A Performance Index as a measure of the host suitability to Drosophila suzukii Matsumura (Diptera: Drosophilidae)

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Abstract

Drosophila suzukii Matsumura, known as spotted wing drosophila (SWD), is an Asiatic invasive fruit pest that has spread over the world in the last fifteen years, due to its high reproductive rate, its tolerance to different environmental conditions, the international fruit trade, and its wide range of host plants. In Buenos Aires, Argentina, blueberry is a major susceptible crop, although other cultivated and non-cultivated fruit species are frequent. The aim of this study was to evaluate the host suitability of commercial and non-cultivated fruit species (blueberries, plums, mulberries and cherries) at two stages of maturity by estimating an index that takes into account biological and biometric parameters. The development and survival of SWD cohorts reared on different fruits were followed from egg to adult emergence. Then, adults were sexed and some biometric traits were measured. The indices: Wing loading, Wing aspect and the Relative Performance Index (RPI) were estimated. The shortest developmental time and the maximum egg to adult survival were observed in the specimens developed in mulberry, in both stages of maturity. Only the length of the thorax showed significant differences between treatments in both sexes, and the largest adults were those reared in the ripe mulberries. The RPI, which relates performance and biometric variables, was the best parameter to evaluate the host suitability of SWD. So, it could be used as an indicator of the nutritional quality of fruits available in a region and to evaluate the importance of alternative hosts in the population dynamic of SWD.

Introduction

Spotted wing drosophila (SWD), *Drosophila suzukii* Matsumura, is an invasive species native of Southeast of Asia that has spread in this century to different countries of Europe (Calabria et al. 2012), North and South America (Hauser et al. 2009; Deprá et al. 2014; Santadino et al. 2015; Mello García et al. 2022), and more recently Africa and Oceania (Kwadha et al. 2021; Aouari et al. 2022; EPPO 2023). This successful invasion is due to its high reproductive rate, its tolerance to different environmental conditions, its wide range of host plants and the international fruit trade (Kimura 2004; Calabria et al. 2012). Females have a serrated ovipositor that allows them to lacerate the epicarp of healthy pre-harvest fruits to oviposit (Lee et al. 2011; Walsh et al. 2011). The larvae develop inside the fruit and allow the entry of pathogens that cause its premature decay (Walsh et al. 2011; Cini et al. 2012). This fly can develop in several commercial and non-cultivated fruit species (Cloonan et al. 2018), and the damage is especially important in soft-skinned fruits and some stone fruits (Lee et al. 2011; Bellamy et al. 2013; Little et al. 2017). Excluding strawberry (*Fragaria x ananassa* (Duchesne ex Weston)) for being a horticultural production, the blueberry (*Vaccinium corymbosum* L.) is the main thin-skinned fruit crop cultivated in the Buenos Aires province, followed to a lesser extent by the blackberry (*Rubus fruticosus* L.), raspberries (*Rubus idaeus* L.) and cherries (*Prunus avium* L.) (Censo Nacional Agropecuario 2018). In addition, in this region there are other susceptible species like plums (*Prunus salicina* L.) and mulberries (*Morus* sp. L.). The latest one is frequently implanted for shade or as an ornamental tree.

There are physical and chemical characteristics of fruits that are related to the performance of SWD offspring, since they affect their survival and developmental time (Silva-Soares et al. 2017; Young et al.

2017; Alhmedi et al. 2019). In addition, several studies have shown that the nutrition of larvae affects body measures of the drosophilid adults, including the size and shape of the wings (Bitner Mathé and Klazcko 1999; Shingleton et al. 2009; Fanara and Werenkraut 2017; Pajač Živković et al. 2018; Cabrera 2019; Little et al. 2020; Jardeleza et al. 2022). The capacity to change body measures in function of environmental and nutritional conditions is known as phenotypic plasticity, and is an important trait in invasive species. It provides rapid adjustments to the new environment, especially considering that after introduction, genetic variation is reduced due to bottlenecks caused by the small initial size of the colonizing population (West Eberhard 1989; Geng et al. 2007; Geng et al. 2016). Therefore, it is expected that *D. suzukii* fed with different diets express this plasticity (Lee et al. 2011; Burrack et al. 2013; Jaramillo et al. 2015; Little et al. 2017; Cabrera 2019; Little et al. 2020).

The aim of this study was to evaluate the host suitability of different commercial and non-cultivated fruit species by estimating different indices that take into account biometric and biological parameters.

