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POLLINATION PATTERNS IN *Ficus deltoidea*: BEHAVIOURAL INSIGHTS INTO *Blastophaga* sp. ENTRY AND INTERACTIONS

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ABSTRACT

Ficus deltoidea, part of the diverse *Ficus* genus and native to Malaysia, is noted for its medicinal properties apart from having 13 different varieties in Malaysia. Its main pollinator, *Blastophaga* sp., is vital in its reproductive processes. This study explored the pollination dynamics in *F. deltoidea* complex, focusing on the entry rates and behaviours of *Blastophaga* sp. from the variety of *deltoidea* through the dissection of the figs. Field research in Johor, Malaysia, between August and December 2023 concentrated on observing male and female figs during the phase where pollinators entered the figs. The results revealed that *Blastophaga* sp. can enter multiple figs, indicating a tendency to visit figs already entered by other fig wasps. This pattern was observed in both male and female fig trees. Only one fig wasp body remained inside a developing fig recorded the highest value among all the figs dissected., where the maximum number of bodies found in a single fig was five in the male and four in the female. This suggests that the receptive phase of a fig permits multiple entries by female fig wasps, possibly influenced by the opening of the ostiole, which in turn affects pollinator preferences and behaviours. Understanding these interactions enhances knowledge of the mutualistic relationship between figs and fig wasps, contributing to fig trees' ecological balance and sustainability.

Keywords: entry rate, fig trees, fig wasps, mutualism, pollination biology

ABSTRAK

Ficus deltoidea adalah sebahagian daripada genus *Ficus* (pokok ara) dan ia merupakan tumbuhan asli Malaysia. Tumbuhan ini terkenal bukan sahaja kerana khasiat perubatannya tetapi juga kerana mempunyai 13 varieti berbeza di Malaysia. Pendebunga utamanya

Blastophaga sp. (penyengat ara), memainkan peranan penting dalam proses pembiakan pokok ara ini. Kajian ini meneroka dinamika pendebungaan dalam kumpulan *F. deltoidea*, dengan fokus kepada kadar kemasukan dan kelakuan *Blastophaga* sp. daripada varieti *deltoidea* melalui kaedah diseksi. Kajian lapangan telah dijalankan di Johor, Malaysia, antara Ogos hingga Disember 2023 yang memberi tumpuan kepada pemerhatian fasa buah ara jantan dan betina semasa fasa pendebunga telah memasuki buah ara tersebut. Hasil kajian menunjukkan bahawa *Blastophaga* sp. boleh memasuki lebih dari satu buah ara, menunjukkan kecenderungan untuk mengunjungi buah ara yang telah dimasuki oleh penyengat ara yang lain. Corak ini diperhatikan pada kedua-dua pokok ara jantan dan betina. Tambahan lagi, hanya satu badan penyengat ara yang paling banyak dijumpai di dalam buah ara yang sedang berkembang di mana bilangan maksimum badan yang direkodkan ialah lima di dalam buah ara jantan dan empat di dalam buah ara betina. Ini mencadangkan bahawa fasa reseptif buah ara membenarkan kemasukan berganda oleh penyengat ara betina, yang mungkin dipengaruhi oleh pembukaan ostiol, seterusnya mempengaruhi pilihan dan kelakuan pendebunga. Memahami interaksi ini meningkatkan pengetahuan tentang hubungan mutualisme di antara pokok ara dan penyengat ara, serta sumbangnya kepada keseimbangan ekologi dan kelestarian pokok ara.

Kata kunci: kadar kemasukan, pokok ara, penyengat ara, mutualisme, biologi pendebungaan

INTRODUCTION

The fig tree, a member of the Moraceae family and the *Ficus* genus (Van Goor et al. 2018), is one of the largest genera among land plants, comprising 850 species (Cook & Raplus 2003; Kjellberg et al. 2022). Found in tropical and subtropical areas worldwide (Clement et al. 2020), including regions in Indo-Australasia, the Neotropics, Afrotropics, and southern Africa (van Noort 2003), fig trees bear pseudofruit with a distinct closed urn-shaped inflorescence known as a fig (Leite et al. 2021). The genus *Ficus* exhibits functional diversity in growth forms (hemi-epiphyte, epiphyte, climbers, tree, rheophytes, lithophyte, and shrub), breeding systems (monoecious and dioecious), and pollination modes (active and passive) (Chen et al. 2009; Clement et al. 2020).

