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A TRANSGENERATIONAL EFFECTS OF OIL SUPPLEMENTED DIETS ON FRUIT FLIES (*Drosophila melanogaster*) PROGENIES

EFEK TRANSGENERASI PEMBERIAN SUPLEMENTASI MINYAK TERHADAP PROGENI LALAT BUAH (*Drosophila melanogaster*)

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Abstract

The causes of obesity are multifactorial, one of which is the parental diet. Fruit fly (*Drosophila melanogaster*) has homologous genes with humans and is a potential model organism for research on human diseases. This study aims to examine the transgenerational effects of a modified high-fat diet on the number of progenies, sex ratio, and body weight in eight generations of fruit flies. Four types of diets consisted of different fat compositions were used banana, cornmeal, cornmeal + 3% virgin coconut oil (VCO), and cornmeal + 3% palm oil. Data were analyzed using SPSS with ANOVA and DMRT post hoc analysis. Results showed significant differences (P <0.05) in the number of progenies between the diet without oil and with added oil. A higher number of progenies were found in the diet without oil with an average of 85 flies (banana diet) and 85.04 flies (cornmeal diet) compared to the results in the oil diet with 19 flies (cornmeal + 3% VCO) and 76.67 flies (cornmeal + 3% palm oil)The sex ratio and the body weight were not significantly different between each diet, suggesting that there are other factors involved. There were significant differences between the early and late generations for number of progenies and body weight, but not for sex ratio. The VCO was difficult to mix in the media so palm oil has the potential to be used for further investigations to find a better formula for high-fat diet food sources in an obesity study using fruit flies.

Keywords: Diet; *Drosophila melanogaster*; Inheritance; Progenies; Transgenerational

Abstrak

Penyebab terjadinya obesitas bersifat multifaktorial, salah satunya adalah pola makan orang tua. Lalat buah (Drosophila melanogaster) memiliki gen yang homolog dengan manusia dan merupakan organisme model yang potensial untuk penelitian penyakit manusia. Penelitian ini bertujuan untuk menguji pengaruh transgenerasi pola makan tinggi lemak yang dimodifikasi terhadap jumlah keturunan, rasio jenis kelamin, dan berat badan pada delapan generasi lalat buah. Empat jenis pakan dengan komposisi lemak berbeda digunakan yaitu pisang, tepung jagung, tepung jagung + 3% Virgin coconut oil (VCO) dan tepung jagung + 3% minyak sawit. Data dianalisis menggunakan SPSS dengan analisis post hoc ANOVA dan DMRT. Hasil penelitian menunjukkan perbedaan yang signifikan (P <0,05) pada jumlah keturunan, khususnya antara diet tanpa minyak dengan diet dengan minyak. Jumlah progeni yang lebih banyak terdapat pada diet tanpa minyak dengan rata-rata 85 lalat (diet pisang) dan 85,04 lalat (diet tepung jagung) dibandingkan dengan hasil pada diet minyak dengan 19 lalat (tepung jagung + 3% VCO) dan 76,67 lalat (tepung jagung + 3% minyak sawit). Rasio jenis kelamin dan berat badan tidak berbeda secara signifikan antara masing-masing pola makan, hal ini menunjukkan bahwa ada faktor lain yang terlibat. Terdapat perbedaan yang signifikan antara generasi awal dan akhir dalam hal jumlah keturunan dan berat badan, namun tidak untuk rasio jenis kelamin. VCO sulit untuk dicampurkan dalam media sehingga minyak sawit berpotensi digunakan untuk penelitian lebih lanjut untuk menemukan formula sumber makanan diet tinggi lemak yang lebih baik dalam studi obesitas menggunakan lalat buah.

***Kata Kunci**: Drosophila melanogaster; Keturunan; Pola makan; Transgenerasi; Warisan*

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INTRODUCTION

Obesity has become a global pandemic and a contributor to high morbidity and mortality rates. Indonesian Basic Health Research (Badan Penelitian dan Pengembangan Kesehatan, 2020) reported that 21.8% of Indonesians aged >18 years are obese, which is a rapid increase compared to 2016 which was only 10.5%. Obesity is caused by many factors, in addition to biological factors such as hormones, psychosocial factors such as lifestyle and socioeconomic status are also suspected to be one of the contributors to obesity. Obesity is usually measured by calculating the body mass index (BMI) which is the metric currently in use for defining anthropometric height/weight characteristics in adults. It can be used to represent an index of an individual's level of size and can be categorized into different BMI groups. Before BMI was used, it was recognized that tall people had a lower death rate than short people with the same weight/height ratio. It was observed that a person's height and leg length could affect the body mass adjusted for height. In the 1970s, a better-documented weight for height data was used and the Quetelet Index was started to be used in population-based studies. Quetelet Index was calculated using body weight (kilograms) divided by height squared (meters) which is now referred to as the body mass index (BMI) (Nuttall, 2015).