Material and methods

Insect rearing and assay conditions

The bioassays and SWD rearing were carried out in the Laboratory of Agricultural Zoology of the National University of Luján, using a GC-300 brood chamber (Lab. Companion ®) under controlled conditions (23 ± 2°C, 60 ± 10% RH, Photoperiod 16L:8D). SWD larvae were fed using fresh and without insecticide raspberries (*Rubus idaeus*) and/or artificial diet as food (García Martínez et al. 2014; Betti 2016; Fanara pers. comm.).

The fruits used for assays were healthy blueberries cultivar Star and cherries cultivar Celeste, which were harvested from an agroecological fruit orchard located in the locality of Lobos; plums cultivar Pizzurno and mulberries, both harvested from trees located in the experimental field of the National University of Luján. Both sites are located in the Northeast of Buenos Aires province. Two stages of maturity, ripening (in the veraison phase) and ripe (optimum harvest maturity), differentiated by the soluble solids content, were evaluated. The juice obtained by crushing a random sample of 3 fruits per species was used to estimate the soluble solids content in degree Brix (°Brix) with a refractometer (Luwig ®) (Lee et al. 2011) (Table 1). To prevent natural fruit infestation by SWD or other insects, some branches with fruits were placed inside organza bags before veraison. Those branches were collected the day before at the beginning of each bioassay, and the fruits collected were checked under the microscope for any natural infestation or damages, and kept in a refrigerator (4°C) until required for bioassays.

Table 1
Concentration of soluble solids measured in degrees Brix for different fruit species in two stages of maturity

Fruits	Stage of maturity	Brix
Blueberry	Ripening	9
	Ripe	11
Cherry	Ripening	13
	Ripe	15
Mulberry	Ripening	7
	Ripe	9
Plum	Ripening	9
	Ripe	11

Performance assay

To obtain cohorts for bioassays, fruits of each species and stage of maturity were exposed to 10 SWD couples in entomological cages rearing (BugDorm-1®) for 24 h. After removing the adults, the number of eggs per fruit were counted under stereoscopic microscope by checking the two respiratory filaments (Beers et al. 2011; Asplen et al. 2015), and then, fruits were individually placed in ventilated 300 ml plastic containers. Pupal formation and adult emergence were daily recorded. The period from oviposition to pupal formation was recorded as egg-larval period, while the period from pupation to adult emergence was considered pupal period. The sum of both periods was considered the developmental time. Twelve replicates were performed for each fruit species and stage of maturity.

Biometric measures

All adults were sexed and kept in a freezer at -18°C until they were measured. The following traits were measured in each specimen (Norry et al. 1995; Loeschcke et al. 1999; Pacheco Fuentes 2013; Cabrera 2019; Lavagnino et al. 2020):

Wing length (WL): linear distance of the longitudinal vein 4 (LV4) from the anterior cross-vein (ACV), to the tip of the left wing (Fig. 1a);

Wing width (WW): distance between the intersection of longitudinal vein 2 (LV2) with the wing margin and between the intersection of longitudinal vein 5 (LV5) with the left wing margin (Fig. 1b);

Thorax length (TL): distance from the anterior margin of the thorax to the posterior tip of the scutellum (Fig. 1c).

Size measurements were determined on photographs taken with a magnifying glass (Stemi 508 model, Zeiss®) with an integrated digital camera and ImageJ software. The distance in pixels was transformed to millimeters from a known scale, through a millimeter sheet.

With these measurements, the indices Wing loading (WLo) and Wing aspect (WAs) were estimated for each sex separately (Azevedo et al. 1998; Loeschcke et al. 1999; Gibb et al. 2006):

$$WLo = \frac{TL}{WW}$$

$$WAs = \frac{WL}{WLo}$$

Finally, three specimens of each sex were randomly selected to estimate the Relative Performance Index (RPI) (Ruiz and Heed 1988; Krebs and Barker 1991, 1993; Fanara et al. 1999):

$$RPI = \frac{VxTL}{DT}$$

Where:

V is the vitality, estimated as mean of survival (%);

TL is the thorax length (mm);

DT is the developmental time (hours).

Thorax length was selected as a measure of the body size because it was the only biometric measure that showed significant differences between treatments in both sexes.

Statistical analysis

All analyzes were performed using the RStudio software (R Core Team 2022) and in all cases, a significance level of 5% ($P < 0.05$) was taken into account.

Egg-larval period, pupal period and developmental time were compared among fruit species (ripening or ripe) using a generalized linear model (GLM) with negative binomial distribution due to overdispersion of the data. Survival was analyzed using the nonparametric Kruskal-Wallis analysis because normality assumption was not met. Differences among treatments were determined by Tukey's test.

