5 g/L                              | 10 g/L                               |
| Yeast                | 8.10%                                       | 142.1 g/L                             | 0 g/L                                |
| –                    | –                                           | 10 g/L                                | –                                    |
| –                    | –                                           | 20 g/L                                | –                                    |
| –                    | –                                           | 60 g/L                                | –                                    |
| –                    | –                                           | 100 g/L                               | –                                    |

–, Absent in the diet.
Development Time (Egg–Pupa)

Here, the feeding of different diet formulations resulted in significant differences in the time required by *B. dorsalis* to develop from egg to pupa (Fig. 4A; $F = 112.63$; df = 3, 36; $P < 0.001$). The flies fed on the 20-g/L yeast diet had the shortest development time ($11.77 \pm 0.07$ d), when compared with the other three diet regimes (10 g/L, $13.22 \pm 0.18$ d; 60 g/L, $12.56 \pm 0.09$ d; and 100 g/L, $14.93 \pm 0.14$ d).

Fig. 1. Daily number of eggs laid per female *Bactrocera dorsalis* fed on diets containing different yeast ratios. In total, 10 replicates were conducted, and the data are presented as means ± SEs. Bars with different letters above them differ significantly at $P < 0.05$.

Fig. 2. (A) Ovaries of 13-d-old female *Bactrocera dorsalis* fed on diets containing different yeast ratios. (B) The differences in the sizes of ovaries from different yeast ratios indicated by the average maximum diameter. In total, 10 replicates were conducted, and the data are presented as means ± SEs. Bars with different letters above them differ significantly at $P < 0.05$. 

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Adult Emergence Rate

Because of the absence of *B. dorsalis* pupae produced on the 0 g/L diet, the fly emergence rate could not be tested on this diet. For the other diets, the *B. dorsalis* adult emergence rates were greater on the 10 g/L (78.71% ± 0.0046) and 20 g/L (78.17% ± 0.035) yeast diets than the other two yeast concentration diets (60 g/L, 63.06% ± 0.011 and 100 g/L, 33.78% ± 0.025; Fig. 4B; \( F = 28.38; \) df = 3, 36; \( P < 0.001 \)). There was no significant difference in the adult emergence rate between 10- and 20-g/L yeast diets.

Discussion

Because yeast and sucrose are the main source of nutrients for adult fly artificial diets, their proportions in the diet is the leading determinant of the *B. dorsalis*’ egg production (Skorupa et al. 2008). For *B. dorsalis*, we found a significant effect of the Y:S ratios on adult fecundity, and its egg numbers significantly declined as the yeast ratio decreased in the diet within certain Y:S ratios (from 1:1 to 0:100). Similarly, it has been reported that diets with a high yeast proportion can increase the fecundity level with high egg production in flies (Lee et al. 2008, Chen et al. 2013, Schultzhaus and Carney 2017).

Additionally, female flies fed on diets containing extremely low Y:S ratios of 1:96 and 0:100 laid no eggs, indicating that a certain amount of yeast intake is necessary for fecundity in *B. dorsalis*. However, we also found that flies fed on diets with relatively high Y:S ratios, from 3:1 to 100:0, had a significantly decreased egg production, and at some levels, flies could not survive and died before egg-laying. The diet with excess of protein might be toxic (Piper and Partridge 2007) and affect physiological and metabolic processes, such as the down-regulation of cellular repair pathways (Martingronert et al. 2008) and the production of reactive oxygen species (Mohanty et al. 2002, Caro et al. 2009). Hence, it might be too costly for producing a nutrient-rich adult diet (Sentinella et al. 2013).

In many insects, dietary yeast and sucrose mixtures play a vital role in the formation of yolk proteins that can trigger the initiation of ovary development, which would be significantly affected by changing the dietary yeast concentrations (Chippindale et al. 1993, Lu et al. 2016). In this paper, the development of ovaries in female flies of *B. dorsalis* was investigated and their development was also changed, following the same variation tendency as *B. dorsalis*’ egg laid among the diets with different Y:S ratios. Therefore, we speculated that the differences in egg production might be the results of
differences in ovarian development. The dietary Y:S mixtures might control the expression of vitellogenin, which influences ovarian development, by regulating some nutritional signaling pathways (Smykal and Raikhel 2015, Chen et al. 2017). Here, adult-acquired development, by regulating some nutritional signaling pathways control the expression of vitellogenin, which influences ovarian differences in ovarian development. The dietary Y:S mixtures might result in a maximum egg production and the development of larger B. dorsalis’ ovaries. Based on our data, as yeast is more costly than sucrose, the 1:3 Y:S ratio-containing (25% yeast and 75% sucrose) adult diet is the best choice for rearing B. dorsalis.

