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Nutritional phenotype underlines the performance trade-offs of *Drosophila suzukii* on different fruit diets

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ABSTRACT

Animals confined to different dietary conditions often exhibit distinct, sometimes contrasting, nutritional phenotypes and performance outcomes. This is especially true for many oviparous insects whose developmental diets can vary depending on the mother's egg-laying site selection. Much research on the relationship between preference and performance in insects has focused on larval success, which overlooks the complexities of dietary effects on diverse performance parameters across life stages and potential trade-offs between those parameters. Furthermore, the connection between diet-induced nutritional phenotype and performance trade-offs is not well understood. Here, using *Drosophila suzukii*, we quantify multiple performance indices of larvae and adults reared on five host fruits of different protein-to-sugar ratios (P:S) which have previously been shown to differ in attractiveness to fly foraging and oviposition. Our results demonstrate robust diet-specific performance trade-offs, with fly fecundity, larval development time, pupal size, and adult weight superior in flies reared on the high P:S raspberry diet, in contrast to the low P:S grape diet; but the reverse was found in terms of adult starvation resistance. Notably, the contrasting performance trade-offs are readily explained by the fly nutritional phenotype, reflected in the protein and energy (glucose and lipid) contents of flies reared on the two fruits. Together, our results provide experimental evidence for metabolic plasticity of *D. suzukii* reared on different fruits and the possibility of using adult nutritional phenotype as a marker for diet and performance outcomes.

Introduction

Diet represents the most important environmental factor for animal survival, growth, reproduction, and various other physiological traits. In many oviparous insects, the developmental diet of immature stages (e.g., larvae) is determined by the mother's egg-laying site selection (Björkman et al., 1997; Fortuna et al., 2013; Gripenberg et al., 2010), which could also shape their long-term performance and life-history phenotypes (Langley-Evans, 2015; Nicholls et al., 2021; Stefana et al., 2017). The preference-performance ("mother knows best") hypothesis assumes maternal oviposition preference evolves toward maximizing offspring fitness (Jaenike, 1978). For example, a meta-analysis of 21-29 early studies on phytophagous insects suggested offspring survival was higher on plant types preferred by ovipositing females (Gripenberg et al., 2010). However, there are also numerous examples in which the correlation between female oviposition preference and offspring performance was poor, with large amounts of variation in egg-laying choices unexplained (Griese et al., 2020; Xi et al., 2019). Implicit

in these examples is the fact that diet is a complex, multidimensional factor where the inputs of different dietary components (e.g., macronutrients) can promote or constrain specific physiological processes, which often leads to trade-offs in performance outcomes (Bellutti et al., 2018). Classic examples include the large body of literature on the impact of dietary protein-to-carbohydrate ratio (P:C) on life history traits in both mammals and insects, such as trade-offs between immunity, lifespan, and reproduction (Fanson et al., 2012; Grandison et al., 2009; Kiilerich et al., 2016; Lee, 2015; Lee et al., 2008; Maklakov et al., 2008; Roeder and Behmer, 2014). These life history traits are strongly associated with animal adaptation to environmental stressors, including food deprivation (Gerofotis et al., 2019; Higginson et al., 2012; Kawecki et al., 2021; Kubrak et al., 2017; Rion and Kawecki, 2007). However, in the vast majority of preference-performance studies, the implications of diet-dependent performance trade-offs were rarely considered.

Drosophila suzukii (Matsumura) (Diptera: Drosophilidae), the spotted wing drosophila, is a polyphagous invasive fly pest native to Asia.

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Distinct from other *Drosophila* species that target rotting fruits, *D. suzukii* can exploit a variety of healthy, ripening fruits, having been shown capable of infesting thirteen different plant families (review by Cloonan et al., 2018). Other non-fruit substrates, ranging from flora to bird manure, have also been suggested as alternative food sources for this pest (Stockton et al., 2019; Tochen et al., 2016). The wide dietary breadth and flexibility in diet choices enable *D. suzukii* to adapt to changing availability of food sources through the seasons or when invading different regions (Aly et al., 2017; Atallah et al., 2014; Jiménez-Padilla et al., 2020; Little et al., 2020; Poyet et al., 2015). Female *D. suzukii* has evolved serrated ovipositors to pierce fruit skins and insert their eggs into the flesh (Hauser, 2011; Stockton et al., 2019; Walsh et al., 2011). The oviposition site selection of *D. suzukii* is crucial for a successful life cycle since the developmental diet of the offspring is confined to the choices made by the mother. To date, research has identified several proximate factors of *D. suzukii* diet and oviposition preferences, which include fruit volatiles (Karageorgi et al., 2017; Keeseey et al., 2015; Krause Pham and Ray, 2015), stiffness of the fruit skin (Karageorgi et al., 2017), bitter taste cues (Dweck et al., 2021), and fruit-associated microbes (Sato et al., 2021; Urbaneja-Bernat et al., 2020). Multiple studies have also examined *D. suzukii* fruit preferences by comparing infestation rates among field-sampled fruits or scoring the number of eggs laid among whole or mashed fruits in the laboratory (Bellamy et al., 2013; Burrack et al., 2013; Olazcuaga et al., 2019; Poyet et al., 2015). There is solid evidence that larval fitness (including survival, development rate, and cold tolerance) is dependent on the dietary P:C or fruit type (Bellamy et al., 2013; Bing et al., 2018; Hardin et al., 2015; Jaramillo et al., 2015; Rendon et al., 2018), and different fruit-based diets have been shown to induce transgenerational changes of the fly microbiome, an important component of fly metabolism (Jiménez-Padilla et al., 2020). However, few studies have examined how *D. suzukii* later-life performance (beyond larval success) varies by host fruit (Jaramillo et al., 2015; Kaçar et al., 2016), and more importantly, how fly nutritional phenotype corresponds to these performance variations.