Biometric traits were compared between sexes using the Kruskal-Wallis test. Also, these body measurements and biometric indices, were compared among fruit/maturation treatments for each sex using an analysis of variance (ANOVA), previously verifying the assumptions of normality and homoscedasticity. Differences among treatments were determined by Fisher's test.

Results

Developmental time from oviposition to adult emergence was similar between sexes ($H = 0.33$; $df = 1$; $P = 0.57$) but varied significantly among treatments ($H = 15.18$; $df = 7$; $P < 0.01$). The specimens developed in both, ripening and ripe mulberries, completed their cycle in the shortest time, while the cycle was significantly longer in those larvae that were fed with plum, whose cycles exceeded 15 days in both stages of maturation. These differences were due to the egg-larval period ($H = 300.93$; $df = 7$; $P < 0.01$), since the pupal period did not show significant difference among treatments ($H = 1.88$; $df = 7$; $P = 0.60$) (Table 2).

Table 2
Developmental time (days) and Survival (%) of *Drosophila suzukii* (mean ± SE) reared on fruits with different maturation stages

Treatment	Egg-larval period	Egg-larval survival	Pupal period	Pupal survival	Developmental time	Egg to Adult survival
Ripening blueberry	9.25 ± 0.704 c	47.06 ± 10.910 b	5.19 ± 0.524 a	90.00 ± 6.667 a	14.7 ± 1.454 c	41.18 ± 9.810 c
Ripe blueberry	7.94 ± 1.075 bc	57.14 ± 6.747 b	5.57 ± 0.899 a	100.00 ± 0.000 a	13.1 ± 0.903 bc	57.14 ± 6.745 bc
Ripening cherry	7.45 ± 0.582 b	60.92 ± 7.803 ab	5.33 ± 0.495 a	88.40 ± 3.478 a	12.8 ± 0.778 b	51.72 ± 6.589 bc
Ripe cherry	7.50 ± 0.645 b	81.48 ± 4.979 a	5.07 ± 0.578 a	96.15 ± 3.845 a	12.5 ± 0.909 b	77.78 ± 5.767 a
Ripening mulberry	6.26 ± 0.423 a	86.96 ± 5.933 a	4.89 ± 0.373 a	90.47 ± 5.019 a	11.1 ± 0.556 a	78.26 ± 6.764 a
Ripe mulberry	6.00 ± 0.577 a	85.37 ± 2.356 a	4.61 ± 0.509 a	100.00 ± 0.000 a	10.6 ± 0.767 a	85.37 ± 2.356 a
Ripening plum	9.58 ± 0.894 c	41.67 ± 7.412 b	5.50 ± 0.678 a	100.00 ± 0.000 a	15.1 ± 1.120 c	41.67 ± 7.409 c
Ripe plum	10.56 ± 1.083 c	66.67 ± 9.478 ab	5.00 ± 0.754 a	100.00 ± 0.000 a	15.6 ± 1.321 c	66.67 ± 9.484 ab
Different letters in each column indicate statistical significance (N = 12) (Tukey's test, $P < 0.05$)						

Survival from egg to pupa was affected by treatments ($H = 33.21$; $df = 7$; $P < 0.01$), but survival of pupae did not differ significantly ($H = 8.84$; $df = 7$; $P = 0.26$), and it was higher than 88% in all treatments (Table 2). For each fruit species, SWD survival from egg to adult was lower when it was developed in the immature stage than in the ripe stage, although there were only significant differences between stages of maturity in cherries and plums. The maximum survival from egg to adult was observed in the specimens raised in mulberries (in both stages of maturity) and in ripe cherries and plums ($H = 38.34$; $df = 7$; $P < 0.01$) (Table 2).

All body measurements were higher in females than in males (WW $H = 63.38$; $df = 1$; $P < 0.01$; WL $H = 65.71$; $df = 1$; $P < 0.01$; TL $H = 54.40$; $df = 1$; $P < 0,01$), whereas the indices WLo and WAs did not show differences between sexes (WLo $H = 0.02$; $df = 1$, $P = 0.88$; WAs $H = 0.29$; $df = 1$; $P = 0.59$). Only the TL was affected by treatments in both sexes (Females: $F = 5.06$, $df = 7$, $P < 0.01$; Males: $F = 2.47$, $df = 7$, $P = 0.03$), while the WW was similar among treatments (Females: $F = 1.86$, $df = 7$, $P = 0.08$; Males: $F = 1.56$, $df = 7$, $P = 0.18$) and WL of females varied significantly according to the diet (Females: $F = 2.61$, $df = 7$, $P < 0.01$; Males: $F = 1.13$, $df = 7$, $P = 0.30$) (Table 3). For males, the highest TL was observed when they were reared on ripening and ripe mulberries and on ripe cherries and ripe plums, while the largest females were obtained from mulberries and blueberries (Table 3). However, TL was similar in adults of the same sex and reared on the same fruit, regardless of the stages of maturity (Table 3).