Ficus deltoidea Jack, native to Malaysia and locally known as 'Mas Cotek,' features golden-colored fine spots on its leaves (Desaku 2005; Mat et al. 2012). In Malaysia, there are 13 known varieties of *F. deltoidea,* with some pollinated by *Blastophaga* spp. (Hatta 2019). This species acts as a true epiphyte, often growing on oil palm trees without harming the host (Benzing 2004), ranging from 0.3 to 7.0 meters in height (Starr et al. 2003). With a dioecious breeding system, *F. deltoidea* produces seeds and rears fig wasps separately (Hatta 2019; Machado et al. 2001), and various parts of the fig offer medicinal benefits (Hakiman & Maziah 2009).

The fig wasp, belonging to the family Agaonidae, is crucial for fig tree reproduction, with *Blastophaga quadrupes* Mayr being the only described pollinator for *F. deltoidea* (Corner 1969). These wasps depend entirely on figs for reproduction sites (Chen et al. 2009) and exhibit distinct morphological characteristics for their roles in the fig's life cycle (Abd Aziz et al. 2021; Tooker 2007). The mutualism between figs and fig wasps are essential ecological interactions, with obligate mutualism being particularly vital, where neither species can reproduce without the other (Kjellberg et al. 2022). The reciprocal benefits in this relationship are crucial for the ecological balance, impacting various rainforest animal populations (Cook & West 2005).

Foundresses, mated female fig wasps carrying pollen, initiate the pollination cycle by entering receptive figs and laying eggs, leading to offspring development and subsequent pollination (Cook & Raplus, 2003; Kjellberg et al., 2022; Hatta et al., 2023). This process, influenced by factors like fig size and structural differences between male and female figs, plays a significant role in fig tree reproduction and mutualism stability (Chen et al. 2009; Yang et al., 2015).

From this study, we aimed to explore the pollinating behaviour of *Blastophaga* sp. in *F. deltoidea* var. *deltoidea*. It is commonly understood that once a foundress enters a fig, she spends her entire lifetime within it. However, various studies have observed that a foundress can exit the first fig she enters and move to an adjacent fig by walking. Specifically, our research addressed the following questions: (1) How many foundresses can enter a single fig? (2) Is this behaviour consistent between male and female figs? (3) Which fig gender tends to host more foundresses?

MATERIALS AND METHODS

Study Site

The study was carried out from August 2023 to December 2023 at the free plantation area in Parit Maimon, Batu Pahat, Johor, Malaysia (1°56'52"N 102°49'18"E) (Figure 1). It involves *F. deltoidea* growing in situ as epiphytes on the trunk of oil palm trees (Figure 2).