In our recent study using five different host fruits (raspberries, strawberries, blueberries, nectarines, and grapes), we have established that *D. suzukii* has clear fruit preferences in foraging and oviposition and that these preferences were not influenced by the fly's developmental diet history or gut microbiome (Shu et al., 2021). In addition to varied attractiveness to *D. suzukii*, these fruits differ widely in nutrient content, with protein-to-sugar ratio (P:S) ranging from 1:4 (raspberries) to 1:22 (grapes). With the expectation that the different fruit diets direct *D. suzukii* to divergent performance outcomes, we hypothesize there are diet-specific performance trade-offs but these trade-offs can only be realized when traits representing diverse aspects of physiology are systematically measured. Here, we quantify multiple performance indices of *D. suzukii* larvae and adults reared on the different fruit diets. Our results show that fly fecundity, larval development time, pupal size, and adult weight were superior in flies reared on the raspberry diet, previously found to be the preferred fruit by *D. suzukii* and had the highest P:S. In contrast, the less-preferred, low P:S grape diet produced the fewest number of offspring, and larval development was severely prolonged, but the adult flies raised on this fruit were superior in starvation resistance. Our nutritional assays indicate raspberry-fed flies had over twice as high protein content than grape-fed flies, while grape-fed flies had elevated glucose, up to ten times more triglycerides coupled with more abundant and bigger lipid droplets in the fat body than raspberry-fed flies. The nutritional phenotypes accompanying flies on these two fruits likely underscore their contrasting performance outcomes. Together, our findings suggest *D. suzukii* fruit preference gears toward maximizing fecundity, offspring growth, and development, but could come at the cost of reduced energy reserves and low starvation resistance. Our results also demonstrate a high degree of developmental and metabolic plasticity of *D. suzukii* in response to different fruit diets, which may help warrant its success as an invasive agricultural pest.

Materials and methods

Fly husbandry

Wild *D. suzukii* were collected from blackberries grown in Hawthorne Florida (29°35'17" N 82°5'2" W) in August 2017. The population was subsequently raised on Formula 4-24® Instant *Drosophila* Medium (Carolina Biological Supply Company) supplemented with 2.5% brewer's yeast (MP Biomedicals) in the laboratory at 24°C, 64% RH, 16:8 L:D cycle. Fruit-based diets were prepared using raspberries (Driscoll's Inc.), nectarines (PLU code: 4378, GEOFRUT Inc.), strawberries (Driscoll's Inc.), grapes (PLU code: 4023, Ahold Inc.), and blueberries (Driscoll's Inc.) purchased from grocery stores. Intact fruits and pitted nectarines were washed with deionized water and then macerated separately in a blender, followed by adding a solution of deionized water (13.7%), agar (0.6%), and Tegosept (0.15%), then dispensed in *Drosophila* vials (25×95mm, VWR, USA). Approximate fruit P:S ratios were calculated using data of protein and total sugar (sucrose, glucose, and fructose) contents obtained from the USDA FoodData Central (<https://fdc.nal.usda.gov/>) (Ahuja et al., 2013).

Fly fecundity and development assays

Groups of three female and three male *D. suzukii* at 5-10 days old fed on the Instant *Drosophila* Medium were transferred into vials containing 10 ml fruit-based diet. The flies were removed after laying eggs for 72h. The number of pupae and adults emerged in each vial were monitored daily, with the larval developmental time to pupation and adulthood recorded. Pupae from multiple vials were randomly picked and measured under a stereomicroscope (Leica). The scale in the stereomicroscope was then calibrated using a ruler (150mm, 1mm graduation). At least four replicate vials were assayed for each fruit.

Starvation resistance assay

After emergence from the different fruit-based diets, adult female flies at 5-10 days old were anesthetized on ice and sorted into groups of 10-20 individuals. We then transferred each group into vials (25×95mm, VWR, USA) provided with 10ml 2% agar. Fly survivorship was monitored at 9AM and 5PM daily until all flies were dead. Each treatment group was run in at least three replicates.

