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INFLUENCE OF FIG SURFACE AREAS ON BROOD PRODUCTION AND GENDER DISTRIBUTION IN *Blastophaga* POLLINATORS OF *Ficus deltoidea*

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ABSTRACT

Fig trees belonging to the genus of *Ficus* (Moraceae) are known for their diversity formed through obligate mutualism with their pollinators, known as the fig wasps (Agaonidae). The interaction occurs in both directions where the fig serves as the breeding site for the wasp, and the wasp in return, pollinate the fig's flower. Studies revealed that fig surface area exhibits influence on the wasp brood productivity by stating that the larger fig surface area is capable of supporting numerous wasp's offspring. Furthermore, the gender distribution of fig wasp of *Ficus* fig is commonly reported to exhibit a female-biased. However, it remains unclear whether fig surface area influences brood productivity (brood size), and the female-bias gender distribution in a Malaysian fig species, *Ficus deltoidea*. Therefore, this study conducted to determine the influence of the fig surface area and the gender distribution of the pollinator, *Blastophaga* fig wasp that oviposited in 100 figs of *F. deltoidea* of var. *angustifolia* and var. *deltoidea* from Banting and Batu Pahat, respectively. The surface area of figs was measured, then dissected, followed by gall extraction for detailed observations. The results indicate the fig surface area and the wasp brood size of var. *deltoidea* are significantly higher than var. *angustifolia* ($P<0.005$). However, in each host variety, the linear regression determined the fig surface area is a weak predictor, addressing only 2% and 25% of variance on the brood size, respectively. In addition, the chi-square determined the gender distribution deviated from 1:1 expected ratio, indicating the imbalanced in the gender distribution and the wasp brood of both host varieties are female-biased. In conclusion, the brood size of *Blastophaga* wasp is not entirely influenced by the fig surface area of *F. deltoidea* var. *angustifolia* and var. *deltoidea*, and female-bias in the wasp was observed across the two host varieties.

Key words: Agaonidae; fig surface area; mutualism; pollination ecology; sex ratio

ABSTRAK

Pokok ara yang tergolong dalam genus *Ficus* (Moraceae) dikenali dengan kepelbagaian mereka yang terhasil melalui kesalingan obligat dengan pendebunga iaitu penyengat ara (Agaonidae). Interaksi ini berlaku secara dua hala yang mana buah ara berfungsi sebagai tempat pembiakan untuk penyengat manakala, penyengat ara pula melakukan pendebungaan untuk buah ara sebagai ganjaran. Beberapa kajian menunjukkan bahawa keluasan permukaan buah ara mempengaruhi penghasilan baka penyengat, yang mana buah ara yang mempunyai keluasan permukaan yang besar mampu menghasilkan bilangan baka penyengat yang lebih tinggi. Tambahan pula, kebanyakan taburan jantina penyengat ara dilaporkan lebih bias terhadap betina. Walau bagaimanapun, pengaruh keluasan permukaan buah ara terhadap penghasilan baka penyengat (bilangan penyengat) serta taburan jantina penyengat yang bias terhadap betina masih belum jelas dalam spesies ara di Malaysia, *Ficus deltoidea*. Maka, kajian ini dijalankan untuk mengenal pasti pengaruh keluasan permukaan buah ara dan taburan jantina bagi pendebunga *Blastophaga* yang telah bertelur dalam 100 buah ara *F. deltoidea* var. *angustifolia* dan var. *deltoidea* dari Banting dan Batu Pahat. Luas permukaan buah ara itu diukur dan dibelah untuk mengeluarkan puru bagi pemerhatian seterusnya. Hasil kajian mendedahkan bahawa keluasan permukaan buah ara dan bilangan baka penyengat var. *deltoidea* adalah lebih tinggi secara signifikan berbanding var. *angustifolia* (P<0.05). Namun, analisis regresi linear bagi setiap varieti perumah memaparkan keluasan permukaan buah ara adalah peramal yang lemah, dengan hanya menunjukkan 2% dan 25% varians dalam bilangan baka yang dihasilkan oleh masing-masing. Selain itu, analisis chi-square menunjukkan bahawa taburan jantina penyengat ara menyimpang daripada nisbah 1:1 yang dijangkakan, sekali gus menunjukkan ketidakseimbangan dalam taburan jantina dan baka penyengat ara bagi kedua-dua varieti perumah adalah bias terhadap betina. Kesimpulannya, saiz brood tebuan Blastophaga tidak dipengaruhi sepenuhnya oleh luas permukaan buah ara *F. deltoidea* var. *angustifolia* dan var. *deltoidea*, manakala nisbah jantina yang memihak kepada betina dalam populasi tebuan tersebut diperhatikan pada kedua-dua varieti perumah.

