

The mating rate of *Drosophila suzukii* reduction due to reproductive interference from *Drosophila melanogaster*

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Research article

Keywords: *Drosophila suzukii*, *Drosophila melanogaster*, interspecific competition, reproductive interference

Posted Date: December 4th, 2020

DOI: <https://doi.org/10.21203/rs.3.rs-39315/v2>

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Abstract

Background *Drosophila suzukii* is widely distributed. Research has revealed that the presence of *Drosophila melanogaster* can reduce the emergence and egg laying of *D. suzukii*. However, the reasons for these phenomena have not yet been reported. To investigate this issue, we sought to answer three questions: Can the presence of *D. melanogaster* reduce the longevity of *D. suzukii*? Does *D. melanogaster* dominate in larval interspecific competition with *D. suzukii*? Does reproductive interference occur between these species; i.e., do individuals of one species (e.g., *D. suzukii*) engage in reproductive activities with individuals of the other (e.g., *D. melanogaster*) such that the fitness of one or both species is reduced?

Results The results showed that the adult offspring number of *Drosophila suzukii* was significantly reduced when this species was reared with *Drosophila melanogaster*. The larval interspecific competition had no significant effects on *Drosophila suzukii* longevity or population size. Surprisingly, *Drosophila melanogaster* imposed reproductive interference on males of *Drosophila suzukii*, which led to a significant decline in the rate of successful mating of the latter species.

Conclusions The presence of *Drosophila melanogaster* causes the population size of *Drosophila suzukii* to decrease through reproductive interference, and the rate of successful mating in *Drosophila suzukii* is significantly reduced in the presence of *Drosophila melanogaster*.

Background

Drosophila suzukii (Diptera: Drosophilidae), known as the spotted-wing drosophila (SWD), is originally from Asia. However, it has become a severe invasive pest in South America and Europe since 2008 [1, 2], causing large economic losses in the fruit production industry [3]. Usually, *Drosophila suzukii* females lay eggs within ripe or ripening fruit via a sclerotized and serrated ovipositor that penetrates the fruit skin, causing physical damage to the fruit [4, 5]. According to the literature, *D. suzukii* can lay up to 600 eggs (approximately 400 eggs on average) during their life span, and the minimum development time from egg at oviposition to adult under optimal temperature is 8 days [6]. Regarding environmental adaptability, *D. suzukii* has a wide range of tolerance to climatic conditions, with successful production of offspring possible at temperatures from 10 to 32 °C [7]. The optimal range for larval development is usually between 20 to 25 °C [8]. In addition, this pest has a wide host range, with more than 150 host species reported to date [9, 10]. Since these factors and the fact that different hosts have different ripening times. Therefore, it is almost impossible to eliminate this pest in a short period of time. Wild hosts as well as ornamental plants can serve as refuges, allowing *D. suzukii* to persist through the winter, even under low temperatures [11].

The use of ovipositors can cause physical damage to intact fruit, and the larvae can accelerate the process of decay. Damaged, decaying fruit is an ideal food source for other phytophagous insects, so competition of *D. suzukii* with other *Drosophila* species, such as *Drosophila melanogaster*, is almost inevitable. Interspecific competition widely exists among insects [12, 13] and includes intraspecific

competition and interspecific competition. The outcome of competition depends on the relative strengths of interspecific competition and intraspecific competition. Both types of competition represent struggles for survival, growth and reproduction for every individual because of limited environmental resources [14, 15]. As a result of interspecific competition, the population of one species tends to decrease while that of the other tends to increase, with strong effects on species coexistence, habitat partitioning, food resource partitioning, and species replacement [16]. The importance of interspecific competition to community structure in plant-eating insects has been discussed by many ecologists [17, 18]. Denno analysed 193 pairs of competitor species and concluded that the interspecific competition affects the abundance and distribution of plant-eating insects [19].