Diet preference assay

Preference assays were performed in 9 cm diameter and 0.5 cm depth sterile Petri dishes that allowed free locomotion but restricted flight. Groups of eight 5–10 days old female flies that had been food-deprived for 15 h (provided with water) were placed into the dishes preloaded with sugar (sucrose)-yeast-casein diets at P:S=1:4 and P:S=1:22 (1cm diameter patches) on opposite sides of the dish (Figure 3A). Both diets had the same total sugar+yeast+casein concentration (90g/L). Relative protein content was manipulated by varying the quantity of casein hydrolysate (Thermo Scientific™), while the yeast concentration was kept constant (8.5g/L, MP Biomedicals) to minimize differences in yeast volatiles and other nutrient components between the diets. (Lihoreau et al., 2016). Fly foraging behavior was recorded in real-time using GigE cameras acA1300-60gc (Basler AG, Germany) for 6 hours under constant light condition and 23°C ambient temperature. Video footage was processed and analyzed by the EthoVision XT 15 software (Noldus, Netherlands). The LOWESS (Locally Weighted Scatterplot Smoothing) method was applied to reduce the tracking noise and the small movements of the fly ("body wobble").

Nutritional assays

Soluble protein, glucose, and triglyceride (TAG) contents of the raspberry- or grape-fed flies were estimated by enzymatic colorimetric

ric assays, using protocols modified from previous studies (Wong et al., 2014; Tennessen et al., 2014). Briefly, pools of five 5-10 days old female flies were weighed on a microbalance (Mettler Toledo XPR2). Fly samples were then homogenized in 125 μ l ice-cold TET buffer (autoclaved 10 mM Tris, 1 mM EDTA, 0.1% Triton X-100, pH 7.6) with 40 μ l matrix D beads (MP Biomedicals) using a bead beater (Percellys Evolution, Bertin Instruments). Twenty microliters of the homogenate were immediately stored at -80°C for subsequent protein assay. The remaining homogenate was heat-treated for 15 mins at 72°C. After heating, the samples were stored at -80°C for future glucose and TAG analyses.

Sample protein content was measured by the DC Protein Assay Kit II (Bio-Rad, 5000112) as per the manufacturer's instruction. In brief, the homogenates were centrifuged, and then 5 μ l of the supernatants or BSA standards were loaded into a 96-well plate in duplicates. 25 μ l of buffer A and 200 μ l of buffer B were then added to each well and mixed by pipetting. The absorbances at 750 nm were obtained after 15 mins incubation at room temperature.

Glucose was measured using the Glucose (GO) Assay kit (Sigma, GAGO-20). Specifically, homogenates were centrifuged, then 5 μ l of the heat-treated homogenate was added to a 96-well plate in duplicates along with the glucose standards, followed by adding 150 μ l of the GO reagent to each sample. After 30 mins incubation at 37°C, 150 μ l of 12N H₂SO₄ was added to end the reaction and the absorbances were measured at 540 nm.

To measure TAG, 5 μ l of samples or glycerol standards were directly loaded into a 96-well plate without centrifugation as lipids are largely insoluble in the TET buffer. This was followed by adding 37 μ l 100 U/ml *Pseudomonas* sp. lipase (Sigma L9515) to each sample and incubation at 37°C in the dark for 10 mins. Control samples without the lipase were included. After incubation, the plate was centrifuged at 3000 rpm for 3 mins. 30 μ l supernatant was transferred to a new well and then added with 150 μ l Free Glycerol Reagent (Sigma F6428). Absorbances at 540 nm were obtained after 5-mins incubation at 37°C.

All colorimetric readings were obtained using a Benchmark Plus microplate spectrophotometer (Bio-Rad).

Lipid staining

Drosophila suzukii fat body was dissected following a video demonstration (Krupp and Levine, 2010) and then stained following the protocol described by Song et al., (2014). Dissected fat body tissue was fixed for 15 mins in 4% formaldehyde/PBS in a spot plate (22mm outside diameter x 7mm deep). Next, the tissue was gently washed with 0.2% Triton/PBS and then stained with 1 mg/ml Bodipy 493/503 (Invitrogen) for 30 mins, followed by 10 mins incubation in DAPI (1:1000, Invitrogen). The tissue was then washed again with 0.2% Triton/PBS and mounted onto a glass slide with the mounting medium (Vector Laboratories VECTASHIELD Antifade). Confocal images were obtained using a Zeiss LSM800 microscope.

Statistical analysis

All data analyses were performed using the statistical computing environment R (version 3.5.1). Pupal length and numbers of viable offspring per mated *D. suzukii* female on the different fruit-based diets were analyzed by Analysis of variance (One-way ANOVA) with the post hoc (Tukey) test. Data from the diet preference and nutritional assays were analyzed by the Student's t-test or Wilcoxon rank-sum test based on whether the data were normally distributed. Larval developmental and adult survival data were analyzed by fitting proportional hazards regression models using coxph implemented in survival R package (version 3.1.8). Kaplan-Meier curves and log-rank tests were performed in survminer R package (version 0.4.6). All *P* values were adjusted by the Bonferroni correction.