Kata kunci: Agaonidae; luas permukaan buah ara; kesalingan; ekologi pendebungaan; nisbah jantina

INTRODUCTION

Plant from the genus *Ficus* (Moraceae) is broadly distributed in tropical regions and classified as one of the largest genera of flowering plants worldwide (Abd Aziz et al. 2021). In Malaysia, *Ficus deltoidea* is commonly found in oil palm plantations and is frequently cultivated as an ornamental plant in residential and urban landscapes (Hatta et al. 2023). This species is also consistently found as an epiphyte in the oil palm plantation, which supports sustainable management within the agroecosystem (Ismail et al. 2023). *Ficus deltoidea* breeds separately in male and female trees, highlighting the importance of pollinators in connecting and facilitating the growth and dispersal of these trees (Nurin Izzati et al. 2026; Yahaya et al. 2025a). The male and female trees also have distinct functional roles: male trees produce figs (syconia) for pollination and as the fig wasps' natal host, whereas female trees produce figs for seedlings (Li & Kokko 2019; Yahaya et al. 2025b). Both male and female figs possess enclosed inflorescences (flowers), but with slight differences in structure. Male figs contain both male and female flowers, while female figs contain only female flowers that receive pollen (Hatta 2019). Despite the differences, the external appearance of the receptive fig is similar, and both emit comparable attractants of chemical scents, leading the mated female fig wasps (foundresses) to penetrate randomly without preference (Nizam et al. 2025).

The genus *Blastophaga* is best known for its mutualistic relationship with *Ficus* trees, whereby these species of *Blastophaga* are extremely host-specific fig wasps (Abd Aziz et al. 2021). In essence, the entire identified *Blastophaga* wasps are exclusively associated with *Ficus* only as their obligatory pollinators (Hatta et al. 2021). These wasps display significant sexual dimorphism, distinguished by the absence of wings and ovipositors in male fig wasps, in contrast to their winged female counterparts (Abd Aziz et al. 2021). These morphological characters exhibit niche specialisation as foundresses in ovipositing and pollinating in the receptive male and female figs, respectively, whereas male fig wasps predominantly focus on mating with the female fig wasps (van Noort 2003).

Previous studies revealed that the fig surface area influences wasp brood productivity (brood size) across various fig wasps species (Dunn 2020; Dunn et al. 2025; West et al. 1997). This relationship is based on the concept that brood volume increases proportionally to the spatial capacity of the fig due to increase number of flower available for oviposition and offspring development (Eernisse 1988). A strong correlation was found between brood size and the successful emergence rates of adult fig wasps, emphasising the need for adequate surface area for effective resource exploitation and development (Paul et al. 2021). Moreover, the complex interactions between the fig surface area (size) and fig wasp reproduction highlight the importance of host traits in shaping reproductive outcomes. In particular, the findings of Kjellberg et al. (2005) suggest that the number of wasps present in a fig directly affects brood sizes, implying that fig internal structures might limit or enhance breeding opportunities depending on environmental contexts.

While both genders have respective critical roles for reproduction, the offspring demonstrate a female-biased ratio, which aligns with the Local Mate Competition (LMC) model (Greeff & Kjellberg 2022). This model indicates that the males mate locally with females within the natal figs and produce offspring that are skewed towards females, as inbreeding is also inevitable in such a confined environment (Li & Kokko 2019). Females, on the other hand, follow the male-first rule by ovipositing male eggs first, followed by female eggs in the remaining ovules (Felício & Pereira 2023). Such an occurrence facilitates the early emergence of males, thereby sustaining the synchronised cycle of figs and pollinators (Hatta 2019). As a result, the brood size of the wasps varies, and the female-biased sex ratio remains across the *Blastophaga* wasps.