Table 3
Biometric traits (mean ± SE) of *Drosophila suzukii* adults reared on different fruits with two stages of maturity

Treatment	WW (mm)[a]		WL (mm)[b]		TL (mm)[c]		WLo[d]		WAs[e]	
	M	F	M	F	M	F	M	F	M	F
Ripening blueberry	1.03 ± 0.042 a	1.34 ± 0.072 a	1.53 ± 0.084 a	2.05 ± 0.088 ab	1.07 ± 0.055 c	1.51 ± 0.076 ab	0.70 ± 0.033 a	0.74 ± 0.039 a	1.49 ± 0.086 a	1.54 ± 0.072 a
Ripe blueberry	1.02 ± 0.042 a	1.33 ± 0.036 a	1.49 ± 0.084 a	2.05 ± 0.044 a	1.11 ± 0.055 bc	1.48 ± 0.038 ab	0.75 ± 0.033 a	0.73 ± 0.199 a	1.45 ± 0.086 a	1.56 ± 0.036 a
Ripening cherry	1.02 ± 0.032 a	1.28 ± 0.042 a	1.54 ± 0.065 a	1.88 ± 0.051 bc	1.13 ± 0.043 bc	1.33 ± 0.044 c	0.73 ± 0.026 a	0.71 ± 0.023 a	1.51 ± 0.067 a	1.48 ± 0.042 a
Ripe cherry	1.12 ± 0.027 a	1.27 ± 0.032 a	1.65 ± 0.055 a	1.94 ± 0.044 abc	1.23 ± 0.036 ab	1.35 ± 0.038 bc	0.75 ± 0.022 a	0.70 ± 0.020 a	1.48 ± 0.056 a	1.54 ± 0.036 a
Ripening mulberry	1.07 ± 0.023 a	1.21 ± 0.051 a	1.65 ± 0.046 a	1.92 ± 0.062 abc	1.24 ± 0.030 a	1.43 ± 0.054 abc	0.75 ± 0.018 a	0.74 ± 0.028 a	1.55 ± 0.047 a	1.59 ± 0.051 a
Ripe mulberry	1.05 ± 0.019 a	1.32 ± 0.032 a	1.68 ± 0.039 a	2.00 ± 0.040 ab	1.21 ± 0.025 ab	1.55 ± 0.034 a	0.73 ± 0.015 a	0.78 ± 0.018 a	1.62 ± 0.040 a	1.52 ± 0.032 a
Ripening plum	1.03 ± 0.051 a	1.14 ± 0.063 a	1.52 ± 0.102 a	1.80 ± 0.076 c	1.07 ± 0.068 c	1.27 ± 0.066 c	0.70 ± 0.041 a	0.70 ± 0.034 a	1.47 ± 0.105 a	1.60 ± 0.062 a
Ripe plum	1.03 ± 0.030 a	1.18 ± 0.056 a	1.56 ± 0.059 a	1.82 ± 0.068 c	1.20 ± 0.039 abc	1.32 ± 0.059 c	0.78 ± 0.024 a	0.73 ± 0.031 a	1.52 ± 0.061 a	1.54 ± 0.056 a

[a]Wing width; [b]Wing length; [c]Thorax length; [d]Wing loading; [e]Wing aspect

Different letters in each column indicate statistical significance between treatments for males (M) and females (F) (Fisher's test, $P < 0.05$)

The correlation analyzes between the biometric parameters were significant ($P < 0.01$) with an r-Pearson coefficient higher than 0.69 (Fig. 2). These results, added to the significant differences observed for TL in both sexes among treatments, prompted the selection of this parameter for estimating the RPI.

The RPI varied according to the fruit and its stages of maturity (F = 29.15; df = 7; P < 0.01). The specimens developed in ripe mulberries presented a maximum index, significantly higher than the rest of the treatments. In addition, for each fruit, the index was higher in the ripe stage than in the ripening one (Fig. 3).

