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FIG WASP ATTRACTION: UNRAVELING PREFERENCES FOR MALE AND FEMALE FIGS IN *Ficus deltoidea* VARIETIES USING A Y-TUBE OLFACTOMETER

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ABSTRACT

Ficus deltoidea (Moraceae) is a dioecious fig species native to Malaysia with seven distinct varieties in Peninsular Malaysia. It maintains a mutualistic relationship with its obligate fig wasp pollinator, *Blastophaga* spp. (Agaonidae). Volatile organic compounds (VOCs) play a vital role in facilitating the interactions between dioecious figs and their specific pollinating wasps. It remains unclear whether *Blastophaga* spp. from two varieties of *F. deltoidea* can differentiate between male and female figs by chemical cues, which may impact their host selection and pollination behaviour. This study investigates whether *Blastophaga* spp. exhibit preferences for male or female figs in two varieties, *F. deltoidea* var. *angustifolia* and var. *deltoidea*, using Y-tube olfactometer assays. This study examined fig wasp attraction, decision time, and the potential influence of fig volatiles on host selection. A total of 132 female fig wasps were tested, with 59 choosing male figs and 73 choosing female figs. A Chi-square test revealed no significant preference between fig sexes (χ^2 (1, N = 132) = 0.49, P = 0.484). However, *Blastophaga* spp. associated with var. *deltoidea* made their choice significantly faster (Md = 77 s) than those in var. *angustifolia* (Md = 90 s) (Mann-Whitney, U = 1700.50, z = 2.17, P = 0.03, r = 0.19). In conclusion, while *Blastophaga* spp. showed no preference between male and female figs of *F. deltoidea*, the faster decision-making in wasps associated with var. *deltoidea* suggests that fig volatiles may influence pollinator behaviour. This supports the intersexual mimicry hypothesis, thereby underpinning the evolutionary stability of their mutualistic nursery pollination.

Keywords: Dioecious fig; fig wasps; sex preference; mimicry

ABSTRAK

Ficus deltoidea (Moraceae) ialah spesies ara diesius yang berasal dari Malaysia dengan tujuh varieti berbeza di Semenanjung Malaysia. Spesies ini mengekalkan hubungan mutualistik dengan pendebunga obligatnya, penyengat ara *Blastophaga* spp. (Agaonidae). Sebatian meruap organik memainkan peranan penting dalam membantu interaksi antara pokok ara dan pendebunganya yang spesifik. Namun, masih belum jelas sama ada *Blastophaga* spp. daripada dua varieti *F. deltoidea* dapat membezakan antara buah ara jantan dan betina berdasarkan isyarat kimia, yang mungkin mempengaruhi pemilihan perumah dan tingkah laku pendebunga. Kajian ini dijalankan bagi mengenalpasti jika *Blastophaga* spp. menunjukkan keutamaan terhadap buah ara jantan atau betina pada dua varieti, iaitu *F. deltoidea* var. *angustifolia* dan var. *deltoidea* melalui ujian olfaktometer berbentuk Y. Daya tarikan, masa membuat keputusan dan potensi pengaruh isyarat kimia dari buah ara terhadap pemilihan penyengat ara telah dikaji. Sebanyak 132 ekor penyengat ara betina telah diuji, dengan 59 memilih buah ara jantan dan 73 memilih buah ara betina. Ujian khi-kuasa dua menunjukkan tiada kecenderungan yang signifikan ditunjukkan oleh penyengat ara terhadap jantina buah ara (χ^2 (1, N = 132) = 0.49, P = 0.484). Walau bagaimanapun, *Blastophaga* spp. daripada var. *deltoidea* membuat keputusan dengan lebih pantas (Md = 77 saat) berbanding dengan var. *angustifolia* (Md = 90 saat) (Ujian Mann-Whitney, U = 1700.50, z = 2.17, P = 0.03, r = 0.19). Kesimpulannya, walaupun *Blastophaga* spp. tidak menunjukkan keutamaan terhadap jantina buah ara, pemilihan yang lebih cepat oleh penyengat ara dikaitkan dengan var. *deltoidea* mencadangkan bahawa sebatian organik meruap daripada buah ara varieti ini mungkin mempengaruhi tingkah laku pendebunga. Penemuan ini menyokong hipotesis mimikri antara jantina sekaligus mengukuhkan kestabilan evolusi dalam sistem pendebungan nurseri ini.