Data availability

Data are available in an excel file in the supplementary materials.

Results

Drosophila suzukii reproductive and developmental successes are determined by its larval diet

Previously, our work has established that when given different fruit choices, female *D. suzukii* tended to forage and oviposit on the raspberries over strawberries, blueberries, nectarines, and grapes (Shu et al., 2021). The relative fruit preferences were largely unaffected by the flies' microbiome, developmental and transgenerational diet histories, signifying a robust innate behavior. Here, our results further show that when confined to fixed fruit diets, flies on the raspberry diet showed the best developmental and reproductive outcomes. Flies on the raspberry diet produced more than double the number of viable offspring than flies on the other four fruits (Figure 1A). Each mated female on the raspberry diet generated 7.4 ± 0.45 offspring, while the lowest number was observed on the grape diet (3.3 ± 0.57 offspring per female, $P < 0.001$, Tukey's HSD). Additionally, eggs laid on the raspberry diet developed into adults the fastest, at a median of 12 days, as compared to blueberry (median: 15 days; $P = 0.015$), strawberry (median: 15 days; $P = 3.8 \times 10^{-6}$), nectarine (median: 19 days; $P = 7 \times 10^{-16}$), and grape (median: 23 days; $P = 2 \times 10^{-16}$, log-rank test) (Figure 1B). The size of pupae also varied by developmental fruit diet, with raspberry, strawberry, and blueberry producing the largest offspring with an average pupal length of $3.07\text{mm} \pm 0.06$, $2.97\text{mm} \pm 0.05$, and $2.89\text{mm} \pm 0.04$, respectively, as compared to nectarine ($2.70\text{mm} \pm 0.05$) and grape ($2.47\text{mm} \pm 0.07$) (Figure 1C). Together, our results confirm that fruit diet type determines *D. suzukii* reproductive and developmental successes.

High performance of reproduction and development on the raspberry diet comes at the cost of low starvation resistance

Despite the apparent benefits of being raised on the raspberries (faster larval development, more offspring, and bigger offspring), female *D. suzukii* were shown to distribute lower but notable proportions of their eggs on the other fruits when all five fruits were presented to the flies (Shu et al., 2021). This gives rise to the possibility that there might be unrecognized benefits of developing on the other fruits, or costs associated with being raised on the raspberry diet that could manifest as physiological trade-offs. Additionally, studies on the related *D. melanogaster* have shown that fly starvation resistance, an important parameter of *Drosophila* performance (Kristensen et al., 2016), is affected by their developmental nutrition (Lee and Jang, 2014; Rehman and Varghese, 2021). F1 female flies raised on the different fruits differed markedly in starvation resistance ($P < 10^{-15}$, log-rank test). Specifically, flies raised on the grape diet showed the strongest starvation resistance response, surviving up to twice as long (median: 4 days) as flies raised on the other four fruits (Figure 2). In contrast to having the best developmental and reproductive performances, flies raised on the raspberry diet were the most vulnerable to starvation (median survival of 2 days) when compared to flies on blueberry ($P < 10^{-4}$, log-rank test), nectarine ($P = 0.024$, log-rank test) and grape ($P < 10^{-5}$, log-rank test) (Figure 2).

The nutritional phenotype of adult *D. suzukii* underlines the diet-dependent performance trade-offs and corresponds to dietary protein-to-sugar ratio (P:S)

The most contrasting performance differences occurred between flies raised on the raspberry and grape diets, which coincides with the largest protein-to-sugar ratio (P:S) differences. Raspberries have a P:S of 1:4 while grapes have a P:S of 1:22 (Table S1). Similar to the