Researches show that variations in BMI often show high heritability. Heritability is the proportion of phenotypic variation caused by genetic and non-environmental factors. However, in 1980–1990, it was reported that obesity may be caused by genetic factors. Children of normal parents have a 10% chance of being obese. The chance will increase to 40–50% if one parent is obese, and will increase to 70–80% if both parents are obese. The use of molecular genetic studies today has also helped to better understand the genetic causes of obesity (Guida et al., 2019; Radha & Mohan, 2016).

Studies using genome-wide association studies reported that genetic variants were only able to explain 2–5% of BMI variations (Choquet & Meyre, 2011). Thus we have to look further into the effects of non-genetic factors on the inheritance of obesity. Environmental factors, especially family eating patterns greatly affect a person's physical condition. Diet, physical activity, and socioeconomic status can alter the association between genetic predisposition and BMI (Brandkvist et al., 2019). The inheritance of obesity due to the diet of parents, especially mothers-to-be, is also known to be affected by epigenetics. Epigenetics is the study of changes in gene expression and phenotype that occur without changes in the DNA sequence. Recent studies indicate that epigenetics may be a potential mediator that plays a role in gene-environment interactions in the development of obesity and its associated comorbidities. The various pathways connected to inflammation, metabolism, oxidative stress, hypoxia, and other factors characterize obesity as a complex, multifactorial disease. Therefore, there is still more to learn before we fully understand how the obesity-related epigenome works (Mahmoud, 2022).

The fruit fly (*Drosophila melanogaster*) is a well-known model organism for studying inheritance patterns. Recent studies have reported that fruit flies have the potential to be one of the organisms that can be used as experimental models of disease in humans (Cheng et al., 2018). The epigenetic effect can be seen for several generations (Heard & Martienssen, 2014) but in research for high food diet for *Drosophila* many are only for one or two generations or only for several weeks. In this experiment, the fruit flies were reared for eight generations with 2 weeks for one life cycle (one generation).

In this research, modification of the fruit fly diet was carried out with the aim of producing a high-fat diet using VCO and palm oil that could be used as a predisposition to fruit fly as a model organism in obesity research. Virgin coconut oil (VCO) is a product made from fresh coconut meat that is processed at low temperatures so that the important content in the oil can be maintained (Anwar & Salima, 2016). The main content of VCO is about 90% saturated fatty acids and about 10% unsaturated fatty acids. The saturated fatty acid of VCO is dominated by lauric acid. VCO contains ± 53% lauric acid and about 7% caprylic acid. Both are medium-chain fatty acids commonly called Medium Chain Fatty Acids (MCFA) (Wardani, 2007). The difference between VCO compared to palm oil is the content of lactic acid bacteria and lauric acid. VCO contains lactic acid bacteria and has a higher lauric acid content compared to palm oil. Coconut oil also contains stearic acid which is not found in palm oil (Suryani et al., 2020). However, the main reason for using both oils in this experiment is that they are widely used in Indonesia, and palm oil, has caused a concern in its effect on our health.

Considering that dietary intake and epigenetic mechanisms influence the development of obesity as a major contributor to cardiometabolic disease, it is necessary to research the potential of an experimental model of obesity in vivo and look at the effect of parental diet on the progenies. Using *Drosophila* as a model organism, this research aimed to find the effect of diets containing VCO and palm oil as a high food diet on the number of progenies, sex ratio, and body weight of several generations (transgenerational) of *Drosophila*.