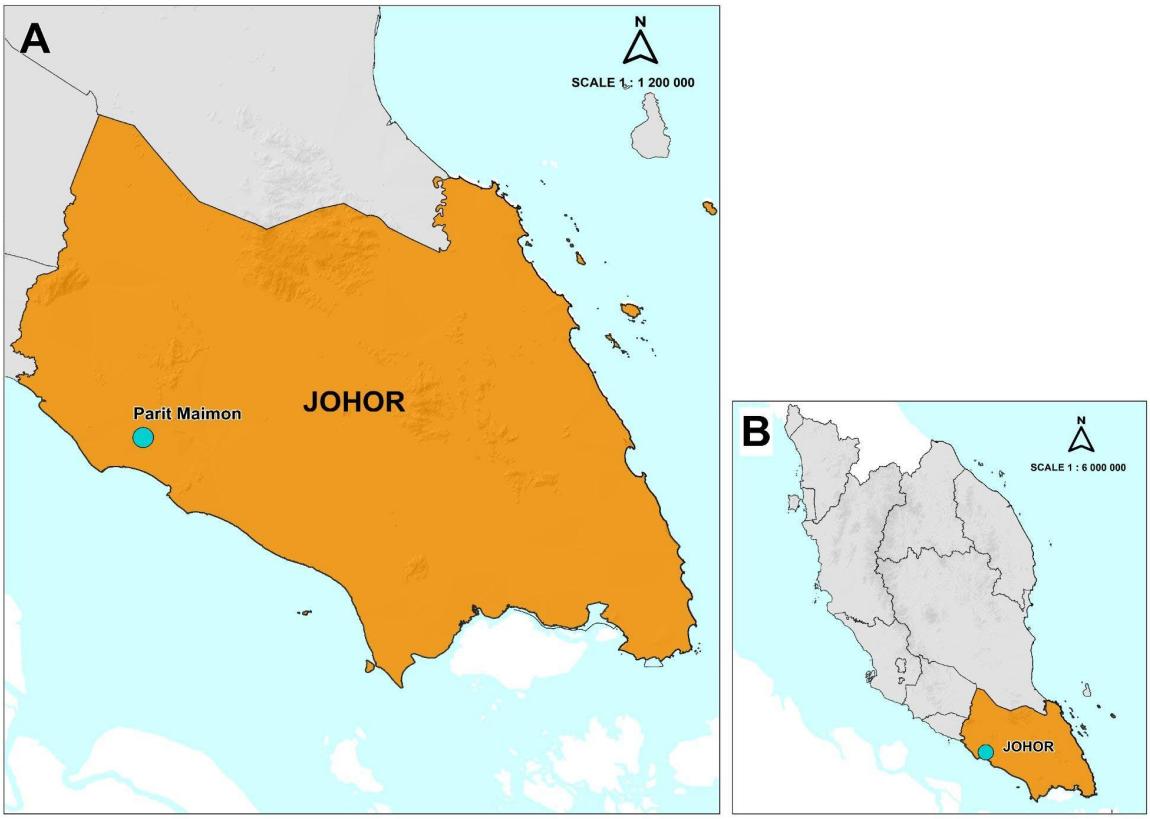

Figure 1 Oil palm plantation that supports epiphytic *Ficus deltoidea* in Batu Pahat, Johor

Figure 2. *Ficus deltoidea* var. *deltoidea* growing as an epiphyte at Parit Maimon, Batu Pahat, Johor (in red circle)

Sampling Methods

The research was carried out in Batu Pahat, where *F. deltoidea* thrives as both free-standing trees and epiphytes. To examine how many female fig wasps could enter a single fig, 100 male and 100 female figs from 100 trees of each sex (10 figs per tree) were explicitly taken during the phase where the fig wasp had already entered a fig. Still, the body has not decayed yet (Hatta 2019). This phase is characterised by the figs being entered by foundresses (Figure 3), with developing offspring and expanding galled ovules in the male figs and seed production in the female figs. A female fig wasp body can also be seen clearly in this phase as they have not decayed. The presence of wings and foundress bodies inside the figs were also documented. Figs with the presence of wings indicate that the fig was the first one to be entered by one or more females, while the figs without the presence of wings are likely to be entered by a fig wasp that has entered another Figure It only provides a minimum estimate of how many foundresses entered each fig because foundresses that lacked wings on entry could not be accounted for (Hatta 2019).