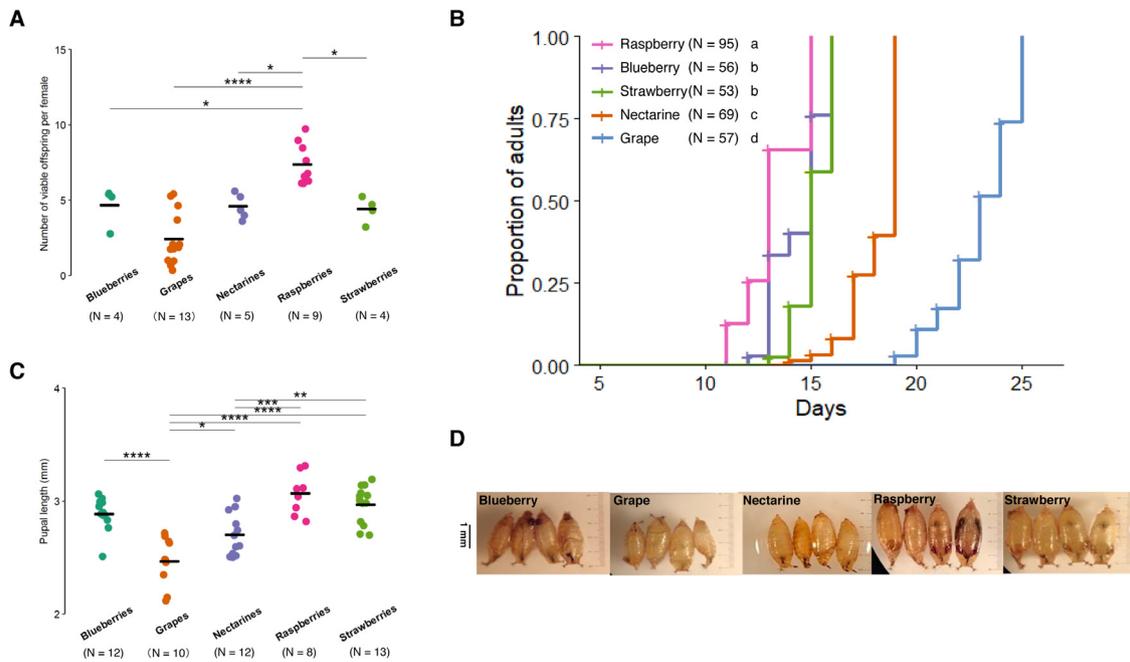
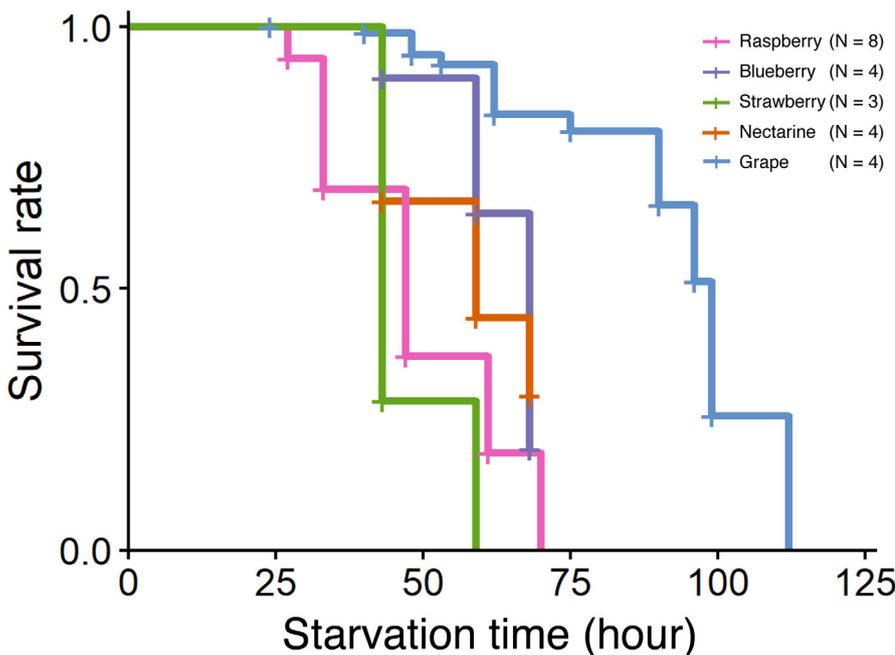


Figure 1. Reproduction and development of *D. sukukii* on five different host fruits. (A) Number of viable offspring produced per female. (B) Developmental time from eggs to adults. (C) Pupal length. (D) Representative images of pupae raised from the different fruits. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$ (One-way ANOVA, Tukey's HSD). P values were adjusted by Bonferroni.



pronounced foraging and oviposition preferences for raspberries over grapes (Shu et al., 2021), female flies had a higher tendency to forage on P:S 1:4 over P:S 1:22 diets when we set up the choices using sugar-yeast-casein diets (Figure 3B).

We next examined how *D. sukukii* nutritional phenotype correlates with the dietary P:S and flies' performance outcomes on the two fruits. Flies raised on the high P:S raspberry diet had a greater body mass (female: $P=0.0067$; male: $P=0.0004$), and their soluble protein levels were over twice as high as flies raised on the low P:S grape diet (female: $P=0.003$; male: $P=0.008$) (Figure 4A and B). In contrast, the energy levels of flies on the grape diet were significantly higher than those on the raspberry diet. Grape-fed females and males showed 31.1% and 15.2%

higher glucose levels than their raspberry-fed counterparts, respectively (female: $P=0.002$; male: $P=0.038$) (Figure 4C). The TAG levels of grape-fed flies were over five times higher than in raspberry-fed flies for females, and over ten times higher for males (female: $P=1.8 \times 10^{-5}$; male: $P=0.004$) (Figure 4D). The exceptionally high lipid storage in grape-fed flies was further demonstrated by the confocal images of their fat bodies, which carried more abundant and larger lipid droplets ($5.8 \pm 0.52 \mu\text{m}$ in diameter) than in raspberry-fed flies ($1.5 \pm 0.28 \mu\text{m}$ in diameter) (Figure 4E and F). Together, our results suggest that the nutritional phenotypes of *D. sukukii* correspond to the P:S of their developmental fruits and likely account for the contrasting trade-offs between reproduction, development, and starvation resistance.