MATERIALS AND METHODS

This research is an experimental study, using a completely randomized design with four fruit fly diets and carried out for eight generations. Parental flies (*Drosophila melanogaster*) in F_0 were wild-type captured in Sleman, Yogyakarta. Four types of diets were used, with the composition of each media given in Table 1. The basic ingredients were: aquadest, palm sugar, yeast, agar, banana (Ambon variety), cornmeal, virgin coconut oil (VCO), and palm oil. The differences in the four types of media used were banana diet (diet 1), cornmeal diet (diet 2), cornmeal + 3% VCO (diet 3) dan cornmeal+ 3% palm oil (diet 4). There were no treatments using a mixture of banana and oil due to the texture of the banana which caused the oil to separate in the media (unpublished result). The equipment needed in the experiment were glass bottles, filter paper, a saucepan, a wooden spoon, a foam plug, an oven (Memmert GmbH), tweezers, an autoclave, an analytical balance (OHAUS), and magnifying glass.

For each type of food, there were three replications (3 bottles). Three pairs of parental flies were placed in each bottle at the start of each generation. Fruit flies were kept in bottles containing 20 mL of food and kept at a temperature of 22 °C with a relative humidity of 60% and a 12-hour light-dark cycle. The number of progenies (imago) was counted on day 14 after parental flies were placed in each diet. Diethyl ether was used to make the flies easier to capture and sex identification was done by using a magnifying glass to identify female fruit flies which have a longer abdomen and no genital combs on their legs while male fruit flies have a shorter abdomen and sex combs on their legs. Flies body weight was measured for samples of 5 fruit flies that were anesthetized and then weighed using an analytical balance. Data analysis on the number of progeny, sex ratio (numbers of males/ number of females), and average weight of fruit flies was carried out using IBM SPSS 26. The statistical analysis used was an analysis of variance (ANOVA) followed by DMRT post hoc analysis.

Table 1. Composition of four *Drosophila* diets used in the experiment

Diets	Composition
Diet 1. Banana	500 g banana, 150 g palm sugar, 500 ml aqua dest, 12 g yeast, 7 g agar
Diet 2. Cornmeal	125 g cornmeal, 76 g palm sugar, 1 L aqua dest, 12 g yeast, 7 g agar,
Diet 3. Cornmeal + 3% VCO	125 g cornmeal, 76 g palm sugar, 1 L aqua dest, 12 g yeast, 7 g agar, 30 mL VCO
Diet 4. Cornmeal + 3% palm oil	125 g cornmeal, 76 g palm sugar, 1 L aqua dest, 12 g yeast, 7 g agar, 30 mL palm oil

RESULTS

Intergenerational Effect of Different Diets on The Number of Progenies

The variation of diets used in this study has been modified to find ingredients that were easy to find but still provide nutrients to support the growth and reproduction of *Drosophila*. The food that is often used in *Drosophila* propagation in our laboratory was made from bananas as a source of carbohydrates. However, the addition of coconut oil and palm oil in the banana media as a source of lipids showed that the oil could not blend with the banana in the media, resulting in an oil layer on top of the media causing fruit flies to easily fall in the food media (unpublished results). Modification of the food source was done using media from cornmeal which is widely used as *a Drosophila* food source (Diop et al., 2017; Guida et al., 2019). Bananas and cornmeal act as a source of carbohydrates and protein for the *Drosophila* diet. The addition of VCO and palm oil for a high food diet was chosen because both oils are widely used by humans for cooking thus we hope that it can stimulate the same effect in *Drosophila*.

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Thirty percent of oil in the media was initially used in our preliminary research (unpublished result) according to result finding of Guida et al. (2019) but produced an oil layer causing all the fruit flies to die. In this study, we modified the high-fat food using cornmeal and reduced the percentage of oil to 3% to reduce the oil layer. However, in the food containing VCO, this layer still persists thus resulting in a significant decrease in the number of progenies in the generations after F_1 in the media containing cornmeal + 3% VCO.