According to niche theory, closely related species overlap in resource needs, so competition can be very strong when two species first meet. The results of competitive interaction are either competitive exclusion of one of the species or niche reduction until coexistence becomes possible [20]. A previous study revealed that in the lab environment, the presence of *D. melanogaster* can significantly reduce emergence and egg laying in *D. sukuzii* through interspecific competition [21]. One possible explanation for these effects is the production of a pheromone called *cis*-vacacenyl acetate (*cVA*) by males of *D. melanogaster* that is used in courting, aggression, and aggregation signalling and has a disruptive effect on *D. sukuzii* [21]. The number of successful matings by males of *D. sukuzii* is reduced when they encounter this pheromone. Correspondingly, in previous work [22], we found that when adults of *D. melanogaster* and *D. sukuzii* were reared together for three generations, the whole population of *D. sukuzii* eventually died. Thus, in the present study, we attempted to explore alternative potential factors contributing to this phenomenon.

The competitive interactions of two closely related species over resources entail time and energy costs and risk of injury. The allocation of time and energy by these two fly species to interspecific competition results in decreased egg laying, and individuals might suffer physical damage, affecting longevity. Decreases in both egg laying and adult longevity could be important factors contributing to the extinction of *D. sukuzii* populations. Recent studies show that both *D. sukuzii* and *D. melanogaster* have strong appetites and overlapping feeding niches [20][23]. Therefore, in our experiments, we investigated the effects of interspecific competition on the longevity and fecundity of the two flies. We studied both adult competition and larval competition between *D. melanogaster* and *D. sukuzii*. Reproductive interference is a kind of interspecific sexual interaction wherein the reproductive success of females of one species could be reduced due to interference by another species [24]. The frequencies of conspecific courting and mating, female fecundity, and female fertility can be influenced by reproductive interference, and time, energy, nutrients, or gametes can be wasted in heterospecific sexual interactions, causing fitness losses for the individuals involved [25]. Reproductive interference might be a factor resulting in the population reduction of *D. sukuzii* and is a possibility examined in this study.

Results

Offspring number and longevity comparison of the two fly species under the two rearing conditions

The offspring number of *D. suzukii* was significantly decreased from that under independent rearing when this species was reared with *D. melanogaster* (Fig. 1a). Under the independent rearing condition, the offspring number of *D. suzukii* (117.37 ± 24.28) was significantly higher than that observed in the mixed rearing condition (40.47 ± 8.23 , $t_{17} = 3.13$, $P = 0.006$). The same pattern was found in *D. melanogaster*. offspring number in the independent condition (494.50 ± 36.92) was much higher than that in the mixed rearing condition (269.53 ± 47.05 , $t_{18} = 3.76$, $P < 0.01$).

Regarding longevity, the two fly species were affected differently under the two conditions (Fig. 1b). The longevity of *D. suzukii* in the independent condition (54 ± 2.70 days) did not significantly differ from that in the mixed condition (61.6 ± 3.04 days, $t_{36} = -1.85$, $P = 0.07$). However, in *D. melanogaster*, the longevity in the independent rearing condition (70.1 ± 1.05 days) was significantly higher than that in the mixed rearing condition (79.25 ± 3.05 days, $t_{38} = -2.838$, $P = 0.007$).

Larval interspecific competition

We calculated the numbers of pupation events and eclosion events of each of the two species in a larval interspecific competition experiment (Table 1). The results showed that for *D. suzukii*, eclosion number did not significantly differ between the independent and mixed rearing conditions ($c^2 = 3.52$, $df = 1$, $P = 0.061$); similarly, *D. suzukii* pupation number did not differ between the conditions ($c^2 = 3.14$, $df = 1$, $P = 0.077$). In *D. melanogaster*, neither eclosion number ($c^2 = 0.515$, $df = 1$, $P = 0.473$) nor pupation number differed substantially between the two rearing conditions ($c^2 = 0.002$, $df = 1$, $P = 0.905$).

Table 1 The numbers of pupation and eclosion events under the independent and mixed rearing conditions

Species and rearing condition	No. of successful pupation events	No. of failed pupation events	No. of successful eclosion events	No. of failed eclosion events
<i>D. suzukii</i> (independent)	140	60	128	72
<i>D. suzukii</i> (mixed)	59	41	52	48
<i>D. melanogaster</i> (independent)	134	66	122	78
<i>D. melanogaster</i> (mixed)	68	32	66	34