Kata kunci: Pokok ara diesius; penyengat ara; pilihan jantina; mimik

INTRODUCTION

Ficus, a large pantropical genus within the Moraceae family, has close to 1000 species worldwide and approximately 350 species in Asia, placing it among the largest genera of land plants (Corner 1965; Weiblen & Bush 2002). It exhibits diverse life forms, including shrubs, trees, herbs, climbers, creepers, free-standing trees, epiphytes, hemiepiphytes, rheophytes, and lithophytes (Cruz et al. 2022; Tnah et al. 2016), allowing them to occupy various ecological niches. Other than their ecological significance, *Ficus* species have long fascinated researchers due to their specialised pollination system, often referred to as ‘nursery pollination’, which relies on an obligate mutualism with fig wasps (Agaonidae) which has been ongoing for approximately 60 to 100 million years (Cruaud et al. 2012; Compton et al. 2010). The figs serve as both a habitat and a food source for wasps. It enters figs through the opening of the ostiole (Liu et al. 2011), where it facilitates pollination while using the fig as a breeding site for its offspring. In return, this pollination ensures the reproductive success of the fig (Zhang et al. 2014), making it a classic example of co-evolutionary specialisation.

Ficus species employ two distinct reproductive strategies: monoecy and dioecy, each with different pollination outcomes (Kjellberg et al. 2001). Some species exhibit gynodioecy, where individual plants have both female and hermaphroditic flowers (Deng et al. 2015). In monoecious plants, a single tree, such as a *Ficus*, contains both male and female reproductive functions. When a mated female wasp, also known as a foundress, enters the fig through the ostiole, it will pollinate the female flowers inside and oviposit in ovules in some of the flowers. The wasp larvae develop within the fig, feeding on the developing seeds. Once mature, the wingless male fig wasps mate with the winged females inside the fig (Eisikowitch 2015). Emerging female wasps collect pollen before exiting to search for receptive figs where they can oviposit and continue the cycle. The pollinated flowers develop into viable seeds, which are dispersed by animals when they consume the mature fig ("fruit"). Male wasps lack wings, so they cannot spread from the fig in which they emerged (Janzen 1979; Weiblen 2000). Hossaert-McKey & Bronstein (2001), described this interaction as an evolutionary trade-off in which the fig effectively “pays” for pollination and seed dispersal by allocating a portion of its ovules to support the development of pollinating fig wasp offspring.

Dioecious figs have separate male and female trees (Hossaert-McKey et al. 2016). Female figs contain only long-styled female flowers, while male figs contain short-styled gall flowers (modified female) and male flowers (Hatta 2019). According to Kjellberg et al. (1987), gall flowers serve only as wasp brood sites and never produce seeds. Therefore, a foundress can reproduce when she enters a male fig, but it does not produce any seeds (Grison-Pigé 2002; Kjellberg et al. 2001). Meanwhile, if the foundress enters a female fig, she can pollinate but cannot lay eggs due to the long flower styles, resulting only in seed production (Hatta et al. 2023). Consequently, in the dioecious fig-pollinator wasp mutualism, female wasps that enter a female fig incur a fitness cost, as they cannot lay eggs and produce offspring (Hossaert-McKey et al. 2016). This separation of sexes necessitates cross-pollination between male and female trees, which often rely on specialised pollinators, such as fig wasps, for successful reproduction (Moe et al. 2011; Hossaert-McKey & Bronstein 2001; Kjellberg et al. 1987). Dioecy can create unique challenges for these plants, as both male and female trees must be close to one another to reproduce effectively (Hatta et al. 2023; Marcotuli et al. 2020).

To overcome these challenges, research suggests that some dioecious *Ficus* species have evolved intersexual mimicry, where female figs produce a volatile scent similar to that of male figs (Huang et al. 2023). This mimicry may prevent fig wasps from distinguishing between the sexes of the trees, thereby preserving the mutualistic relationship between male and female trees and ensuring pollination of both sexes (Hossaert-McKey et al. 2016; Soler et al. 2012). If the fig wasp can differentiate, it potentially leads to reproductive failure in female trees and local extinction of the species (Chen et al. 2022; Patel et al. 1995). Moreover, dioecious males and females figs exhibit different characteristics that influence fig wasp attraction. For instance, female figs tend to remain attractive longer than male figs, which may lead to selective pressures favouring fig wasps that can effectively navigate these differences (Huang et al. 2023; Suleman et al. 2011). This dynamic creates a scenario in which female figs may mimic the olfactory cues of male figs to attract pollinators, a strategy that underscores the complexity of their interactions (Borges et al. 2013; Suleman et al. 2011).