The number of progenies was investigated because it is linked to fitness or the ability of the species to reproduce. Investigation of fitness is usually represented by the species's fecundity, where it is estimated by the number of eggs laid. Fecundity is a plastic trait that can be affected by many environmental factors (Nouhaud et al., 2018). ANOVA with post hoc analysis using DMRT for a number of progenies between media for all generations showed that significant differences are found between the cornmeal diet containing palm oil with the other diets (Table 2). A higher number of progenies were found in the diet without oil with an average of 85 flies (banana diet) and 85.04 flies (cornmeal diet) compared to the results in the oil diet with 19 flies (cornmeal + 3% VCO) and 76.67 flies (cornmeal + 3% palm oil)

In this study, later generations (F_7–F_8) showed that the number of progenies is significantly different from some of the earlier generations in the media without VCO (table 2), specifically in generations F_3–F_5. However, there are significant differences in the number of progenies between generations F_1 and F_2 with generations F_6, F_7, and F_8. The number of progenies was initially high (average= 71.42) then decreased in generation F_4 (average= 53.75) and later increased again in later generations, reaching an average of 77.08 in F_8.

Table 2. The average number of total progenies of *Drosophila melanogaster* for eight generations in four types of diets

Generation	Average number of progenies in different diets				
	Banana	Cornmeal	Cornmeal + 3% VCO	Cornmeal + 3% palm oil	Average number of progenies per generation
F_1	52.33 ± 6.35	81.33 ± 6.03	82.67 ± 3.06	69.33 ± 2.89	71.42 ± 13.38^{cd}
F_2	88.33 ± 2.89	84.00 ± 12.29	23.67 ± 37.58	68.33 ± 8.02	66.08 ± 31.8^{cd}
F_3	83.00 ± 6.25	83.67 ± 5.13	7.33 ± 6.42	67.00 ± 3.46	60.25 ± 32.99^{ab}
F_4	66.33 ± 10.5	75.33 ± 3.21	6.00 ± 10.39	67.33 ± 3.21	53.75 ± 29.76^{a}
F_5	84.67 ± 6.51	84.33 ± 6.51	11.33 ± 12.66	66.67 ± 8.62	61.75 ± 32.25^{ab}
F_6	94.33 ± 7.09	86.67 ± 17.93	6.67 ± 11.55	88.33 ± 7.09	69.00 ± 30.02^{cd}
F_7	113.00 ± 4.36	100.33 ± 2.08	6.33 ± 10.97	88.67 ± 3.79	77.08 ± 43.93^{d}
F_8	98.00 ± 7.94	84.67 ± 13.32	8.00 ± 13.86	97.67 ± 9.81	72.08 ± 40.26^{cd}
Average number of progenies per diet	85.00 ± 18.83^{a}	85.04 ± 10.60^{a}	19.00 ± 28.72^{c}	76.67 ± 13.25^{b}	

Intergenerational Effect of Different Diets on The Sex Ratio of *Drosophila*

Sex allocation in certain species reflects the adaptive ability in different environments including those that are not favorable to the species (Rosenfeld & Roberts, 2004). The sex ratio was calculated using the number of males divided by the number of females so an average of more than 1 means that there were more females than males. The sex ratio between media and between generations was not significantly different (Table 3) even though the average sex ratio in generations F_7 and F_8 is lower than in F_1 and F_2. There is mainly a fluctuation in the sex ratio with no significant difference between the generations. The sex ratio between the four diets also shows no significant difference even though the number in the media is slightly lower (1.36) in the media containing palm oil compared to the sex ratio in the other three diets. No significant difference in sex ratio between media or between generations shows that both media and population generation did not affect the sex ratio of *Drosophila* in this experiment.

Intergenerational Effect of Different Diets on Body Weight of *Drosophila*

In this experiment, statistical analysis showed that a significant difference ($P < 0.05$) was found between the weight of flies in the media containing VCO compared to the other three media (Table

4). This difference could be due to VCO not being able to mix in the media and causing a layer of oil on the media surface which caused the flies to die or be unable to obtain food hence causing a lower weight.

Significant differences were also observed in flies body weight between generation F_1 with later generations (F_4–F_8). The reduced body weight occurred in media containing banana, cornmeal only, and cornmeal + VCO but not in media containing palm oil. In the cornmeal + 3% palm oil, the average weight in generations F_7 and F_8 was slightly higher than that of earlier generations.