Reproductive interference reduced the rate of successful mating in *D. suzukii*

We found that the presence of *D. melanogaster* affected the courting and mating behaviour of *D. suzukii* (see Additional file 1 e-h). In addition, the rate of successful mating in *D. suzukii* was affected by the presence of *D. melanogaster* (Table 2), being significantly decreased in the mixed rearing condition compared with the independent rearing condition ($c^2=3.84$, $df=1$, $P=0.05$). However, in *D. melanogaster*, the successful mating rate did not significantly differ between the two rearing conditions ($c^2=0.41$, $df=1$, $P=0.522$). Furthermore, our results showed that the courting time of *D. suzukii* did not significantly differ between the independent (728.72 ± 200.07 s) and mixed (1392.25 ± 393.22 s, $t_{13}=1.64$, $P=0.125$) conditions. Similarly, in *D. suzukii*, the number of courting behaviours ($U=16$, $P=0.472$) and mating time did not significantly differ between the independent (1738.1 ± 159.92 s) and mixed (1412.5 ± 182.75 s, $t_{12}=-1.16$, $P=0.268$) conditions.

In *D. melanogaster*, courting time did not significantly differ between the independent (442.54 ± 96.26 s) and mixed (202.3 ± 51.81 s, $t_{21}=2.02$, $P=0.057$) conditions. However, in this species, the number of courting behaviours before mating was significantly lower in the mixed rearing condition than in the independent rearing condition ($U=102.5$, $P=0.022$), whereas mating time was not significantly different between the independent (987.69 ± 60.93 s) and mixed (961.9 ± 64.92 s, $t_{12}=0.287$, $P=0.777$) conditions.

Regarding misdirected courting, in the mixed rearing condition, *D. suzukii* exhibited significantly greater numbers of misdirected courting behaviours than *D. melanogaster* ($U=40$, $P=0.0057$). Males of *D. suzukii* exhibited 13 heterospecific mating attempts; i.e., attempted matings with female *D. melanogaster*. Surprisingly, males of *D. melanogaster* did not attempt heterospecific mating. In addition, heterospecific mating occurred twice, between *D. suzukii* males and *D. melanogaster* females.

Table 2 The effects of reproductive interference on courting and mating behaviour

Species and rearing condition	Courting time (s)	Mating time (s)	Successful mating rate
<i>D. suzukii</i> (independent)	728.72 ± 200.07	1738.1 ± 159.92	55% (11/20)
<i>D. suzukii</i> (mixed)	1392.25 ± 393.22	1412.5 ± 182.75	20% (4/20)
<i>D. melanogaster</i> (independent)	442.54 ± 96.26	987.69 ± 60.93	65% (13/20)
<i>D. melanogaster</i> (mixed)	202.3 ± 51.81	961.9 ± 64.92	50% (10/20)

Discussion

Consistent with a previous study [21], our results showed that the number of offspring of *D. suzukii* was significantly reduced when this species was rearing in mixed groups with *D. melanogaster* (Fig. 1). Datta *et al.* (2008) suggested that the presence of *D. melanogaster* could change oviposition preference,

resulting in reduced egg laying by *D. suzukii*. Males of *D. melanogaster* produce a pheromone, *cis*-vacccenyl acetate (*cVA*) [26], which is natural repellent to *D. suzukii* females searching for oviposition sites. Our results suggested that in addition to affecting oviposition preference, reproductive interference by *D. melanogaster* likely contributed to the significant decrease in offspring number in *D. suzukii*.

Reproductive interference between invasive and native species has received much attention. Reproductive interference is a kind of interspecific sexual interaction wherein the female reproductive success of one species is reduced because of the interference by another species [24]. In our behaviour experiment, we found that the presence of females and males of *D. melanogaster* resulted in reproductive interference with males of *D. suzukii*, which selected *D. melanogaster* females as their mating targets in some cases (see Additional file 1 f). Usually, reproductive interference is categorized into seven types: signal jamming, heterospecific rivalry, misdirected courting, attempted heterospecific mating, erroneous female choice, heterospecific mating and hybridization [27]. Three types of reproductive interference, misdirected courting, attempted heterospecific mating and heterospecific mating, were observed in our study.