For larval diets, the solid diets based on carrot (Daucus carota L.; Christenson et al. 1956) and liquid diets (Chang et al. 2004) have been developed for fruit flies. The disadvantages of solid diet are the inconsistent quality of the bulking agent, the risk of pesticide contamination, the metabolic heat, and most seriously, the disposal of the spent diet, which can result in a large amount of waste that could contain living pupae and larvae that constitute a great threat to the ‘fruit fly-free’ regions (Chang et al. 2004, Chang 2009). Although liquid diets do not contain biological bulking agents and are suitable for rearing some fruit flies, including Bactrocera cucurbitae (Schroeder et al. 1971), C. capitata (Ling et al. 2007), Anastrepha fraterculus (Vera et al. 2014), and B. dorsalis (Anato et al. 2017). There are still some issues in large-scale rearing processes (Chang 2004, Chang 2009), namely, the cleaning and frequent replacement of substrates, the separation of ingredients, and, owing to fermentation, the diet becoming viscous, which can lead to larval mortality (Pascacio-Villafán et al. 2018).

In the present study, to overcome the drawbacks of solid and liquid diets as described above, we developed a new gel larval diet by adding agar to the B. dorsalis larval diets. Gelling agents may improve fly larval diets by removing the physical substrates, preventing the settling of dense materials and preventing fermentation. They are also convenient for insect movement and pupation and are easy to handle (Moadeli et al. 2017). Agar is highly clear, stable, nontoxic, and resistant to metabolism during culturing, making it the ideal gelling agent for fruit fly larval diets (Henderson and Kinnerley 1988, Jain et al. 2005). The previous studies showed that agar is used as an economical and effective gelling agent in the diets of B. tryoni (Moadeli et al. 2017), Bactrocera oleae (Hanife 2008), and C. capitata (Paškořová 2007).

Therefore, the gel larval diet was used in this study and we found that the dietary yeast concentration had significant effects on larval performance, and flies could not survive on the yeast-free diet, which further indicated that yeast is an indispensable nutritional component of artificial B. dorsalis diets. In addition, high yeast concentrations had negative impacts on larval development, with extremely low pupal production, suggesting detrimental effects of high yeast ratios on development (Nestel et al. 2004). Bactrocera dorsalis appeared to develop better on 20 g/L, as assessed by a higher pupation rate, pupal weight and adult emergency rate, and shorter development time, than on any other dietary treatment. When compared with previous artificial diets, the present gel diet (20 g/L yeast) also allowed a higher pupal production (88%) and adult emergence (78%) than the solid diet (8% and 37%, respectively) or liquid diet (74% and 61%, respectively), indicating that this diet had great potential for rearing B. dorsalis larvae for SIT-based programs (Anato et al. 2017).

However, we realized that there were some limitations in our experimental designs and data analyses. For example, the present study mainly focused on analysis in testing the effect of different adult diet regimes on fecundity ability, but not clearly clarified the changes in ovary size and egg production that were caused by yeast, sucrose, or their interactions. Therefore, the additional two-factor interaction model analysis could be used to study the contribution of each component (yeast and sucrose) and their interactions on fecundity ability of B. dorsalis in the future (Pascacio-Villafán et al. 2016). In addition, another limitation was that we varied the yeast content of larval diet without changing all other larval diet components, which could result in the final amount of experimental diets varied. Consequently, we were not sure that the response of insects to diet was caused by the proportion of their ingredients or the absolute amounts of the larval diets. To overcome this problem, the two-component mixtures (including yeast and corn) experiments (each component is in the design space) could be applied to confirm the total amount of larval diet remains constant (Lapointe et al. 2008, Pascacio-Villafán et al. 2017).

In conclusion, the main aim of this research was to determine the most suitable dietary yeast and sucrose mixtures that resulted in a high fecundity level and preferable larval performance for the mass-rearing of B. dorsalis. Firstly, we found that the Y:S ratio-containing (25% yeast and 75% sucrose) could result in a maximum fecundity of B. dorsalis. Then, after assessing the literature (Moadeli et al. 2017), we developed a gel larval diet for B. dorsalis by adding a gelling agent (agar) to our diets. The present gel larval diet has overcome some disadvantages of previous solid and liquid diet of B. dorsalis, and 20-g/L yeast gel diet allowed a higher pupal weight, pupal production, adult emergence, and shorter development than the both previous solid and liquid diet, and thus can be seen as a potential media for a large-scale mass-rearing of B. dorsalis. Although this study was conducted at a small-scale in the lab, we believed that the data obtained provide important reference information for the large-scale factory rearing of B. dorsalis to be applied in SIT-based methods.

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