Discussion

Drosophila suzukii has greatly expanded its worldwide distribution due to its high polyphagia, among other reasons (Kimura 2004; Cini et al. 2012; Calabria et al. 2012). However, the observations of this work suggest that the quality of the food resources present in an area may differ between fruit species and their stage of maturity, since both could affect the development, survival and adult biometric traits of the fly population, which is in agreement with what was observed by other authors (Poyet et al. 2014; Jaramillo et al. 2015; Lee et al. 2015; Arnó et al. 2016; Bernardi et al 2017).

The developmental time was affected by the fruit species, but it did not vary between stages of maturity for the same fruit (Table 2). It varied between 10.6 and 15.6 days, which indicates that the duration of cycle can be 50% longer depending on the food of the larvae. The shortest developmental time was found in mulberries, regardless of their stage of maturity, whereas the highest values were observed in plums and blueberries. Some authors have found developmental times of SWD reared in blueberries and cherries slightly lower than those observed in this work (Jaramillo et al. 2015; Alhmedi et al. 2019; Cai et al. 2019). This difference could be due to the fact that these studies were carried out at a temperature between 23 and 25 ºC, slightly higher than the conditions of this study (21–25°C). No studies about the developmental time of *D. suzukii* in plums and mulberries were found, so these results would constitute the first data on the biology of SWD in these hosts. Several works have concluded that the larvae reared on an optimal diet have shorter developmental time (Edgar 2006; Markow and O'Grady 2008; Jaramillo et al. 2015). In this sense, mulberries, even in a stage prior to maturation, were the best food for SWD rearing. Added to this, the mulberries in both stages of maturity were the treatments where the maximum survival was recorded, higher than 78%. Similarly, survival in ripe cherries was almost 78%, an intermediate value to that observed by other authors (40 to 90%) (Lee et al. 2011; Alhmedi et al. 2019; Cai et al. 2019), while in ripe blueberries, survival was 57%, higher than it recorded by other works (between 30 and 55%) (Lee et al. 2011; Burrack et al. 2013; Cai et al. 2019). For ripe plum, survival was 66.7%, almost three times higher than that observed by Cabrera (2019), who used an artificial diet composed mainly of plum macerates. In this case, the other ingredients of the diet could be affecting its nutritional quality, so the data is not directly comparable.

In each fruit species, higher survival was observed in ripe stage than in ripening one, although only in cherries and plums the difference was statistically different (Table 2). In agreement, other authors compared the susceptibility of various fruits to SWD and found in most of them that when Brix levels increased, more SWD developed on (Lee et al. 2011; Little et al. 2017; Kamiyama and Guédot 2019). In the same way, Arnó et al. (2016) observed in two strawberry varieties higher percentages of pupae in red than in ripening or unripe fruits, possibly due to higher sugar content. In this sense, Little et al. (2017)

suggest that SWD larvae can develop in a wide range of sweetness and acidity, as long as their sugar and protein needs are met, since it is known that the proper balance between these nutrients is essential for the development of SWD (Young et al. 2017).

All body measurements were larger in females than in males, which is in agreement with other authors (Jaramillo et al. 2015; Cabrera 2019). On the other hand, the WW did not differ among treatments, while only females showed differences in the WL, which does not agree with Jaramillo et al. (2015), who found no differences in wing length according to the diet of the larvae of SWD. In relation to the TL, both sexes showed significant differences according to the diet. These differences were not observed for the same fruit in different stages of maturity, and when the larvae were fed with ripe or ripening mulberries, the adults of both sexes were in the group with the highest TL (Table 3). The size of adults in many cases is correlated with performance components such as fecundity, longevity, mating behavior and resistance to stress (Kingsolver and Huey 2008) and it has been found that larger adults can reach higher speeds and accelerations during flight, which could influence the flight and dispersal capacity (Fraimout et al. 2018; Pajač Živković et al. 2018).

Both indices, the WLo and the WAs, did not present significant differences among treatments. The wing loading is related to the flight capacity, the flight is more energetically efficient when the WLo is lower, since the wings are larger in relation to the body (Angelo and Slansky 1984; Berwaerts et al. 2002; Gibb et al. 2006; Fanara and Werenkraut 2017). On the other hand, the wing aspect is related to the flight pattern, when this value is higher it indicates that they have a faster flapping flight, while if it is lower it indicates a gliding flight (Norberg 1990; Wootton 1992; Fanara and Werenkraut 2017). Therefore, these flight characteristics would seem to be unaffected by the diets offered in this study. However, these results differ from those reported for other drosophilid species exposed to different diets (Fanara and Werenkraut 2017). While these indices only take into account biometric traits, the RPI can be considered as a measure of fitness, because relates these characteristics to biological ones, since it increases with viability and body size and decreases with developmental time (Klingenberg and Spence 1997. The results of this work show, on the one hand, that in all the fruits, this index was significantly higher when they were ripe, and on the other, that the value obtained for the larvae fed with ripe mulberry was significantly higher than that of the rest of the treatments. In the same way, Fanara and Werenkraut (2017) determined that for cactophilous drosophilid species the RPI varies according to the diet supplied.