Despite the substantial research on numerous *Blastophaga* wasp species, studies of how the fig morphology influences the brood size of the pollinators and the relationship between sex ratio and the brood size of *Blastophaga* species associated with different varieties of *F. deltoidea* remain limited and mostly ignored. Hence, we conducted a study on *Blastophaga* spp. from two varieties of *F. deltoidea*: var. *angustifolia* and var. *deltoidea*, to decipher whether the size of the fig determines the number of the brood size and whether these fig wasps exhibit a female-biased sex ratio and variation in their brood size. This study aims to provide baseline data in understanding the fig-wasp relationship and focuses on two objectives; (1) to determine the relationship between the fig surface area and the brood size of fig wasps derived from two varieties of *F. deltoidea*, (2) to investigate the brood size of fig wasps between, and (3) to determine the production of offspring. These evaluations provide an insight into the surface area of the fig, sex allocation and brood size variation in *Blastophaga* spp. associated with two varieties of *F. deltoidea*.

MATERIALS AND METHODS

Study Sites

The figs were obtained from two oil palm plantations, each exhibiting similar vegetation however, populated by distinct varieties of *F. deltoidea.* The plantation in Kuala Langat, Selangor (2.8668° N, 101.5626° E) populated by *F. deltoidea* var. *angustifolia* and operated by private company. Nevertheless, plantation in Batu Pahat, Johor (1.9618° N, 102.8088° E) populated by *F. deltoidea* var. *deltoidea*, and cultivated by small holders and community in Parit Sulong. Only fig trees that grows as an epiphyte on the crevices of the oil palm trunk was chosen to be evaluated in this study. Both study sites were shown in Figure 1.