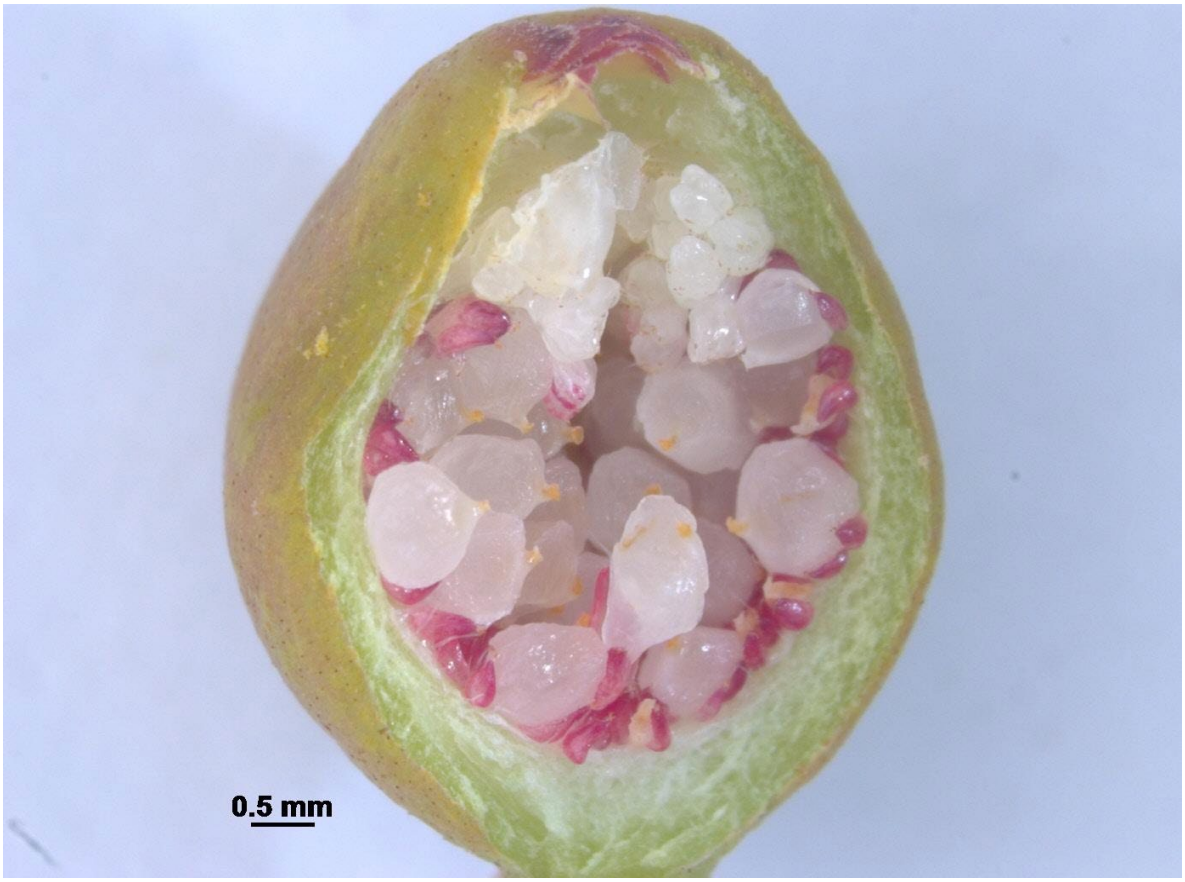

Figure 3. Phase C in fig on *Ficus deltoidea* var. *deltoidea* that showed developing galls

Additionally, the orientation of the fig wasps' heads to determine whether they were positioned to lay eggs, pollinate the ovule, or die before these activities were also recorded. If the body was inside the fig cavity or oriented outwards through the ostiole, it could lay eggs or pollinate the ovules. Conversely, if the head was positioned in the ostiole facing towards the cavity, it suggests that the wasp died before it could reach the female flowers.

Data Analysis

Pearson correlations were used to investigate the relationship between the percentage of visited figs and the average number of dead foundresses in both male and female trees. Fisher's Exact Test was employed to assess the count of foundresses remaining inside the figs, the frequency of figs entered by a single foundress, and variations in the head position of the foundress within the figs, particularly when some expected values were below five. All analyses were conducted using the Statistical Package for Social Sciences (SPSS) Statistics 20.

RESULTS AND DISCUSSION

The Entry Rate of *Blastophaga* sp. from *Ficus deltoidea*

The prediction of the minimum number of *Blastophaga* sp. entry into male and female figs can be derived by assessing the remaining number of fig wasp bodies. For male figs, 10 random figs were sampled from 10 different fig trees of *F. deltoidea* var. *deltoidea.* As depicted in Table 1, 100 collected male figs were dissected to observe any presence of fig wasp bodies. Forty-four out of the 100 figs were found without foundresses' bodies inside the Figure The percentage of visited figs (consisting of the foundress body) ranged from 20% to 100% (Table

1). The mean number of fig wasp bodies in a single fig ranges from 0.20±0.42 to 2.20±1.23, 1.87 (Table 1).

Table 1. The number of naturally-visited male figs with foundress bodies. Mean values do not include figs with no foundress corpses

Tree	Number of figs	Figs with foundresses (%)	Figs without foundresses (%)	Number of foundress corpses per fig		
				Mean	SD	Range
1	10	60	40	0.60	0.52	1
2	10	20	80	0.40	0.84	0-2
3	10	70	30	1.60	1.65	1-5
4	10	70	30	1.50	1.43	1-4
5	10	20	80	0.40	0.84	0-2
6	10	50	50	0.80	0.92	1-2
7	10	100	0	2.20	1.23	1-4
8	10	20	80	0.20	0.42	1
9	10	70	30	2.20	1.87	1-5
10	10	80	20	1.70	1.64	1-5
Total	**100**	**50**	**50**	**1.16**	**1.38**	**1-5**

The count of *Blastophaga* sp. within an individual male fig varied from one to five. As shown in Figure4, most figs contained only a single fig wasp body. There was a decrease in frequency as the number of foundresses per fig increased. It is important to note that the values exclude pollinators that may have been trapped while attempting to enter the figs. Instead, only foundress bodies either in the fig cavity or with the body stuck head-outwards in the ostioles were noted.