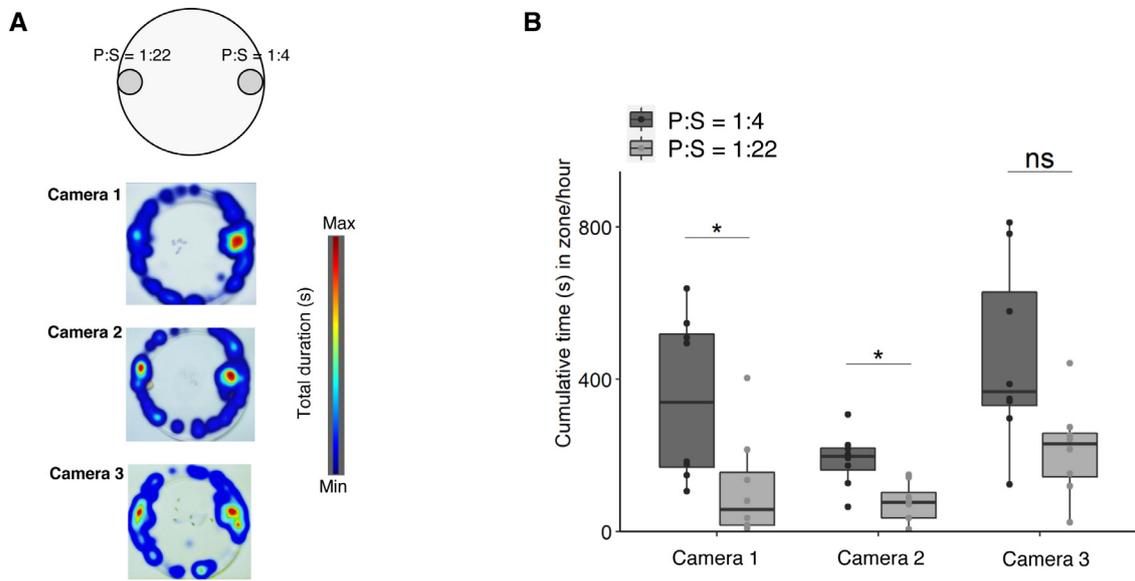


Figure 3. Foraging of *D. suzukii* female flies toward P:S=1:22 and P:S=1:4 diets made of sucrose, yeast, and casein. (A) The heatmaps and (B) boxplots represent the cumulative time spent in the P:S=1:4 or P:S=1:22 zone. Each arena containing eight female flies was tracked by one camera for 6 hours. Three cameras were set up in the experimental run. Wilcoxon rank-sum test was performed. *P* values were adjusted by Bonferroni. **P* < 0.05. ns stands for non-significant (*P* > 0.05).