Several species of dioecious figs have been studied globally, including *Ficus deltoidea, Ficus carica, Ficus. erecta, and Ficus formosana* (Nizam et al. 2025). Among them, *F. deltoidea,* a species native to Malaysia, has an intricate mutualistic relationship with the fig wasp *Blastophaga* spp., Seven varieties are commonly recognised in Peninsular Malaysia: *F. deltoidea* var. *deltoidea*, var. *angustifolia*, var. *trengganuensis,* var. *bilobata*, var. *intermedia*, var. *kunstleri*, and var. *motleyana* (Fatihah et al. 2014). Studies have documented three distinct species of *Blastophaga* spp. as pollinators for three different varieties of *F. deltoidea* (Hatta et al. 2021). A key characteristic of *F. deltoidea* is its asynchronous fig production, where trees produce figs throughout the year and are present in high densities within a region (Hatta 2019). This ensures the continuous availability of receptive figs, reducing the time adult female fig wasps search for a host after emerging from their natal figs (Yahaya et al. 2025a). Given that *Blastophaga* spp. must locate and enter figs within a very short adult lifespan of approximately

24-48 hours, the timing of their arrival is critical because successful pollination depends on entering figs when female flowers are receptive (Naser 2023). The complete life cycle of fig wasps, from egg to adult emergence within the fig syconium, typically lasts several weeks, depending on environmental conditions. Their ability to rapidly find and enter receptive figs is a key factor in their success (Zhang et al. 2011). Their flight decisions may be influenced by chemical cues released by male and female figs, especially since their host trees produce figs asynchronously, aligning with the emergence patterns of pollinators (Hatta et al. 2021; Naser 2023).

Thus, the objective of this study was to determine whether *Blastophaga* spp. show preferences for male or female figs in two *F. deltoidea* varieties, var. *angustifolia* and var. *deltoidea*. These two varieties were selected because they were readily available at the study site and produced sufficient numbers of receptive male and female figs during the experimental period, enabling controlled behavioural assays using a Y-tube olfactometer. The assays were used to determine whether female fig wasps show preferences for male or female figs, the time taken to reach each fig, and whether fig volatiles influence host selection. These findings contribute to a better understanding of how chemical cues mediate pollination dynamics in dioecious *F. deltoidea.*

MATERIALS AND METHODS

Planting Material and Fig Identification

Ficus deltoidea is a dioecious species in which male and female figs occur on separate trees. Male and female trees were identified based on reproductive structures observed during fruiting cycles. Male figs contain gall flowers and developing fig wasps, whereas female figs contain only long-styled female flowers that develop into seeds. Receptive figs used in the olfactometer assays were therefore collected from previously identified male and female trees of var. *angustifolia* and var. *deltoidea* (Hatta 2019). Although figs of var. *angustifolia* are generally smaller than those of var. *deltoidea*, the criteria used to distinguish male and female figs are consistent across varieties.

Fig Wasp Collection

Blastophaga spp. were selected from figs at the fig wasp-releasing stage (Early D phase, the stage when adult fig wasps emerge from mature figs), typically measured from 0.45 cm to 0.55 cm in diameter (Hatta 2019). Early D phase figs were collected on each experimental day to obtain freshly emerged female *Blastophaga* spp. for behavioural assays. These figs were randomly harvested from multiple trees located within an oil palm plantation in Parit Maimon, Batu Pahat, Johor (1°57’19.4” N and 102°48’47.3” E). Between 10 to 15 figs were kept overnight in muslin-covered plastic containers to allow the emergence of wasps. Female *Blastophaga* spp. have a very short adult lifespan of approximately 24-48 hours, which they must locate receptive figs for oviposition and pollination (Naser 2023). Host-seeking behaviour begins almost immediately after emergence. Therefore, newly emerged female wasps were used within a few hours of emergence and were tested individually in the olfactometer assays. The experiments were conducted between 10:00 a.m. and 3:00 p.m., coinciding with the peak activity of *Blastophaga* spp. (Naser 2023). The experiment was conducted in a dark room at ~26°C in the Biology lab of Faculty of Applied Sciences with relative humidity at approximately 60-70% RH to minimise external variables.

Y-Tube Olfactometer Set Up

A Y-tube olfactometer was employed to assess the preferences of *Blastophaga spp.* for the odour of male versus female receptive figs of *F. deltoidea* varieties *angustifolia* and *deltoidea.* The Y-tube allowed fig wasps to travel equidistantly towards either odour source, ensuring unbiased access (Chen et al. 2009; Proffit et al. 2020). The Y-tube was placed on a flat white table illuminated by cool white light from two table lamps, directed towards the Y-tube arms to reduce visual distractions. Only chemical cues from randomly collected receptive figs (B phase, the stage when female flowers are receptive and emit volatiles that attract pollinating fig wasp) measuring approximately 0.2 cm were presented to the respective fig wasps during the trials. The glass Y-tube used (stem: 8 cm; arms: 9 cm at a 55° angle; i.d.: 1.5 cm) followed the specifications of Chen et al. (2009) (Figure 1).