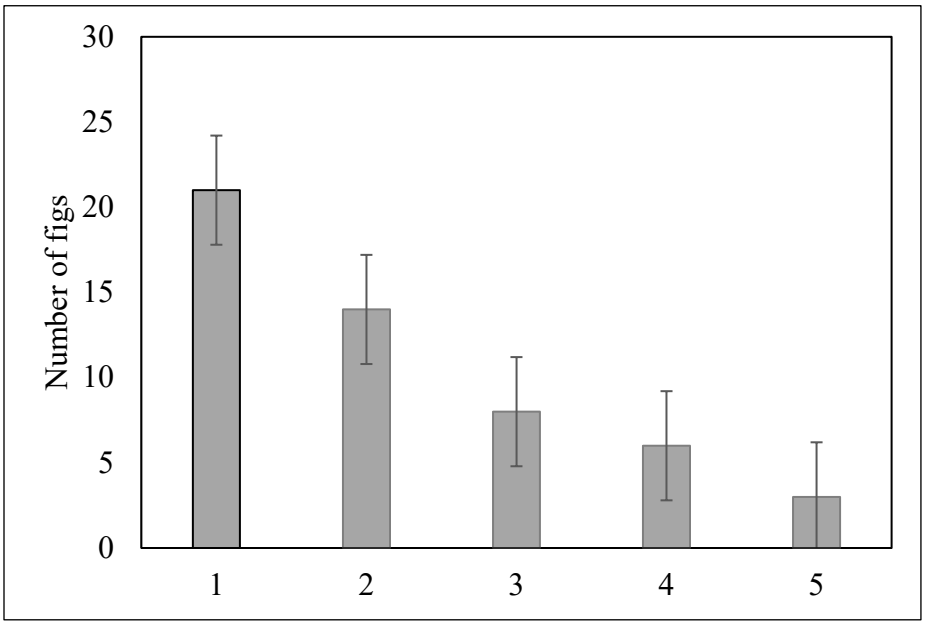

Figure 4. The mean number of *Blastophaga* sp. foundresses remaining inside male figs of var. *deltoidea* that had gall developing

On the other hand, for female trees, among 100 collected and dissected figs, 65 were found without foundresses' bodies inside the Figure The percentage of visited figs with the foundress' body ranged from 0% to 60% (Table 2). The mean number of fig wasp bodies in a single fig ranges from 0.0±0.0 to 1.0±1.05 (Table 2).

Table 2. The number of naturally-visited female figs with foundress bodies either in the fig cavity or with the body stuck head-outwards in the ostioles. Means do not include figs with no foundress corpses

Tree	**Number of figs**	**Figs with foundresses (%)**	**Figs without foundresses (%)**	**Number of foundress corpses per fig**		
				Mean	**SD**	**Range**
1	10	60	40	1.00	1.05	1-3
2	10	40	60	0.50	0.71	1-2
3	10	40	60	0.60	0.84	1-2
4	10	60	40	1.00	1.05	1-3
5	10	50	50	0.60	0.70	1-2
6	10	20	80	0.20	0.42	1
7	10	30	70	0.30	0.48	1
8	10	20	80	0.20	0.42	1
9	10	0	100	0.00	0.00	0
10	10	30	70	0.70	1.34	1-4
Total	**100**	**50**	**50**	**0.52**	**0.83**	**1-4**

The number of the *Blastophaga* sp. inside a female fig ranged from one to four. As depicted in Figure 5, most figs contained just one fig wasp body. Similar to the observations in male figs, the number declined as the count of foundresses increased.

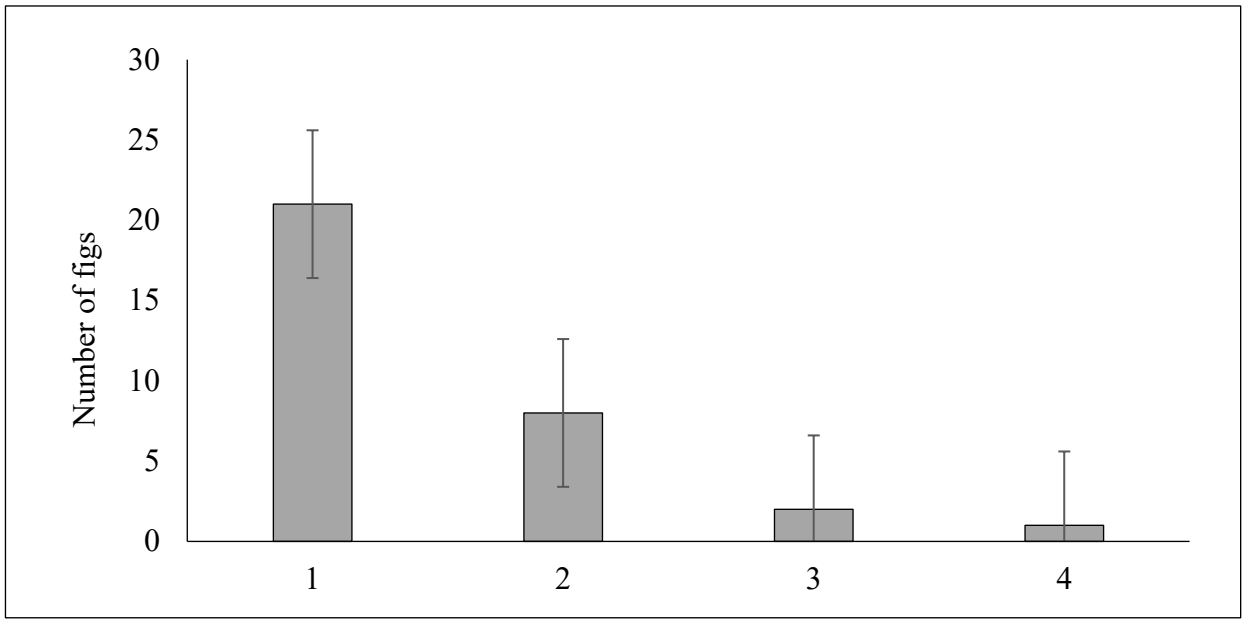

Figure 5. The mean number of *Blastophaga* sp. foundresses remaining inside female figs of var. *deltoidea* that had seeds developing