The higher RPI found in ripe mulberry treatment is due to the fact that specimens developed in this fruit showed a large size associated with the shortest developmental time and a high survival rate. In the same way, Cabrera (2019) used this index to compare the fitness of SWD reared with different diets and densities, and found the highest RPI with the diet where obtained greater viability and shorter developmental time. In addition, other authors also found that when the developmental time is shorter, the size of the SWD adults is larger (Silva Soares et al. 2017; Bezerra da Silva et al. 2019).

The mulberry tree is a Chinese species used in cut and carry systems for more than 5000 years and to feed the silkworm (*Bombyx mori* L.) (Martín et al. 2007). In Argentina, it was introduced for ornamental

purposes, becoming an invasive plant since it grows spontaneously (Tolaba and Novara 1996; Duarte Baschini and Dellafiore 2021). An alternative host can be considered beneficial if it strongly attracts the pest instead of the crops and, in addition, greater control efforts could be performed it, with the aim of reducing the population and preventing future attacks (Lee et al. 2015). However, in the region of this study, the mulberry bloom in late winter and its fruits are ripe in early November, shortly before many of the commercially important fruits such as raspberries, plums and some varieties of blueberries and cherries. This makes it one of the first food and oviposition resources in the region for SWD, mainly for the females of the wintering generation. In addition, the results indicate that the adults developed in mulberry would have morphological characteristics that would facilitate the dispersal and search for both mates and new food and oviposition resources, which would make this tree an alternative host of excellent quality,that should be avoided in the vicinity of susceptible fruit crops.

Declarations

Acknowledgments

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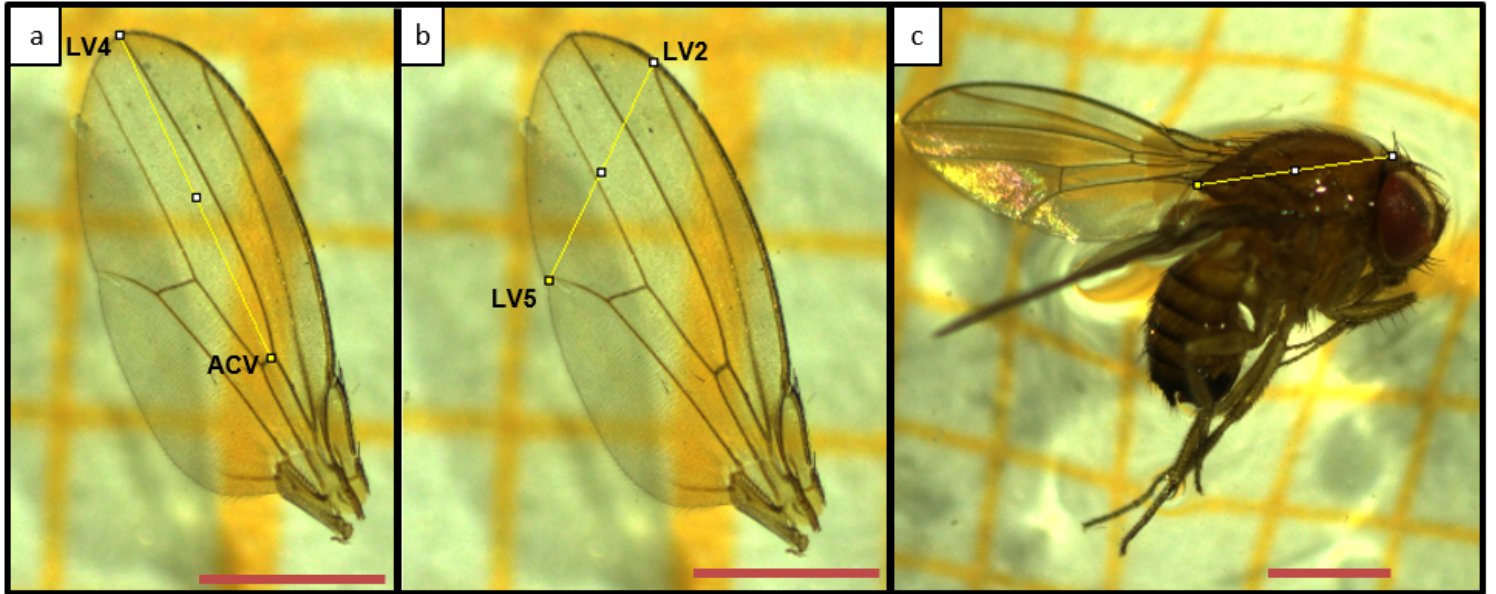
Figures