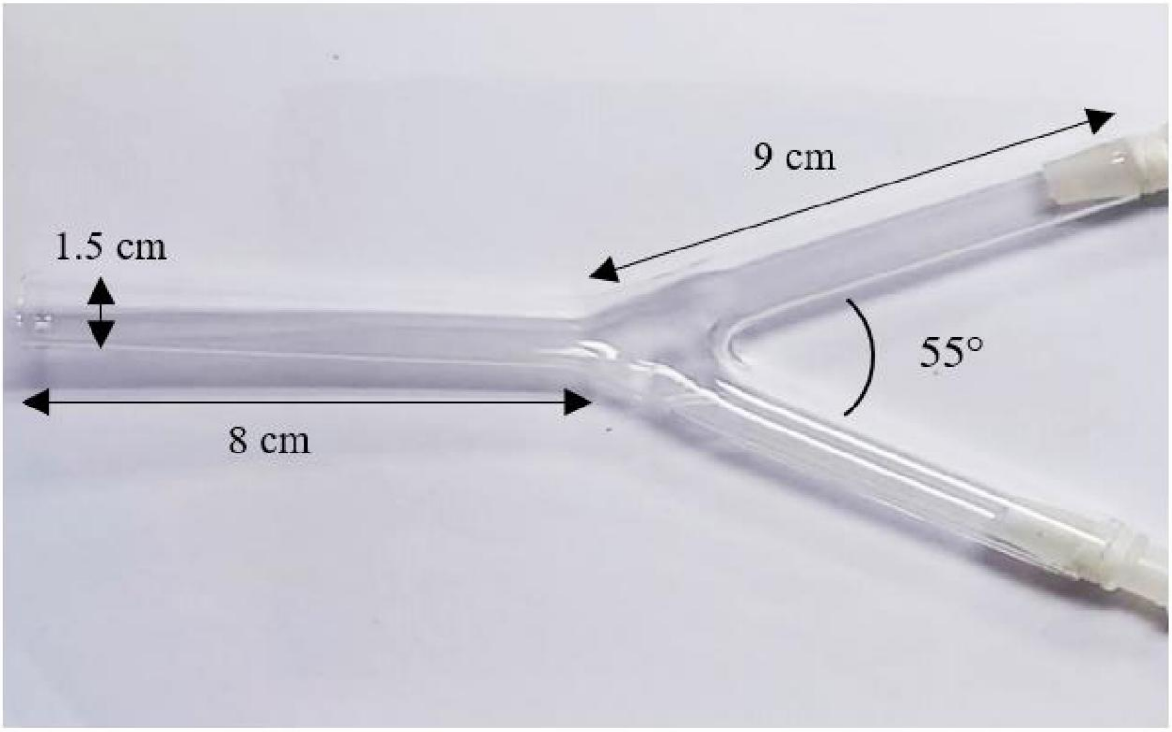

Figure 1. Glass Y-Tube

Each arm of the Y-tube olfactometer was connected to a 500 mL glass beaker containing male or female receptive figs. (Figure 2). In each beaker, branches bearing five to eight fresh figs were used as odour sources, depending on the availability of figs on the sampling day. The same number of figs was used in both beakers within each experimental trial to standardise volatile emission intensity between treatments. For var. *angustifolia*, the fig diameter ranged between 0.37-0.47 cm for males and 0.39-0.47 cm for females, while for var. *deltoidea*, the diameters ranged from 0.42-0.49 cm for males and 0.44-0.50 cm for females. A white cardboard divider was placed between the Y-tube and the beakers to eliminate visual stimuli. An airstream (200 mL min^{-1} per arm) was purified with activated charcoal, humidified with distilled water purified with activated charcoal, and humidified with distilled water to carry odours.