Among the tested adult males of *D. suzukii*, 95% (19 of 20 groups) showed misdirected courting behaviour. Usually, misdirected courting is performed or initiated by males, which are often indiscriminate in mate choice, as they invest less energy in reproduction [28]. In our study, we found that misdirected courting was initiated by males of *D. suzukii*. Such males may fail to recognize conspecific females and preferentially court heterospecific females or even males [29, 30]. Previous studies reported that heterospecific females with larger body size than conspecific females were attractive to males because large body size indicates high fecundity [31, 32]. This finding contrasts with our observations that *D. suzukii* males were attracted to *D. melanogaster* females, which are smaller than *D. suzukii* females. Therefore, we deduce that *D. suzukii* males fail to recognize conspecific females and that *D. melanogaster* females possess features that can attract *D. suzukii* males. *D. melanogaster* sex pheromones are cuticular hydrocarbons (CHC) that mediate chemical communication for both sex and species recognition [33]. These CHC may make *D. melanogaster* females attractive to *D. suzukii* males and prevent scent-mediated attraction to conspecific females.

Consistent with previous reports [34], in our observation experiments, all of the heterospecific mating attempts followed misdirected courting, and *D. melanogaster* males showed no heterospecific mating attempts. The behaviour of heterospecific mating has been investigated in many studies, such as Takafuji (1988), Fujimoto *et al* (1996), and Takafuji *et al* (1997) [35-37]. However, there is no study reported *D. suzukii* males underwent heterospecific mating with *D. melanogaster* females. Usually, reproductive interference can be regarded as a "mistake" resulting in incomplete species recognition. Thus, time, energy, nutrients, or gametes are wasted in heterospecific sexual interactions, causing fitness losses of the individuals involved [25]. The frequencies of conspecific courting and mating, female fecundity, and female fertility can be influenced by reproductive interference [25].

In this study, potential factors resulting in population decline in *D. suzukii* due to *D. melanogaster* were explored. However, inconsistent with our expectations, the lifespan of *D. suzukii* was not reduced when

this species was reared with *D. melanogaster*. Our results suggest that competition with *D. melanogaster* might not lead to physical damage to *D. suzukii* adults thus might not affect adult longevity. Therefore, the population decline of *D. suzukii* was unlikely to be caused by a reduction in lifespan in *D. suzukii* adults reared and competing with *D. melanogaster*. In addition, larval interspecific competition might not be a factor affecting *D. suzukii* population decline, as rearing condition had no significant effect on pupation rate or eclosion rate (Table 1).

Conclusions

In this study, we found that *D. suzukii* population size was significantly decreased when individuals of this species were reared with *D. melanogaster* vs. reared alone, which was consistent with previous research. Potential factors underlying this phenomenon, including longevity, larval interspecific and reproductive interference, were studied. The experimental results showed that longevity and larval interspecific competition had no significant effects on population size in *D. suzukii*. However, *D. melanogaster* imposed reproductive interference on *D. suzukii* males, significantly reducing the rate of selecting conspecific females as mating targets in these males, and apparently decreasing the rate of successful mating rate. This phenomenon warrants further research, including research into the features of *D. melanogaster* that cause *D. suzukii* males to not recognize conspecific females. We speculate that *Drosophila melanogaster* may release a substance, such as a sex hormone, that distracts *D. suzukii* males.

Material And Methods

Fly stocks

Adults of *Drosophila suzukii* were collected from a Hui Wang blueberry orchard in Nanling, Anhui Province, China, in 2012 (30.92°N, 118.34°E). *Drosophila melanogaster* individuals were collected from Anhui Normal University, Anhui Province, China, in 2010 (31.33°N, 118.37°E). Under laboratory conditions, adults of the two species were independently reared in nylon cube cages (35×35×35 cm) at 25±1 °C under a light: dark photoperiod of 14:10 and a relative humidity of 60 ± 5%. Both flies species were fed a solid food diet [38], which was changed out daily.

Longevity and fecundity

For this experiment, 20 male-female pairs of newly emerged (<24 h) individuals of each of the two fly species were selected. Ten pairs of each species were independently reared in food-containing tubes (one pair per tube), and the remaining pairs were reared in mixed-species groups (two pairs per tube). The longevity of each adult fly was recorded daily. To investigate egg laying, one pair of *D. suzukii* or *D. melanogaster* individuals was placed into a transparent tube pre-loaded with 20 ml solid food. Additionally, treatments with the two species reared together were conducted. The next day, the adult flies

in each tube were anaesthetized by CO₂ and transferred to another transparent tube with new solid food and maintained there until death. The number of adult offspring that emerged was counted daily from the first adult eclosion at three days to the death of the adult female. Ten replicates of each fly species and rearing type were established. All tubes containing flies and all replacement tubes were maintained in incubators under the same conditions of light:dark photoperiod (14:10), temperature (25±1 °C), and humidity (60±5%) and were checked daily.