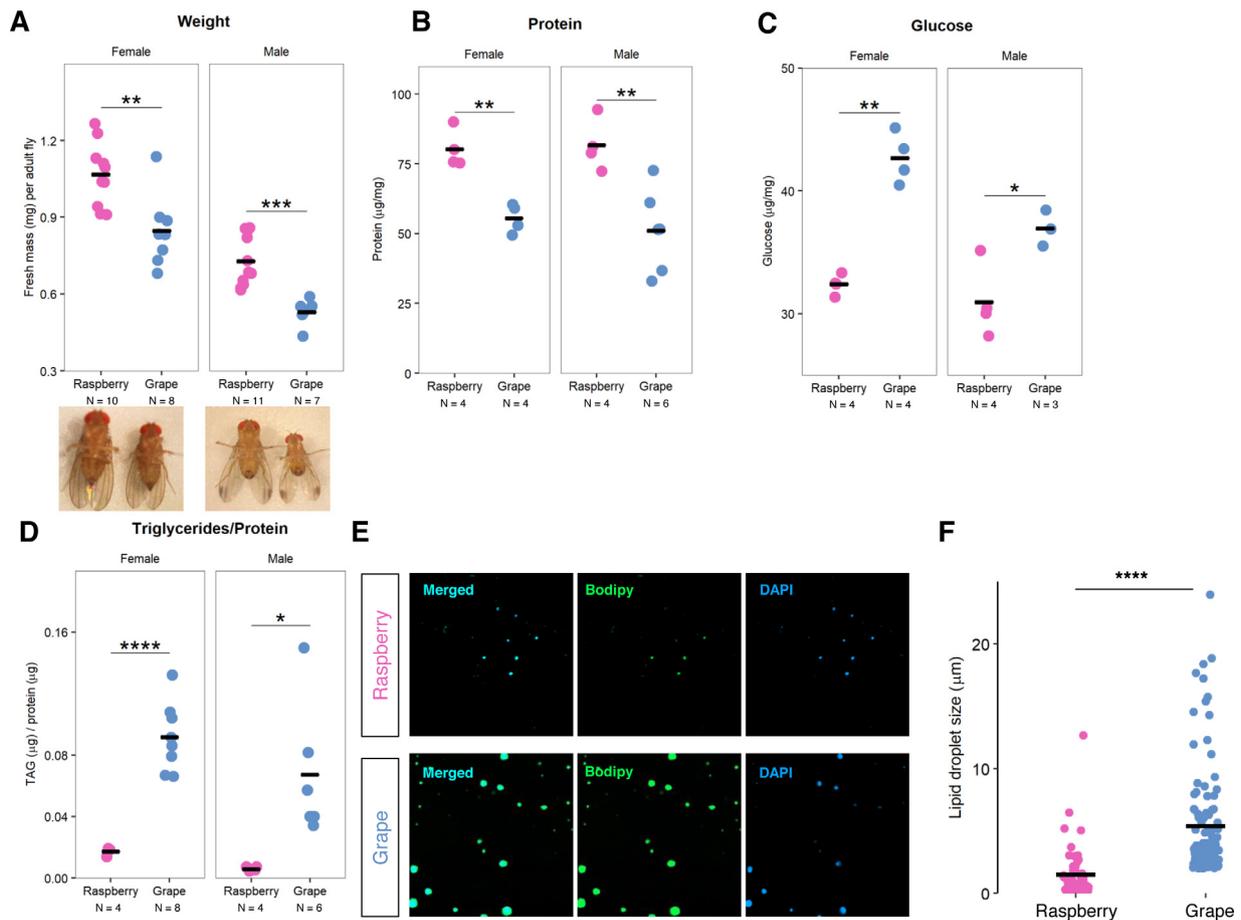


Figure 4. Nutritional phenotypes of adult female *D. suzukii* on the raspberry and grape diets. (A-D) Comparisons of fresh weight, protein, glucose, and triglyceride levels. (E) Confocal images of fat bodies stained with BODIPY and DAPI to show lipid droplets and nuclei, respectively. (F) Lipid droplet size quantified by imageJ based on the representative confocal images. Each dot represents a single lipid droplet. *P* values were Bonferroni-adjusted **P* < 0.05, ***P* < 0.01, ****P* < 0.001, *****P* < 0.0001.

Discussion

The broad host range and well-characterized fruit preferences of *D. suzukii* (Abraham et al., 2015; Bellamy et al., 2013; Cloonan et al., 2018; Shu et al., 2021; Silva-Soares et al., 2017; Young et al., 2018) provide an opportunity to explore the preference-performance relationship in the context of trade-offs. By systematically quantifying multiple traits that represent diverse aspects of *D. suzukii* life history (development, reproduction, and nutrition) on host fruits previously shown to have varied attractiveness to *D. suzukii*, our study illustrates that a positive preference-performance association with juvenile growth and development could pair with a negative association on adult starvation resistance, and vice versa. The implication is that there are fitness costs and benefits associated with each oviposition site selection that can manifest at different life stages. The significance of these costs/benefits likely depends on a range of ecological factors and may therefore drive variability in egg-laying choices.

Another major finding of our study is that the diet-specific performance trade-offs can be explained by the nutritional phenotype. Proteins and carbohydrates are two prominent dietary macronutrients; although they are near identical in caloric value, they fulfill different organismal functions (Simpson and Raubenheimer, 2012). Dietary protein provides the essential amino acids for somatic growth, cellular protein synthesis, and tissue repair. It is also the principal source of nitrogen that serves as a building block for essential nitrogenous molecules, such as nucleic acids, whereas the primary function of dietary carbohydrate is to provide and store energy (Le Gall and Behmer, 2014). Studies across animals have demonstrated that dietary protein-to-carbohydrate ratio (P:C) or P:S influences performance trade-offs (Clark et al., 2015; Cotter et al., 2011; Fanson and Taylor, 2012; Tatar and Carey, 1995; Zanco et al., 2021). For example, in *D. melanogaster* and mice, the longevity-reproduction trade-off was shown to correlate with dietary P:C, with reproduction generally optimized on higher P:C diets than those which maximize adult longevity (Lee et al., 2008; Solon-Biet et al., 2015b). Consistent with this pattern, fecundity was the highest on mating pairs confined to the high P:S raspberry diet, which also generated larvae with the fastest development and adults with significantly higher protein titers. This result supports the consensus that raspberry is among the best host fruits for *D. suzukii* reproductive success (Aly et al., 2017; Bellamy et al., 2013; Olazuaga et al., 2019). In contrast, oviposition on the low P:S grape diet condemned the offspring to poor larval performance, concurred with the previous observation, but the resulting adults were highly resistant to starvation as reflected in their richer energy reserves. Hence, the fly nutritional phenotype is a predictor for diet-specific performance trade-offs and appears to correspond to the fruit P:S.