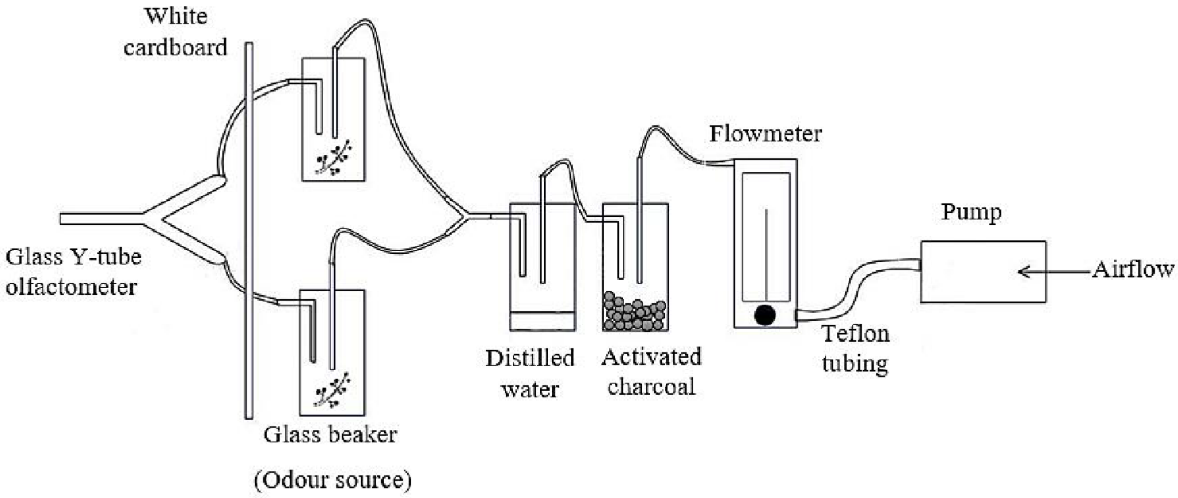

Figure 2. Experiment setup on the preferences of fig wasps towards male and female figs

Sex Preference Test by *Blastophaga* spp.

Each *Blastophaga* spp. was introduced at the Y-tube's stem opening and given up to 10 minutes to choose between the left or right arm. A choice was recorded when a fig wasp crossed the decision line, located 1 cm past the Y-tube bifurcation, and remained there for more than 1 minute. The time taken to reach the decision line was also recorded. However, individuals that did not make a choice within the first 5 minutes were excluded from the analysis, as delayed responses were considered unlikely to reflect active orientation towards the odour source. A total of 66 female *Blastophaga* spp. were tested for var. *angustifolia*, with a maximum of 20 individuals tested per day. The experiments were therefore conducted over four experimental days for this variety. An equal number of fig wasps (n = 66) were tested for var. *deltoidea* using identical protocols, also over four experimental days. Each individual fig wasp represented one replicate in the Y-tube assay. The Y-tube was cleaned with pure ethanol and air-dried after each trial to prevent contamination. Fresh receptive figs were collected daily and replaced every two hours as odour sources. The positions of the glass beakers were alternated between the Y-tube arms after six consecutive trials to avoid directional bias.

Statistical Analysis

A chi-square test was performed to examine the association between the choices of two *Blastophaga* spp. towards the fig's sex. A two-tailed binomial test was used for the dual-choice experiment of the Y-tube olfactometer to test the null hypothesis that the same number of *Blastophaga* spp. were attracted to both male and female odour sources. The Mann–Whitney U test was used to compare the time taken by *Blastophaga* spp. associated with var. *deltoidea* and var. *angustifolia* to choose between fig sexes. All statistical analyses were performed using IBM SPSS Statistics version 28.

RESULTS AND DISCUSSION

A total of 132 *Blastophaga* spp. were tested for their preference between male and female figs. Of these, 59 *Blastophaga* spp. chose male figs, while 73 *Blastophaga* spp. chose female figs. A chi-square test revealed no statistically significant association between fig wasp choice and fig sex (χ^2 (1, N = 132) = 0.49, P = 0.484). Further analysis using two-tailed binomial tests indicated similar patterns for *Blastophaga* spp. associated with both *F. deltoidea* var.

angustifolia and var. *deltoidea*. For var. *angustifolia*, 32 wasps (48%) preferred the arm with male fig odour, while 34 wasps (52%) preferred the arm with female fig odour (P = 0.90; N = 66). Similarly, for var. *deltoidea*, 27 wasps (41%) preferred the male fig odour, while 39 wasps (59%) preferred the female fig odour (P = 0.18; N = 66). These results suggest that *Blastophaga* spp. associated with *F. deltoidea* do not exhibit a significant preference for either male or female fig odours (Figure 3).