Larval competition

We hypothesized that larval interspecific competition would lead to a change in *D. suzukii* population size. To determine the effect of larval interspecific competition on adult emergence, we reared the two fly species under two conditions. Because interspecific competition has a density-dependent effect on population dynamics, when the density of one species increases, the density of the other decreases [24]. Furthermore, the species with the higher initial density is likely to exclude the species with lower initial density [39, 40]. Therefore, in our experiment, we maintained the same density in the two rearing conditions to control for the influence of density on competitive ability (10 larvae per 10 g solid food in the independent condition; 10 larvae per species per 10 g solid food in the mixed condition).

Both fly species were fed on yeast water for 8 h, and then two cups containing solid food were used for egg collection. Twenty larvae of each species were placed in a cup containing 10 g solid food for independent rearing after egg incubation. For the mixed rearing condition, 10 larvae from each species were placed together in a cup containing solid food. All the cups were maintained in incubators with the following condition settings: light:dark photoperiod, 14:10 h; temperature, 25±1 °C; and humidity, 60±5%. The numbers of pupation events and adult eclosions were counted daily. Ten of twenty replicates for each species were established for determining eclosion counts, and the remainder were established for pupation counts.

Observations of courting behaviour of the two flies under independent and mixed conditions

To ensure that the flies used for behavioural observations were unmated, we placed pupae into EP tubes for emergence. All tubes were maintained in incubators with the following condition settings: light:dark photoperiod, 14:10 h; temperature, 25±1 °C; and humidity, 60±5%. Observation started 24 h after eclosion. For the independent condition, one pair of *D. suzukii* or *D. melanogaster* individuals was placed in a quartz cylinder (height: 0.5 cm, diameter: 3 cm) with a 0.5 mm quartz lid. An appropriate amount of solid food was placed in each cylinder before each observation period. For the mixed condition, one pair of each fly species was placed together a cylinder for observation. We recorded a 40-min video of courting and mating behaviour with a microscope (VHX-5000, Osaka Japan, Keyence Corporation). The frequency

of courting behaviour and total mating time were recorded. We conducted observations of 20 replicates of each of the independent and mixed conditions for the two fly species.

Data analysis

We performed a Kolmogorov-Smirnov normality test on all collected data. The longevity, offspring number, courting time, and mating time data fit normal distributions, so these data were analysed by Student test (*t*-test). The data that did not fit a normal distribution, such as the frequencies of correct courting, misdirected courting, and heterospecific mating attempts, were analysed by the Mann-Whitney U test. The successful mating rate, pupation rate, and emergence rate were analysed by the Chi-square test. All these tests were performed with R 3.6.1.

Availability of data and materials

The data that support the findings of this study are uploaded to the open repository Dryad(https://datadryad.org/stash/share/ovg5_qZtvaHuupqejQOi4kgviw3ky_vZ6vFJ8uwx-oU; https://datadryad.org/stash/share/NbDe_Pn5EkX9N93Q092MGLiPPDFy4-JZMW4DdgjSYBg).

Abbreviations

SWD: Spotted-wing drosophila

cVA: *cis*-vaccenyl acetate

Is: Independent rearing *D. suzukii*

Ms: Mixed rearing *D. suzukii*

Im: Independent rearing *D. melanogaster*

Mm: Mixed rearing *D. melanogaster*

CHC: cuticular hydrocarbons

Declarations

Acknowledgements

We gratefully thank Sheng Zhang and Yumei Tao of Anhui Normal University for their assistance. And we thank the anonymous reviewers for many useful comments.

Funding

This work was supported by the National Natural Science Foundation of China (31672351, 31172145), the Natural Science Foundation of Anhui Province (1408085MKL24), and the Fund from the Provincial Key Laboratory of Conservation and Utilization for Important Biological Resources in Anhui.

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Contributions

YC, MZ, WH, and JL conduct the experiments. YC contributed to data curation and statistical analysis, and first drafted the writing. PL and HH contributed to idea and design of the study, and comments and revisions; All authors contributed critically to the drafts. All authors read and approved the final manuscript.