The “obesity-like” phenotype of *D. suzukii* reared on low P:S fruits may reflect the “protein leverage hypothesis”, i.e., the priority to satisfy protein needs over needs for other macronutrients (Raubenheimer and Simpson, 2019; Simpson and Raubenheimer, 2005). The hypothesis predicts that animals prioritize protein intake in feeding, as has been shown in various insects and mammals (Gosby et al., 2011; Le Gall and Behmer, 2014; Raubenheimer et al., 2015; Solon-Biet et al., 2015a; Warbrick-Smith et al., 2006). Protein leverage was found to be pronounced during *D. melanogaster* larval development. When fly larvae were confined to nutritionally imbalanced diets of low P:C, they overconsumed carbohydrates to attain protein intake critical for development and metamorphosis (Almeida de Carvalho and Mirth, 2017). Therefore, a possible explanation is that *D. suzukii* larvae under the low P:S fruits overconsume sugars to regulate their protein intake, resulting in several folds higher in lipid storage and elevated starvation resistance. Alternatively, the larvae may consume the same amount of the fruits but the low P:S fruits were more energy-dense (grapes are ~30.2% more caloric than raspberries). It remains open the extent to which protein leverage impacts *D. suzukii* energy stores on high P:S fruits compared to low P:S fruits if the fruit diets were controlled to the same caloric

content. Future work will also focus on developing robust quantitative feeding assays to test if consumption varies by host fruit.

One aspect that remains to be tested is the extent to which the fruit nutritional content contributes to *D. suzukii* fruit preference relative to non-nutritive cues (e.g., fruit odor, taste, or hardness as indicated in earlier studies). Insects possess peripheral and endocrine receptors to sense nutrients from food (Behmer, 2009). The role of dietary P:S in animal foraging preference has been demonstrated in several insects, including aphids, locusts, grasshoppers, and flies (Raubenheimer and Simpson, 2003; Simpson et al., 1993; Wong et al., 2017; Young et al., 2018). In *D. suzukii*, two previous studies have examined the association between oviposition preference and dietary P:S using semi-defined artificial media (Silva-Soares et al., 2017; Young et al., 2018). Using sugar-yeast diets of three different P:S (1:1, 1:4, and 1:8), Silva-Soares et al. (2017) found that *D. suzukii* preferred laying eggs on the P:S 1:8 diet and least preferred the 1:1 diet. Young et al. (2018) provided *D. suzukii* eight choices of corn syrup-whey-casein diets with varying P:S ratios (1:12, 1:6, 1:3, 1:1, 2:1, 4:1, 8:1, 24:1) and showed that the flies preferred laying eggs onto the P:S 1:12 diet the most. These data suggest *D. suzukii* generally prefers low P:S food sources in oviposition, coupled with the observations that larvae survived better on low P:S artificial media (Rendon et al., 2018; Silva-Soares et al., 2017). However, several studies using whole or mashed fruits did not find such a pattern. These include Aly et al. (2017) that showed female *D. suzukii* preferred laying eggs on raspberries over green grapes, our earlier work showing *D. suzukii* laying significantly more eggs on the raspberry diet than the grape diet when offered five different fruit choices, and a study involving 12 different fruits that found *D. suzukii* laid more eggs onto fruit diets at high to moderate P:S (blackberry and blackcurrant) (Olazuaga et al., 2019). Olazuaga et al. further showed that the fruit phosphorus level was strongly associated with *D. suzukii* oviposition preference, and there was no correlation between preference and emergence rate (Olazuaga et al., 2019). The different preference and performance outcomes observed across studies, particularly between those using artificial and fruit diets, could be attributed to a combination of factors including fly nutritional or satiety status, fly microbiome makeup, fly genotype, diet nutritive and non-nutritive cues, and laboratory assay setup. More research will be needed to delineate the contribution of these factors to *D. suzukii* preference and performance.

While our results indicate that the fruit diets can project the flies to distinct nutritional phenotypes and performance trade-offs, it is unclear whether these traits are reversible. Swapping host fruits at different developmental stages will help clarify the metabolic plasticity of *D. suzukii* in response to diet switching. Future experiments will also expand the performance traits to be measured (such as longevity) to establish a more comprehensive picture on diet-induced performance trade-offs in this significant agricultural pest.

Declaration of Competing Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

CRediT authorship contribution statement

Runhang Shu: Investigation, Methodology, Writing – original draft. **Laurice Uy:** Investigation, Methodology. **Adam Chun-Nin Wong:** Conceptualization, Methodology, Funding acquisition, Writing – review & editing.

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Supplementary materials

Supplementary materials associated with this article can be found, in the online version, at doi:10.1016/j.cris.2021.100026.

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