Preferences of Fig Wasps in Entering Figs

In male figs, there was a significant negative correlation (Pearson correlation, r = -0.899, n = 10, *P<0.05*) between the percentage of foundress-free visited figs on a tree and the mean number of dead foundresses within visited figs (Figure 6). A similar negative and significant correlation observed in female figs (Pearson correlation, r = -0.93, n=10, P<0.05) (Figure 7).

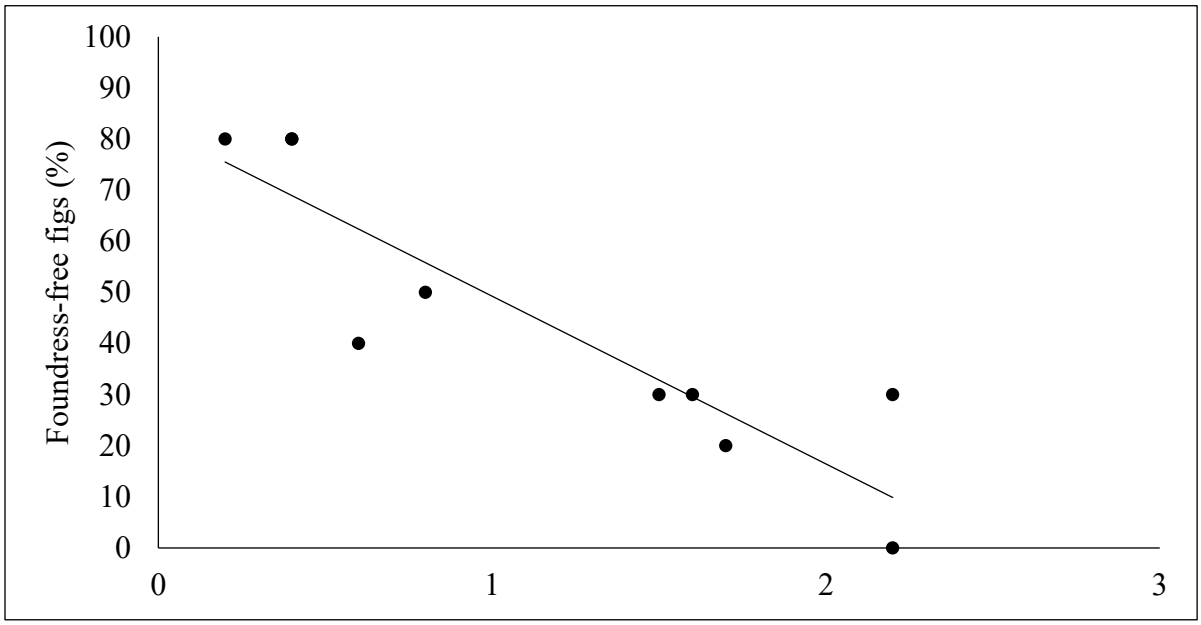

Figure 6. Relationship between the percentage of male figs with no foundress bodies present and the mean number of dead foundresses in a single fig wasp. Each data point represents 10 figs from one male tree