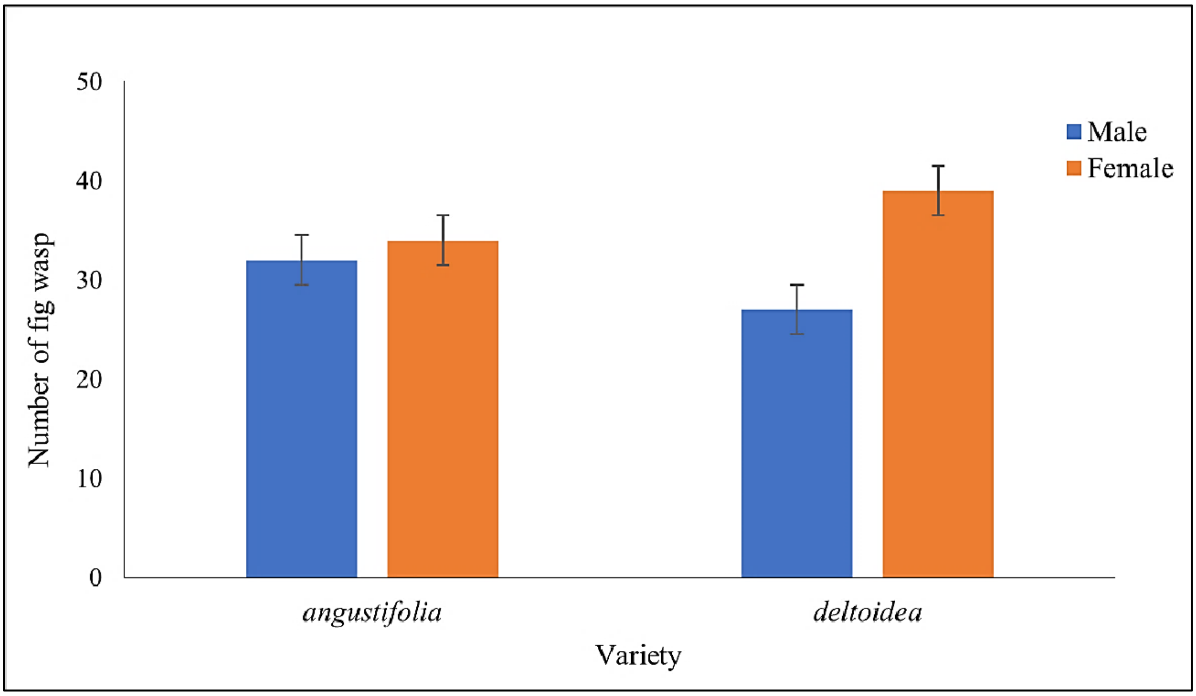

Figure 3. Preferences of fig wasps from var. *angustifolia* and var. *deltoidea* towards male and female receptive figs of their own variety

The time taken for individual female *Blastophaga* spp. to choose between male and female receptive figs is summarised in Table 1. For var. *angustifolia*, the mean decision time towards male figs was 104.75±55.51 s (range: 36-252 s), which was slightly shorter than the time taken to reach female figs (109.26±53.56 s, range: 42-228 s). In contrast, *Blastophaga* associated with var. *deltoidea* reached male figs more quickly (77.30±31.29 s, range: 49-234 s) than female figs (98.46±57.68 s, range: 39-269 s).

Table 1. Time taken for a single *Blastophaga* spp. foundress to choose male and female receptive figs

Variety of the Foundress	**Time Taken Towards Male Figs (Sec)**	**Time Taken Towards Female Figs (Sec)**
	Mean±SD	**Mean±SD**
var. *angustifolia*	104.75±55.51	109.26±53.56
var. *deltoidea*	77.30±31.29	98.46±57.68

The Mann-Whitney U test was used to evaluate differences in the time taken by fig wasps associated with *F. deltoidea* var. *deltoidea* and var. *angustifolia* to choose between fig sexes. The median time taken by fig wasps associated with var. deltoidea to reach receptive figs was 77 s (Md = 77, N = 66), whereas for var. *angustifolia* the median time was 90 s (Md = 90, N = 66). The analysis showed that fig wasps associated with var. *deltoidea* made their choices significantly faster than those associated with var. angustifolia (U = 1700.50, z = 2.17, P = 0.03, r = 0.19). As illustrated in the boxplot (Figure 4), the distribution of decision times differed between the two varieties, with var. *deltoidea* generally showing shorter decision times than var. *angustifolia*.