Figure 1

Biometric measures of *Drosophila suzukii*. a- Wing length; b- Wing width; c- Thorax length. Longitudinal vein 2 (LV2), Longitudinal vein 4 (LV4), Longitudinal vein 5 (LV5), anterior cross-vein (ACV) (Scale bar: 1mm)
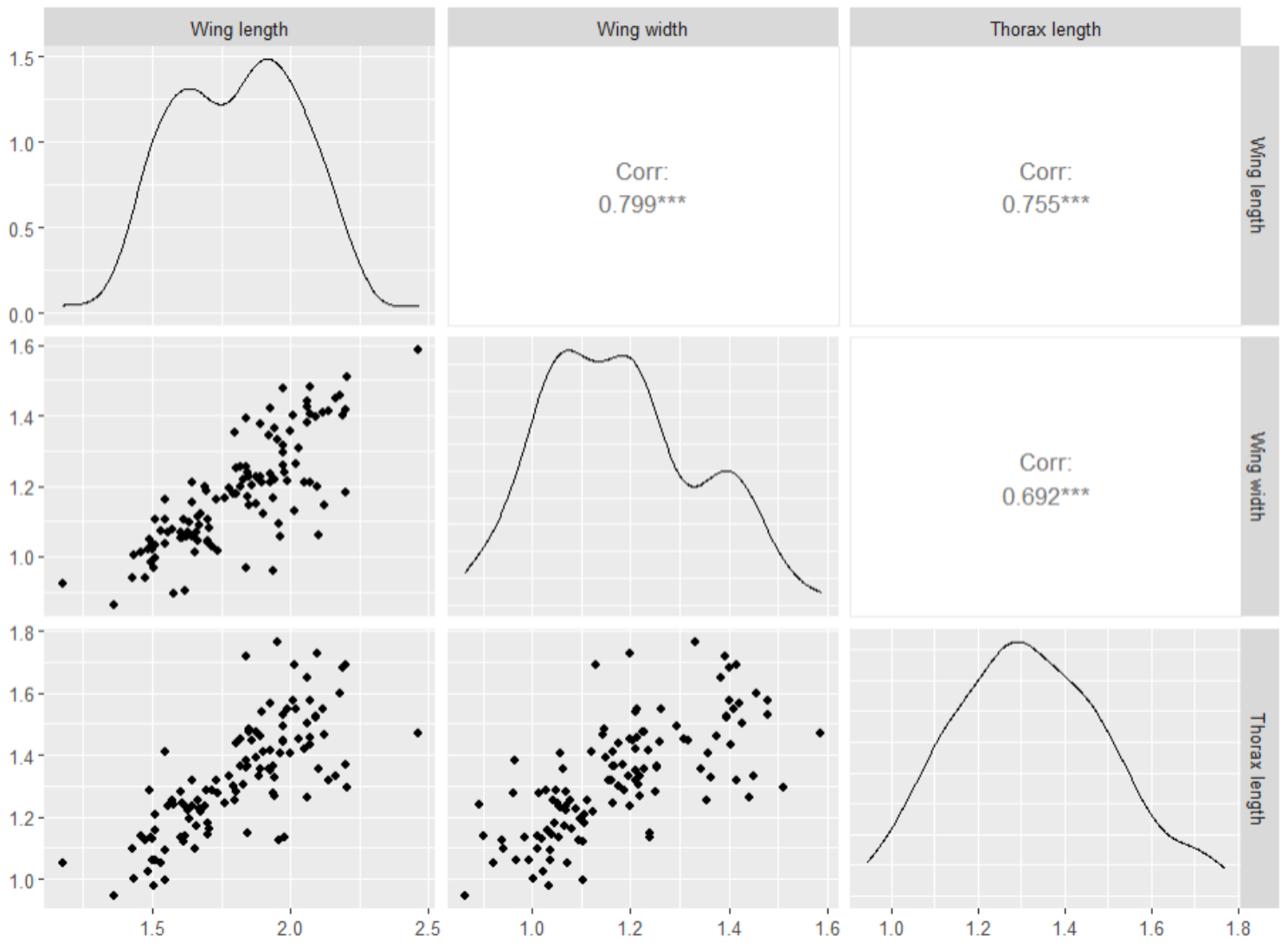
Figure 2