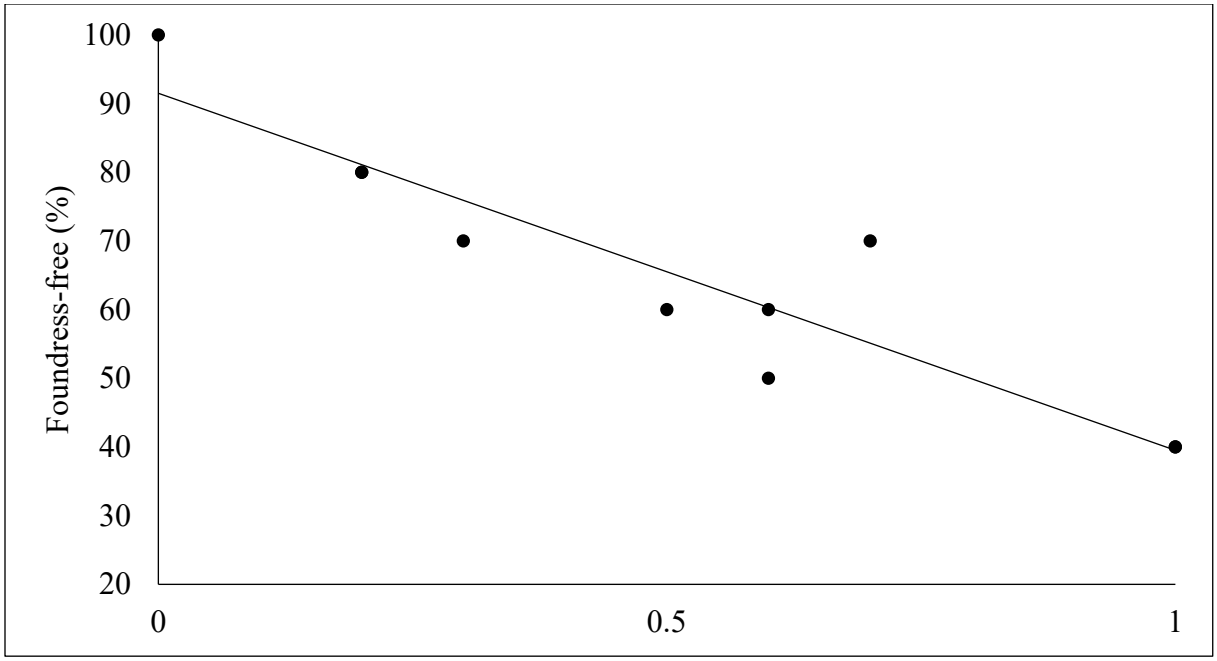

Figure 7. Relationship between the percentage of developing female figs with no foundresses present and the mean number of foundresses in the figs where one or more foundresses were present. Each data point represents 10 figs from one female tree

The Position of Fig Wasp Bodies within the Entered Figs

Among all dissected figs, 164 out of 200 figs contain foundress bodies. From those 164 bodies, 68 were positioned with their heads facing outward towards the ostiole, 64 inside the fig cavity, and 32 with heads toward the cavity. For all 3 positions, male figs recorded a greater frequency than female figs (Figure 8). Most foundresses from male figs were located inside the fig cavity. In contrast, most foundresses of female figs were found with their heads towards the ostiole (Figure 8). Fisher's Exact Test (df = 2, P>0.001) revealed no significant difference in the distribution of foundress locations within the figs between male and female trees.

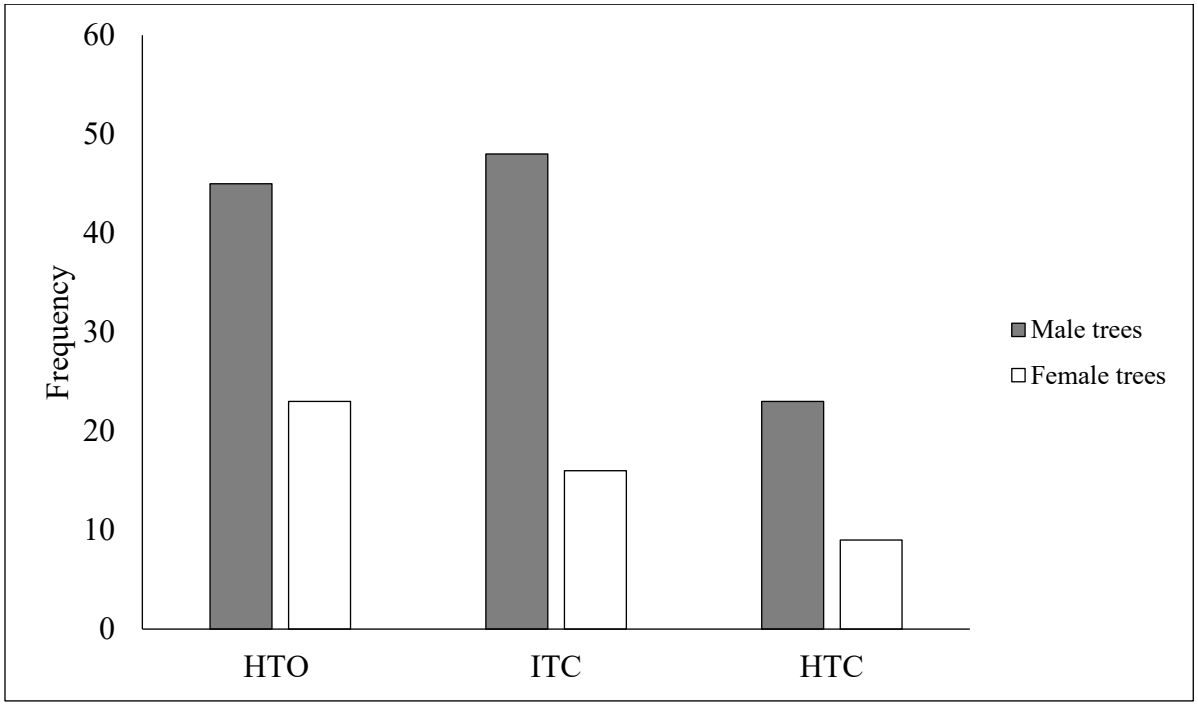

Figure 8 The frequency positions of foundresses in the figs. HTO = head towards ostiole, ITC = body in the cavity, HTC = Head towards the cavity