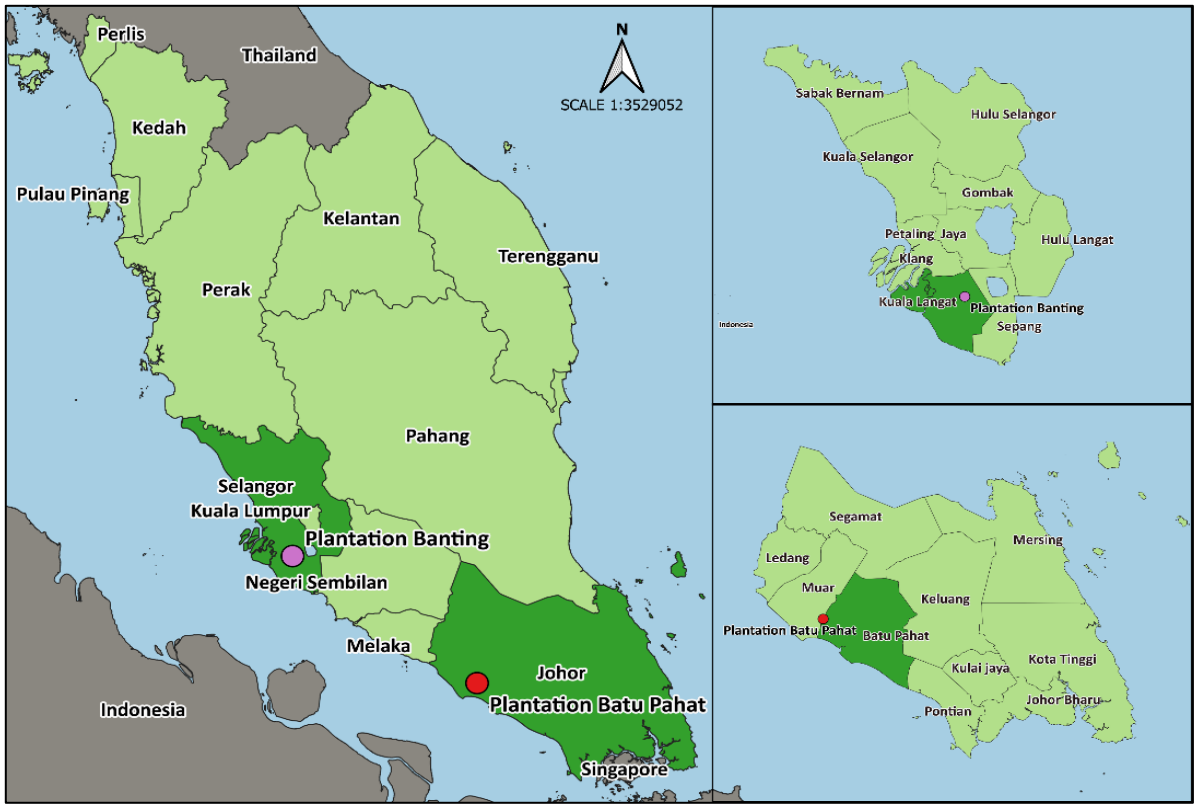

Figure 1. The study sites are shown according to colour coded points. *Blastophaga* wasps associated with *F. deltoidea var. angustifolia* were collected from oil palm plantation Banting (●), and fig wasps associated with *var. deltoidea* were collected from oil palm plantation Batu Pahat (●)

Fig Wasps Collection

Samples collection was initiated by first collecting 50 of nearly ripe figs (D-phase) from male trees of each *F. deltoidea* variety. The figs were identified by their softening surface, the opening of the ostiole, and the presence of developed brownish galls within the fig's cavity (Figure 2). This identification aimed to ensure that the figs were in impending emergence of fig wasp offspring. The collected figs were brought to the lab and measured for length using a calliper with a precision of ±0.01 mm at room temperature (25±1°C). The fig surface areas were obtained by squaring the length measurement, resulting the surface area unit in square millimetres (mm^2). These figs were stored individually in respective containers (7.5cm x 4 cm) and covered with mesh cloth to trap the emerging fig wasps while allowing ventilation. Then,

the emerged fig wasps were counted and differentiated by gender as described by Abd Aziz et al. (2021) before being preserved in 70% ethanol. Both female and male fig wasps exhibit sexual dimorphism: females have wings and an ovipositor, while males do not. To extract wasps that remained unhatched, the figs were sliced into four sections before the galls were gently extracted from the fig's cavity. Each gall was lightly compressed by using two glass slides under a stereomicroscope until the galls were visibly crinkled, and the gall fragments were removed by using fine-point forceps (entomological forceps) to ensure the wasp structures remained intact. All fig wasps observed were recorded based on two variables; the brood size per fig and the gender composition (male-to-female ratio) for subsequent analysis.