Pearson correlation analyses performed between biometric traits (*** significant differences, *P* < 0.05)
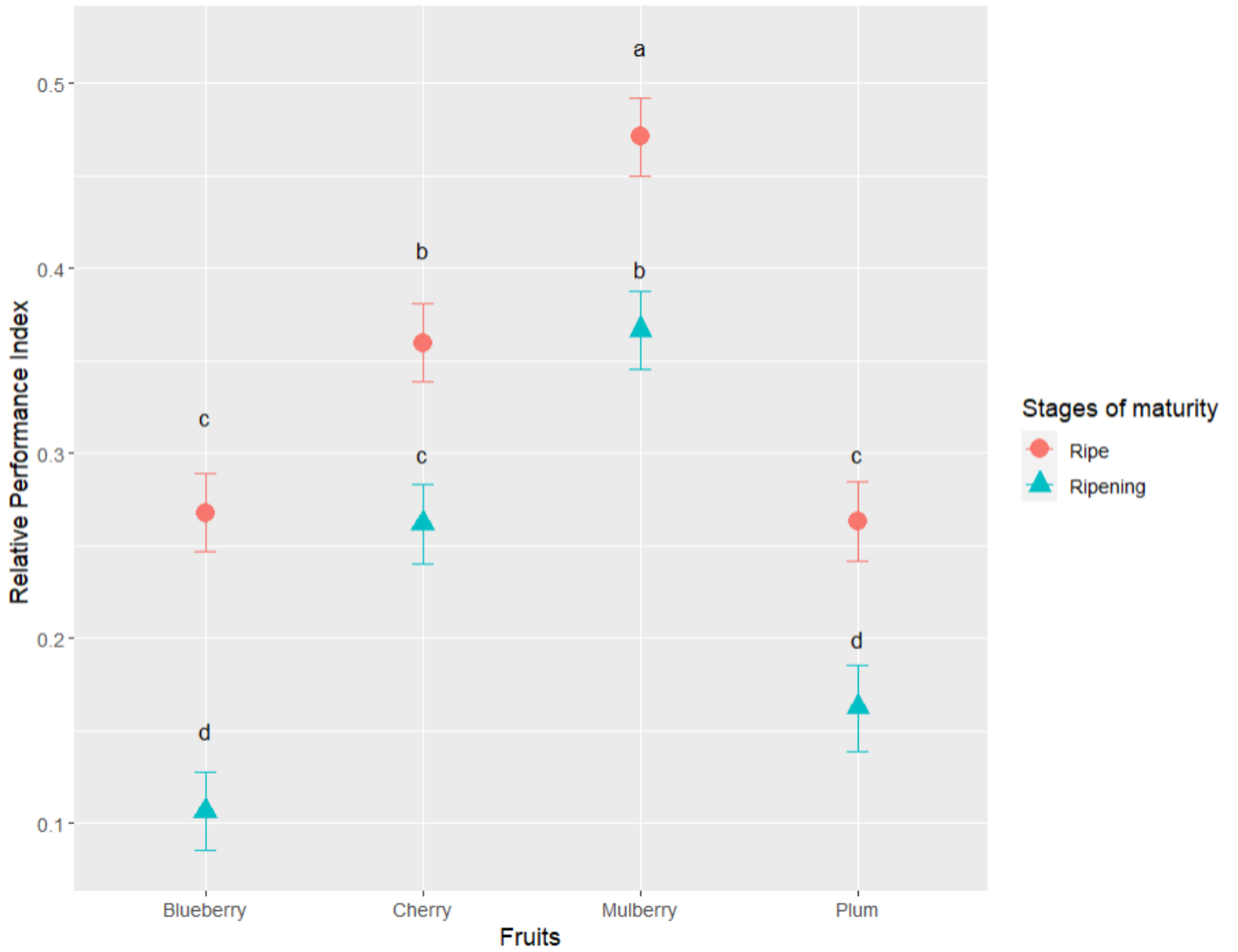
Figure 3

Relative Performance Index (mean ± SE) of *Drosophila suzukii* reared in different fruits and stages of maturity. Different letters indicate significant differences between treatments (Fisher's test, $P < 0.05$)