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Ethics declarations

Ethics approval and consent to participate

The behavioral research in our study were in compliance with the law of the people's republic of China on the protection of wildlife and were approved by the Laboratory Animal Ethics Committee of Anhui Normal University.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Figures

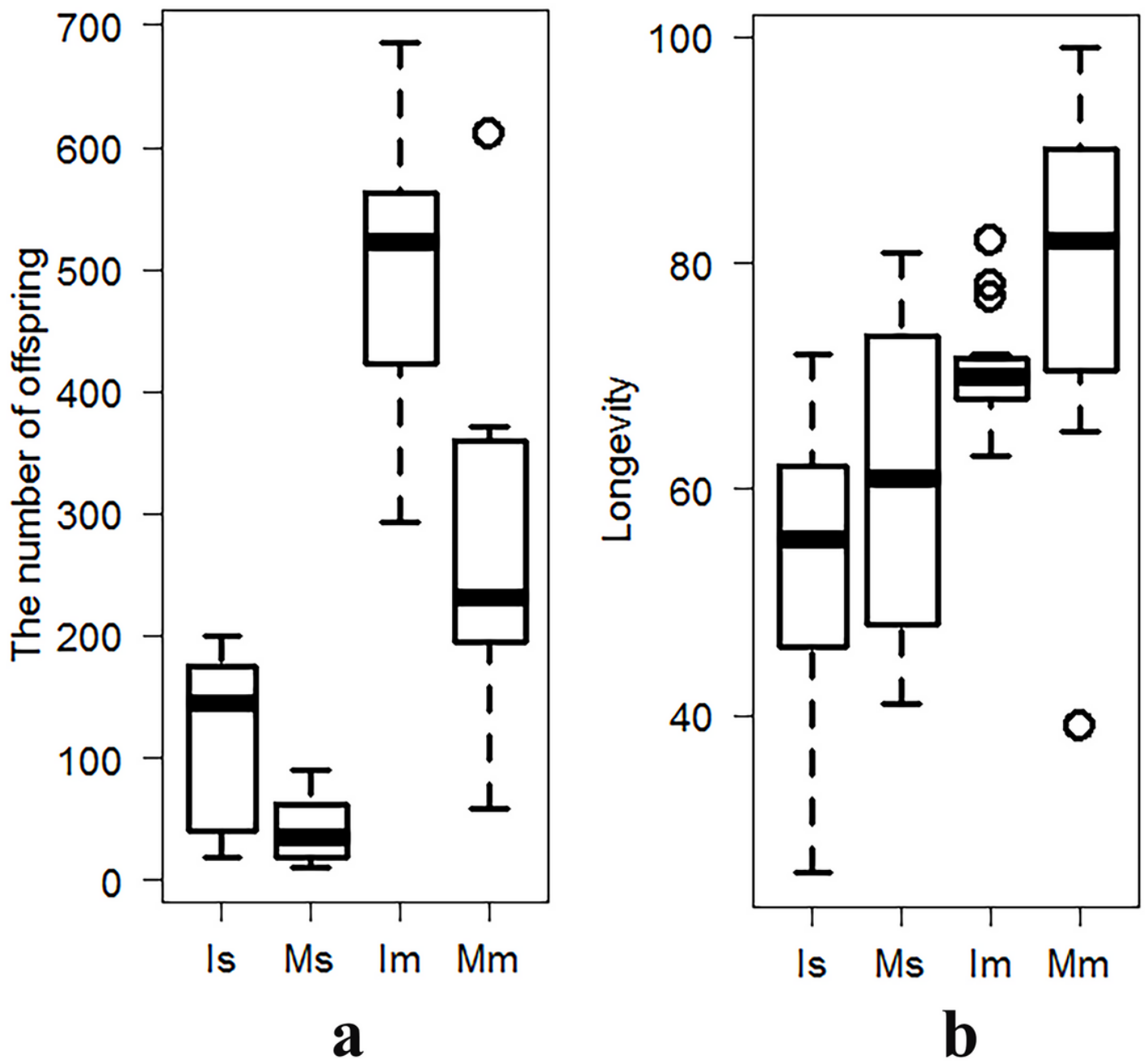


Figure 1

The offspring number (a) and longevity (b) of the two fly species under two rearing conditions. Is = independent rearing, *D. sukuzii*; Ms = mixed rearing, *D. sukuzii*; Im = independent rearing, *D. melanogaster*; and Mm = mixed rearing, *D. melanogaster*.