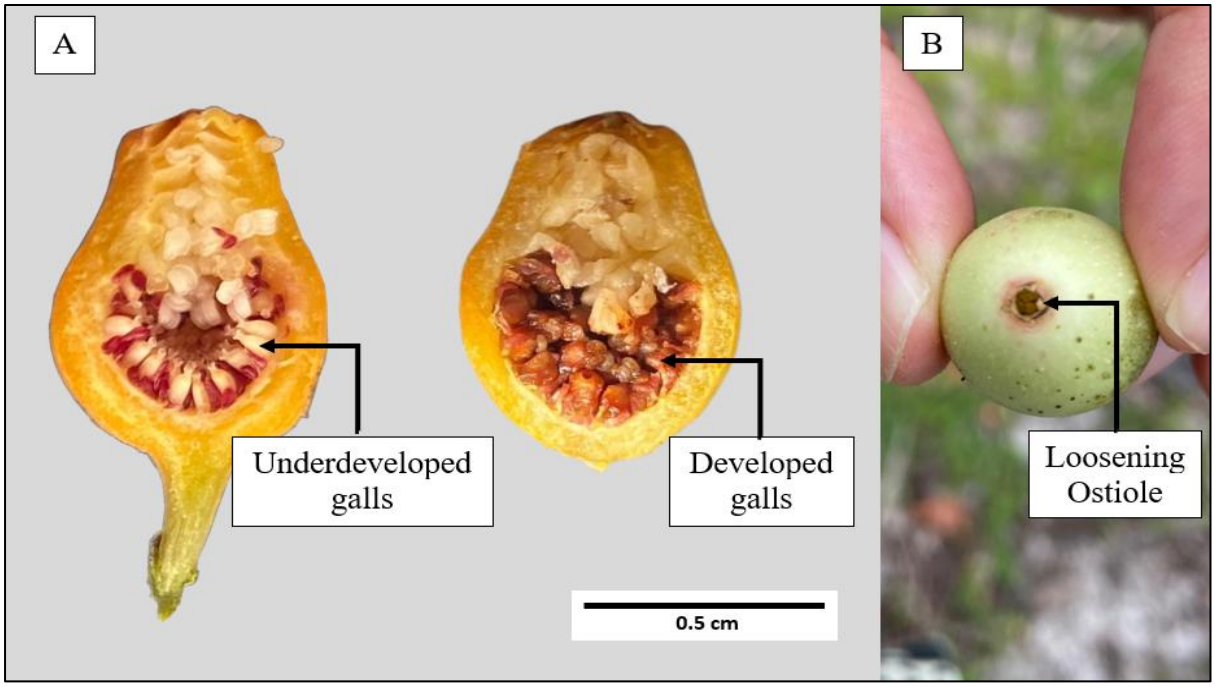

Figure 2. [Picture A] The fig on the left exhibits less pigmented underdeveloped galls (C-phase), indicating that the wasps were still in the developmental stage. The nearly ripe fig on the right exhibits brownish galls (D-phase), indicating that the wasps were nearing the completion of their development before emergence. [Picture B] The D-phase fig was recognised by loosening of the ostiole, allowing the offspring to depart from the fig's cavity

Data Analysis

The collected data were analysed using the Statistical Package for the Social Sciences (SPSS) version 29.0. The data analysis commenced with normality test to determine whether the brood size of *Blastophaga* wasps follows a normal (Gaussian) distribution through Shapiro-Wilk statistic, given that sample size was less than 100 figs per *F. deltoidea* variety. To assess whether there was a significant difference in the wasp brood size between the host varieties (*F. deltoidea* var. *angustifolia* and var. *deltoidea*), Mann-Whitney U test or independent-sample t-test was executed; subjected to the normal assumption result. In addition, the fig surface areas between the hosts were also analysed through similar analytical procedure. In subsequent analysis, the Pearson correlation test was conducted to investigate the strength and direction of association of the wasp brood size and the fig surface area. This finding then followed by simple linear regression to determine the relationship between the fig surface area and the

brood size. Next, the deviation from expected 1:1 gender distribution (male-to-female) within each host variety were determined by using Chi-square goodness-of-fit test. The sex ratio value was determined through the proportion of male wasps to the number of total offspring (sex ratio value = number of male wasps/numbers of total offspring). The male proportion value that showed below 0.5 indicated the gender frequency between male and female were not equal. lastly, the correlation of sex ratio and the wasp brood size was executed according to each host varieties, subjected to the normality test result.

RESULTS

Brood Size and Its Relationship with the Fig's Surface Area

A total of 2730 *Blastophaga* wasps were extracted from *F. deltoidea* var. *angustifolia*, whereas 3684 individuals were obtained from var. *deltoidea* (Figure 3). The wasp brood size per fig ranged between 19 and 112 individuals in var. *angustifolia* and from 32 and 135 individuals in var. *deltoidea*. The Shapiro-Wilk test revealed that the wasp brood size from both hosts were normally distributed ($P>0.05$) for both varieties, allowing further examination using independent-sample t-test for comparison among the host varieties. The t-test then revealed the *P*-value was less than 0.05, indicating the brood size in var. *deltoidea* was significantly higher compared to var. *angustifolia* (t = -4.1073, df = 97.58) (Figure 4). The same result was found where the t-test *P*-value scored less than 0.05, indicating the fig surface areas of var. *deltoidea* was significantly higher compared to var. *angustifolia* (t = -26.794, df = 74.857) (Figure 5).