Table 3. The average sex ratio of *Drosophila melanogaster* for eight generations in four types of diets

Generation	Sex ratio in each diet (number of males/number of females)				
	Banana	Cornmeal	Cornmeal + 3 % VCO	Cornmeal + 3% palm oil	Sex ratio per generation
F_1	2.31 ± 0.42	2.31 ± 0.64	1.82 ± 0.78	2.04 ± 0.37	2.07 ± 0.41[a]
F_2	2.14 ± 0.40	1.77 ± 0.64	1.73 ± 1.55	1.59 ± 0.25	1.81 ± 0.72[a]
F_3	1.89 ± 0.22	1.92 ± 0.13	3.67 ± 4.73	1.40 ± 0.11	2.22 ± 2.21[a]
F_4	1.76 ± 0.94	1.57 ± 0.54	0.42 ± 0.72	0.89 ± 0.80	1.16 ± 0.79[a]
F_5	1.72 ± 0.28	1.61 ± 0.18	1.38 ± 2.27	0.99 ± 0.16	1.43 ± 1.02[a]
F_6	1.82 ± 0.44	1.71 ± 0.39	3.00 ± 5.19	1.32 ± 0.16	1.96 ± 2.32[a]
F_7	1.59 ± 0.36	1.68 ± 0.25	1.25 ± 2.17	1.26 ± 0.58	1.44 ± 0.95[a]
F_8	1.52 ± 0.21	1.41 ± 0.18	1.00 ± 1.73	1.37 ± 0.19	1.33 ± 0.78[a]
Average sex ratio per diet	1.82 ± 0.43[a]	1.75 ± 0.39[a]	1.78 ± 2.59[a]	1.36 ± 0.37[a]	

Table 4. Average body weight of *Drosophila melanogaster* for eight generations in four types of diets

Generation	Body weight in each diet (mg)				
	Banana	Cornmeal	Cornmeal + 3 % VCO	Cornmeal + 3% palm oil	Average body weight per generation
F_1	0.87 ± 0.09	0.78 ± 0.07	0.75 ± 0.03	0.70 ± 0.07	0.78 ± 0.09[a]
F_2	0.76 ± 0.05	0.68 ± 0.05	0.69 ± 0.08	0.79 ± 0.08	0.73 ± 0.08[ab]
F_3	0.71 ± 0.06	0.67 ± 0.06	0.49 ± 0.42	0.76 ± 0.07	0.66 ± 0.21[abc]
F_4	0.63 ± 0.06	0.59 ± 0.01	0.17 ± 0.30	0.69 ± 0.01	0.52 ± 0.03[c]
F_5	0.60 ± 0.02	0.62 ± 0.04	0.37 ± 0.32	0.73 ± 0.08	0.58 ± 0.19[c]
F_6	0.64 ± 0.02	0.61 ± 0.05	0.19 ± 0.33	0.76 ± 0.06	0.55 ± 0.27[c]
F_7	0.79 ± 0.18	0.70 ± 0.02	0.17 ± 0.29	0.81 ± 0.01	0.62 ± 0.31[bc]
F_8	0.48 ± 0.35	0.66 ± 0.05	0.14 ± 0.24	0.83 ± 0.02	0.53 ± 0.32[c]
Average body weight per diet	0.68 ± 0.17[a]	0.66 ± 0.07[a]	0.37 ± 0.33[b]	0.76 ± 0.07[a]	

DISCUSSION

Results showed that the number of *Drosophila melanogaster* in media with oils was lower than the number in media without oil. One factor that might cause this lower number is decreased female attractiveness, resulting in reduced male mating behaviors toward females in high-fat diets (Schultzhaus et al., 2018). A high fat diet (HFD) is also known to affect the ability of males to judge mate attractiveness and likely alters fly condition and sexual traits which affects mating behavior thus affecting the number of progenies in the HFD. The effect of a high-fat diet on *Drosophila* fecundity was also found (Liao et al., 2021) where HFD of the *Drosophila* diet supplemented with 30% coconut oil, caused a lower number of eggs. In that study, the longest observation was for 70 days for the percent of survival and only 1–3 generations for other characters observed.

The increased number of progenies in later generations (F_6, F_7, and F_8) can be due to the adaptation of the population in each type of media causing increased fecundity. Adaptation to food sources and crowded environments can cause changes in fecundity and mortality (Sharma & Shakarad, 2021). Epigenetics mechanisms can also affect changes in progenies from both maternal and paternal mediators. Factors such as diet, stress or external chemicals can induce epigenetic changes in various developmental stages of male or female parents (Sales et al., 2017). *Drosophila melanogaster* reared on an isocaloric diet can influence more than one generation even though the diet has been changed to a standard diet. The effect of a diet high in protein-sugar ratio also showed faster metamorphosis, higher reproduction, and different metabolic pool content (Matzkin et al., 2013). Another reason is that some parental flies in some diets might have longer life spans and may have been counted because in each generation the parental flies were not separated from the new progenies.