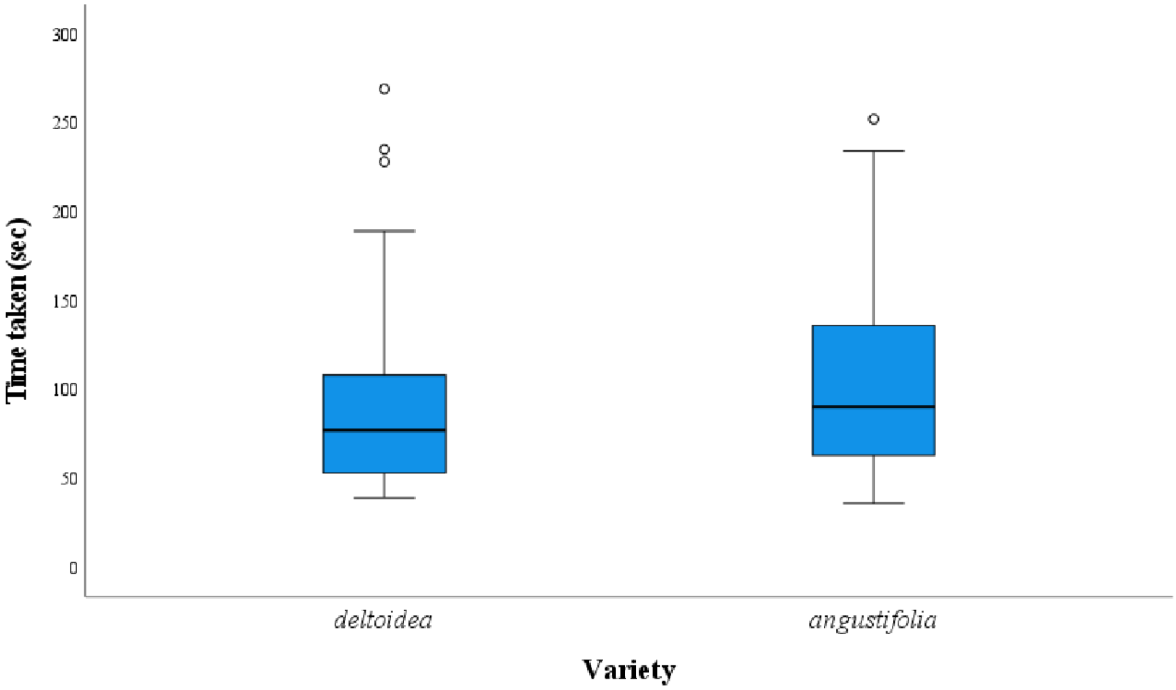

Figure 4. Boxplot showing the decision time (s) of female *Blastophaga* spp. selecting receptive figs of *F. deltoidea* var. *deltoidea* and var. *angustifolia* (n = 66 per variety). The difference between varieties was significant (Mann–Whitney U test, P = 0.03)

In the fig-wasp mutualism, the entry of the fig wasp into female figs is crucial to ensure reproductive success through pollen transfer of *Ficus* (Kjellberg et al. 2001). Female figs function as seed-producing structures (Wang et al. 2009), and successful pollination directly influences fruit development and seed set (Wang et al. 2015). Unlike the male fig, which serves as a breeding site for the fig wasps, female figs have the vital role of ensuring the continuation of the fig's lineage by producing viable seeds through pollination (Molbo et al. 2003). Based on the result, *Blastophaga* spp. associated with *F. deltoidea* from var. *angustifolia* and var. *deltoidea* did not show any significant preference for male or female figs, suggesting their attraction is primarily driven by general fig receptivity cues rather than fig sex.

A study conducted by Nizam et al. (2025) on the volatile organic compounds (VOCs) emitted by receptive figs of *F. deltoidea* reported several compounds shared between male and female figs. In var. *angustifolia*, three VOCs were common to both sexes: β-caryophyllene, β-cubebene, and cycloheptasiloxane tetradecamethyl. Among these, β-caryophyllene was the dominant compound, exhibiting the highest peak area in both male and female receptive figs. In contrast, var. *deltoidea* exhibited a richer VOC profile, with 13 compounds shared between male and female figs, and the volatile blend was composed primarily of sesquiterpenes. Similar to var. *angustifolia*, β-caryophyllene was the most abundant compound, showing the highest peak area in both male and female figs with only minor differences in abundance between the sexes. The high similarity in VOC composition between male and female receptive figs supports the hypothesis of intersexual chemical mimicry in dioecious figs, whereby female figs mimic the odour of male figs to ensure pollinator attraction despite not providing a reproductive site for fig wasp offspring. Such chemical convergence between fig sexes has been widely reported in dioecious *Ficus* species and is considered an important mechanism that prevents pollinators from distinguishing between male and female figs during host location (Anstett et al. 1998; Borges et al. 2008; Chen et al. 2009; Hossaert-McKey et al. 2016; Proffit et al. 2008; Soler et al. 2012). The short adult lifespan and high mortality risk during flight (Bronstein 1988) impose strong selective pressure on *Blastophaga* spp. to locate a host rapidly, often resulting in entry into the first receptive fig encountered (Raja et al. 2008).

Additionally, olfactory receptors (ORs) and odorant-binding proteins (OBPs) mediate sex preference in fig wasps at the molecular level (Chen et al. 2022). These chemosensory mechanisms enable wasps to recognise specific VOC blends, theoretically allowing them to distinguish fig sexes. However, similarity in VOC emissions minimises this ability, effectively overriding the specificity of ORs and OBPs. This compels wasps to visit male and female figs, ensuring successful pollination and reproduction. In dioecious *Ficus* species, male and female trees often synchronise their receptive phases following the fruiting of the male tree to ensure successful pollination and reproduction. Such synchrony enables emerging female wasps to discriminate between male and female figs, as previously studied (Hossaert-McKey et al. 2016).