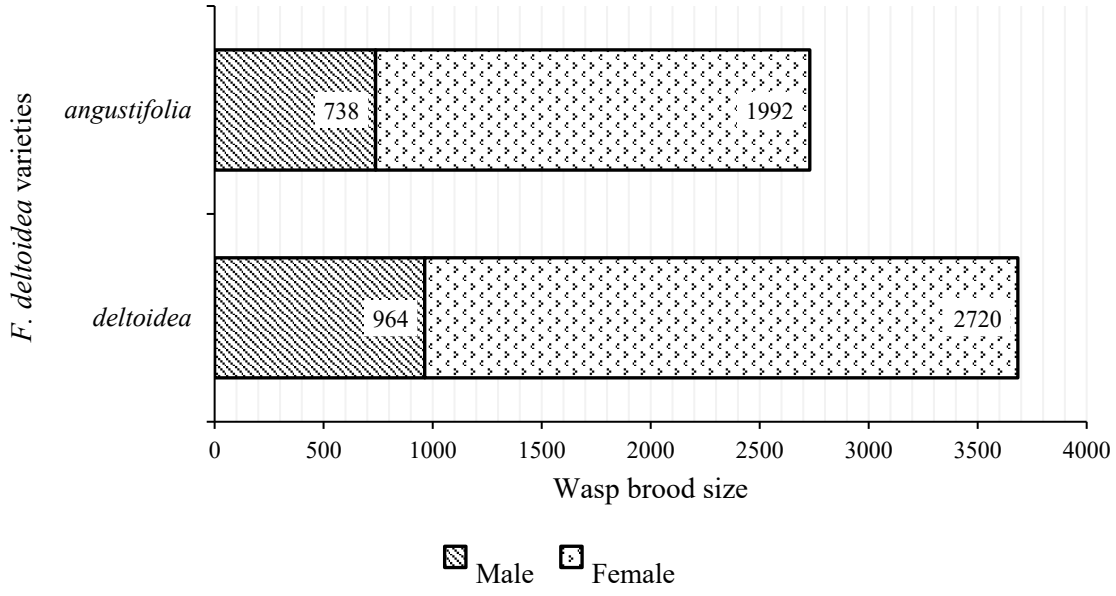

Figure 3. The brood size of *Blastophaga* offspring according to two varieties of *F. deltoidea*. The value in the stacked bar chart represents gender distribution (male-to-female composition)

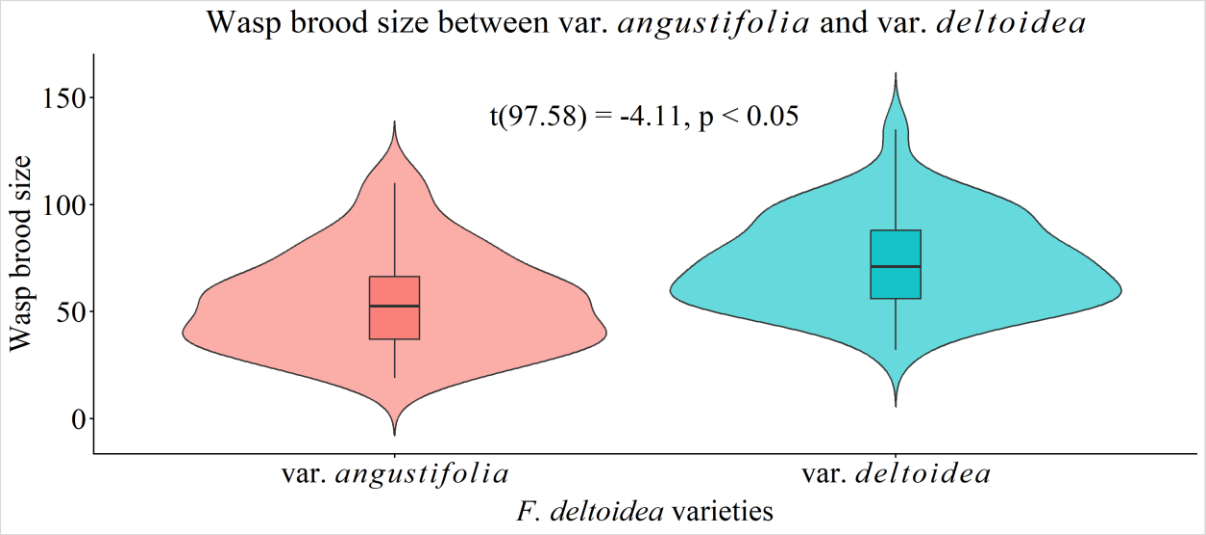

Figure 4. Comparison of wasp brood size showed that var. *deltoidea* with a mean of 72.9 was significantly higher compared to var. *angustifolia* with a mean of 54.6