Even though the average sex ratio of progenies was lower in the later generations, statistical analysis showed that there were no significant differences between media or generations. The lower sex ratio (more daughters in the population) may be affected by other factors. In other research, the number of male and female *Drosophila* can have a constant ratio (1:1) when exposed to different environments (Fauzi et al., 2017). However, some research also showed that the sex ratio can change due to external factors such as where the fruit flies are reared (natural or laboratory environment), the origin of the species, and climatic or microclimate conditions (Salceda & Arceo-Maldonado, 2012). In mammals, external conditions such as overcrowding can also cause a shift in the sex ratio, favoring female progenies. Overcrowding due to rearing in a small closed bottle can be a potential factor in affecting the increased number of females. However, a change in diet such as a high-fat diet given to mice was found to reduce the influence of overcrowding, changing the increase in male progenies instead (Dama et al., 2011; Rosenfeld & Roberts, 2004).

The effect of rearing in a closed space can also cause female flies to mate with both old and young males. Long and Pischedda (2005) found that in *Drosophila melanogaster*, females mated to old males produced more number of daughters than females mated to young males. This may be due to a higher probability of mutations in older males that can be passed on. Thus lower number of sons are produced than daughters to limit the mutations occurring in the population. Further investigation is needed to understand if food sources can affect the sex ratio of *the Drosophila melanogaster* population because changes in sex ratio can affect the species' survival as it affects the species' fitness (Silva-Soares et al., 2017).

Variation in body shape or weight is affected by environmental factors such as nutrition, temperature, and living space. The effects of nutrition have been studied widely in fruit flies and some studies show that some nutritional restriction dan affect body weight. Guida et al. (2019) showed that a high-fat diet using 30% VCO can cause an increase in fruit fly body weight in the first generation but not in the second generation, showing that a much higher concentration of VCO was used and the effect on body weight was not inherited. A study by Krittika and Yadav (2022) also showed that food sources can affect the growth of fruit flies. A low-protein food source affects body weight, relative water content, relative fat content, body size, wing size, and pupal size in *Drosophila melanogaster*.

In this study, the average body weight of *D. melanogaster* in different diets showed significant differences only between the cornmeal + VCO with the other three diets. From observation during the experiment, the decrease in body weight in media containing 3% VCO was mainly due to the layer of oil that occurred on the media surface. This enabled the flies to take nutrients from the media. The layer of oil might also decrease the odor of the food media. Food-related odor is an important signal for appetite in *Drosophila* (He et al., 2022) because in the wild, *Drosophila* usually consume fermented food sources from rotting fruit (Bass et al., 2007).

From the result, it can be observed that the addition of 3% VCO and palm oil in the cornmeal media did not significantly increase the number of progenies, sex ratio, and body weight in eight generations of *D. melanogaster* progenies. The nutrition composition of each diet has not been analyzed and more importantly still needs some adjustment to obtain a better composition so that the addition of oil does not cause an oil layer. However, the addition of oil palm made a better media because no oil layer was produced on top of the media, making it a better potential for further use in the effect of HFD using palm oil for *D. melanogaster*.

CONCLUSION

There were significant differences between the number of progenies in the four types of diets, specifically between the oil media (VCO and palm oil) with the media without oil. The number of progenies between F_1 with F_8 was not significantly different even though there were significant differences with generations F_3–F_5 showing that there may be changes to the ability of the fruit files ability to adapt to the food source. The sex ratio of the *Drosophila melanogaster* was not significantly different either between the different diets or between the eight generations. The fly's body weight in a diet containing VCO was significantly different from the other diets but it was difficult for flies to obtain nutrients from the diet due to the VCO that did not mix easily with other ingredients in the diet. Significant differences were also observed in flies' body weight between generation F_1 with later generations (F_4–F_8). These results suggest that there may be other factors contributing to the number of progenies, sex ratio, and body weight of fruit flies such as the age of individual flies and living space of the population. Further investigation is also needed to find a better formula for high-fat diet food sources that can be used for the epigenetic study of obesity using fruit flies as model organisms.

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