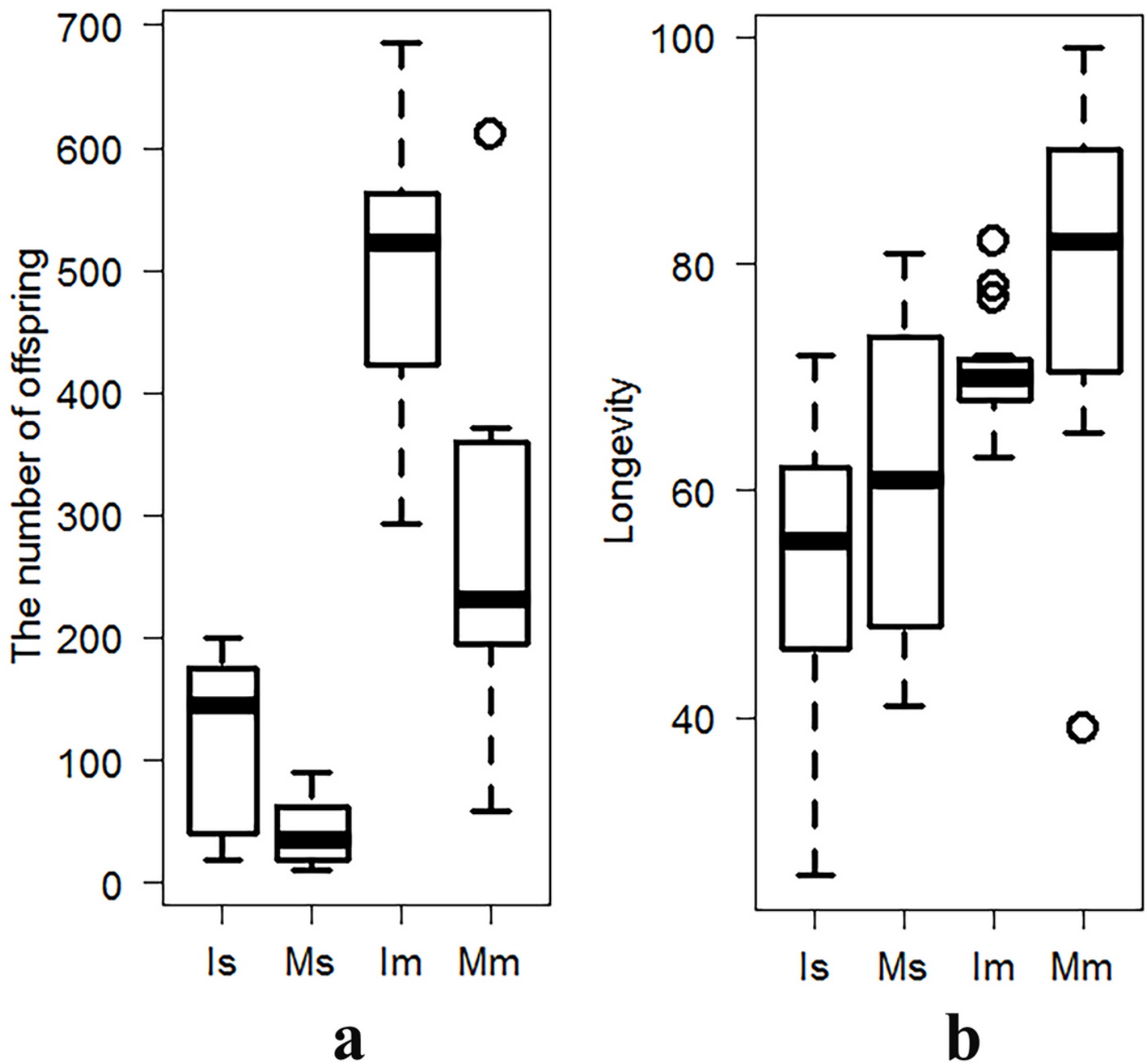


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