Penetrating through the ostiole is the only way of entering the fig's cavities, and it usually opens for a specific duration (Liu et al. 2013). During the receptive phase, the ostiole will open, allowing its respective pollinators to enter. The plant's natural selection enables the ostiole to keep opening for a specific time to let more pollinators enter or re-emerge to have more chances for seed production (Suleman et al. 2013). Among many varieties of *F. deltoidea*, the figs of the variety *deltoidea* produce small-sized figs with fewer flowers (Corner 1969). This is reflected in the findings of this study, where a single foundress can enter up to five male figs and four female figs during the receptive phase. Multiple fig entrance by female fig wasps is possible as they carry loads of pollen (for pollination) and produce eggs (for oviposition), which are more than the number of fig flowers (Jandér 2021). When comparing the entry of foundresses between fig sexes, a single male fig can accommodate more fig wasps than female figs as it has a shorter style length and requires a shorter time for oviposition.

Most of the figs were recorded as having only one fig wasp body inside, and the number of figs was found to be gradually decreasing as the number of fig wasp bodies increased. It contradicts the negative relationship between the number of foundress corpses within figs and the percentage of foundress-free in male and female figs. The highest percentage of foundress-

free trees in both sexes had the lowest mean number of fig wasp bodies. This implies that in crops where a higher proportion of figs were entered exclusively by foundresses that had already visited other figs, fewer foundresses remained in those figs. This correlation may be attributed to variations in foundress frequency among different crops.

It also proves that var. *deltoidea* fig had enough flowers (Hatta 2019) to be pollinated or oviposited by multiple fig wasps (Hatta et al. 2021). It also depicts that the pollinators tend to visit the figs already entered by other pollinators rather than those that are either untouched or entered by fewer pollinators (Hatta et al. 2023). This preference shown by pollinators might be due to easy access in the figs with ostioles still opened even entered by the first pollinator that visited the particular fig (Liu et al. 2013). Thus, the fig wasps can save energy from the hassle of penetrating through the narrow ostiole bract and use time and energy to find as many flowers as possible to be pollinated or oviposited (Ashman 2019).

The success of pollination and oviposition attempts by *Blastophaga* sp. is indicated by the positioning of fig wasp bodies found within the fig cavity. Only those with bodies within the cavity or their heads facing outwards at the ostioles are considered to have done the pollination or oviposition process. It is because they are likely to have reached the flowers to lay eggs or pollinate the ovules, while those with heads facing toward the cavity are likely to have died before reaching the flowers (Hatta 2019). However, the truth behind this hypothesis is impossible to confirm. In both male and female figs, the frequency of fig wasps with heads towards the ostiole and bodies within the cavity are higher than those with heads towards the cavity. It indicates that many fig wasps that entered the figs survive until the oviposition or pollination process is completed.

CONCLUSION

The study shows that *Blastophaga* sp. visits both male and female figs of *Ficus deltoidea*, with male figs experiencing more visits and a wider range of fig wasp corpses per fig compared to female figs. Fig wasps demonstrate a preference for figs previously visited by fig wasps, likely due to easier access through open ostioles. The positioning of fig wasp bodies within figs suggests successful pollination or oviposition. Variability in foundress frequency among different crops impacts the number of fig wasps remaining in figs. *Ficus deltoidea* figs can host multiple fig wasps, with fig wasps favouring figs already visited by others. Overall, these findings shed light on the dynamics of fig wasp entry, behaviour, and preferences, providing insights into the reproductive ecology of *Ficus deltoidea* and the role of *Blastophaga* sp. in its pollination and oviposition processes.

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AUTHORS DECLARATIONS

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Conflict of Interest
All authors declare that they have no conflicts of interest to 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
Yahaya Indah Nilam Sari (YINS) was the principal researcher who executed the experiments, discussed the findings, and wrote the first draft of the manuscript. Siti Khairiyah Mohd Hatta (SKMH) designed the experiments, revised and refined the final manuscript. Nur ‘Aliyaa Nizam (NAN) and Nur Badrina Mohammad Naser (SBMN) executed the experiments, provided materials and references, and co-wrote the manuscript. Nurul Fatihah Abd Latip (NFAL), Norhafizah Mohd Zazi (NMZ), and Noor Akmal Abd Wahab (NAAW) co-wrote the manuscript.

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