However, these findings contrast with those of Hatta (2019) and Yahaya et al. (2025b), who reported a preference for male figs among pollinators in *F. deltoidea* var. *angustifolia* and var. *deltoidea* under natural field conditions, while our study found no significance for male figs under controlled laboratory conditions. This difference may arise due to variations in the experimental design. We conducted our study under controlled conditions, minimising external environmental pressures such as predation or competition. Additionally, all figs utilised during this experiment were at the same stage of receptivity, potentially reducing any variations in volatile profiles between male and female figs that may occur in actual field conditions. The high mortality risk faced by fig wasps in natural conditions may pressure them to locate figs quickly (Patel & Hossaert-McKey 2000), potentially influencing their apparent preference for male figs observed by Hatta (2019).

Moreover, the observed preference for male figs in field studies may be attributed to their greater opportunities for oviposition and protection. A review by Greeff et al. (2022) highlights pollinating fig wasps adjust their behaviours and sex ratios in response to environmental cues and resource availability. Male figs, potentially providing more oviposition sites and better protection from predators, could significantly reduce mortality risks and enhance reproductive success, offering a compelling explanation for this field preference. According to Ghana et al. (2017), in dioecious *Ficus* species male figs contain short-styled female flowers that allow female fig wasps to insert their ovipositor and lay eggs, where larvae subsequently develop within galled ovules. In contrast, female figs contain long-styled flowers that prevent the ovipositor from reaching the ovules, resulting in seed development instead of fig wasp offspring. Therefore, only male figs function as suitable reproductive sites for fig wasps. These structural differences in floral morphology strongly influence fig wasp behaviour and host selection. Such adaptive strategies align with findings that natural pressures shape wasp behaviour in ways that optimise their reproductive fitness (Jousselin & Kjellberg 2001).

Blastophaga spp. associated with var. *deltoidea* reached both male and female figs in significantly less time than those associated with var. *angustifolia*. This difference may be related to variations in ostioles, rougher fig surfaces, or differences in overall fig morphology, which could influence the ability of this species to locate and decide to enter figs. As Frank (1984), Lavi & Sapir (2015), and Sun et al. (2015) reported, fig-wasp attraction is also influenced by cues such as colour, size, and ostiole diameter. The size of the fig ostiole can be a physical barrier that limits pollinator entry (Nizam et al. 2025). The ostiole diameter of receptive figs is typically very small, generally around 0.2-0.5 mm, while adult female *Blastophaga* spp. measure approximately 1-2 mm in body length with a body width of about 0.3-0.6 mm. As the ostiole is the only entry point into the fig syconium, its size relative to the fig wasp body can strongly influence successful entry and pollination. The morphology of figs in var. *deltoidea* may therefore allow *Blastophaga* spp. to inspect and select figs more efficiently. Additionally, the fig wasp populations associated with different types of figs may have distinct response thresholds to chemical or visual cues (Herre et al. 2008; Hossaert-McKey et al. 2016). Rodriguez et al. (2017) discussed this phenomenon and suggested that receptive fig scents assist fig wasps in locating host figs. However, the limited differentiation among odours from different *Ficus* species allows for adaptive flexibility in odour recognition rather than imposing a strict co-evolutionary constraint. This adaptability may enable fig wasps to utilise several host species or adjust to fluctuating environmental conditions.

CONCLUSION

This study provides strong evidence supporting the intersexual mimicry hypothesis in *F. deltoidea*, while also highlighting the influence of experimental design on the behaviour of pollinating fig wasps. Variation in decision time between varieties further suggests that fig morphology and associated cues may influence pollinator behaviour. Together, these findings demonstrate that both chemical signals and physical traits play important roles in shaping *Ficus*-fig wasp interactions. These findings emphasise the importance of integrating chemical ecology and behavioural responses to better understand the stability and persistence of obligate plant-pollinator mutualisms. Future studies integrating controlled experiments with more natural environmental conditions, as well as investigating the sensory mechanisms underlying odour perception, may further improve our understanding of pollinator behaviour in this system.

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AUTHORS DECLARATIONS

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Conflict of Interest

All authors declare that they have no conflicts of interest that could influence the findings reported in this paper.

Ethics Declarations

Ethics declarations do not apply to this research.

Data Availability Statement

This manuscript has no associated data.

Authors' Contributions

Nurin Izzati Mohd Zulkifi wrote the first draft of the manuscript. Nur ‘Aliyaa Nizam conducted the experiments and discussed the findings. Nur Badrina Mohammad Naser executed the experiments, provided materials and references. Siti Noorfahana Mohd Idris co-wrote the manuscript. Siti Khairiyah Mohd Hatta designed the experiments, revised and refined the final manuscript.

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