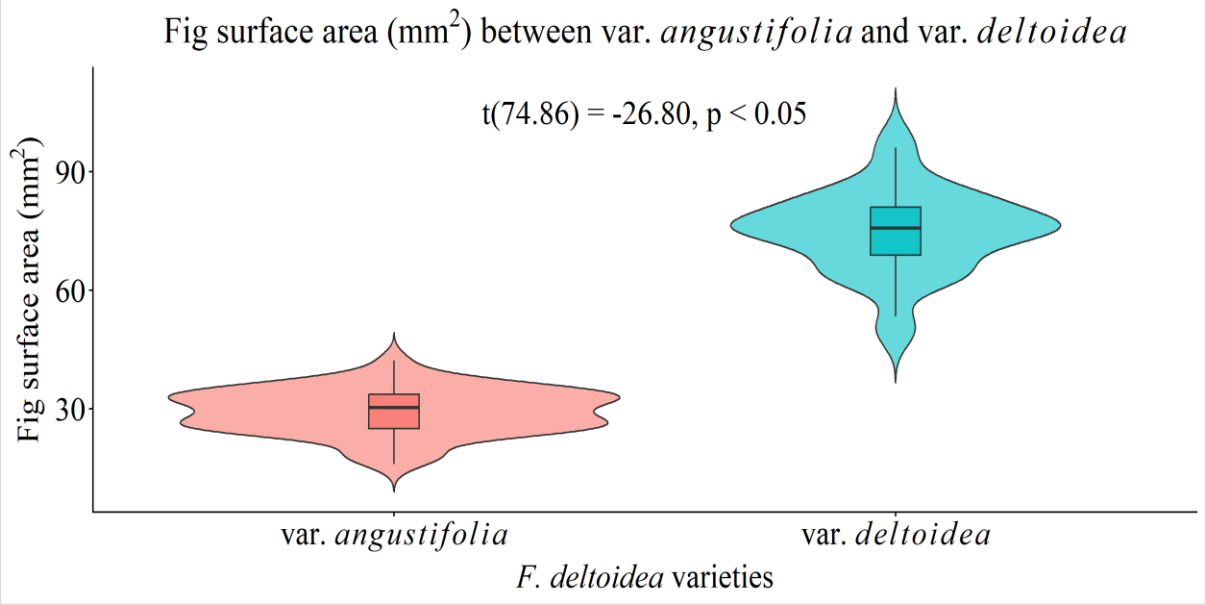

Figure 5. Comparison of fig surface area (mm2) showed that var. *deltoidea* with a mean 74.9 was significantly higher compared to var. angustifolia with a mean of 29.36.

In Pearson correlation test, there were linear positive trends observed in both host varieties which indicated as the fig surface area increase, the wasps brood size tends to increase as well (Figure 6). However, the correlation strengths were different between the varieties. It was showed that the correlation for var. *angustifolia* was classified as weak positive ($r = 0.14$, $n = 50$, $P<0.05$), while var. *deltoidea* was moderately positive ($r = 0.50$, $n = 50$, $P<0.05$). Based on the linear regression equation of var. *angustifolia*, the wasp brood size was expected to increase by approximately 38.8 individuals for each single unit increase in fig surface area (Figure 6). Though, the test also determined that the alteration in fig surface area may only causes 2% ($R^2 = 0.02$) of variance in the wasp brood size, addressing the fig surface area is a weak predictor of wasp brood size. For var. *deltoidea*, wasp brood size was expected to increase

by approximately 3.1 individuals for each unit increase in fig surface area (Figure 6) and it may cause 25% ($R^2 = 0.25$) of variance in wasp brood size. This result then suggests the fig surface area is a moderate predictor of brood size.

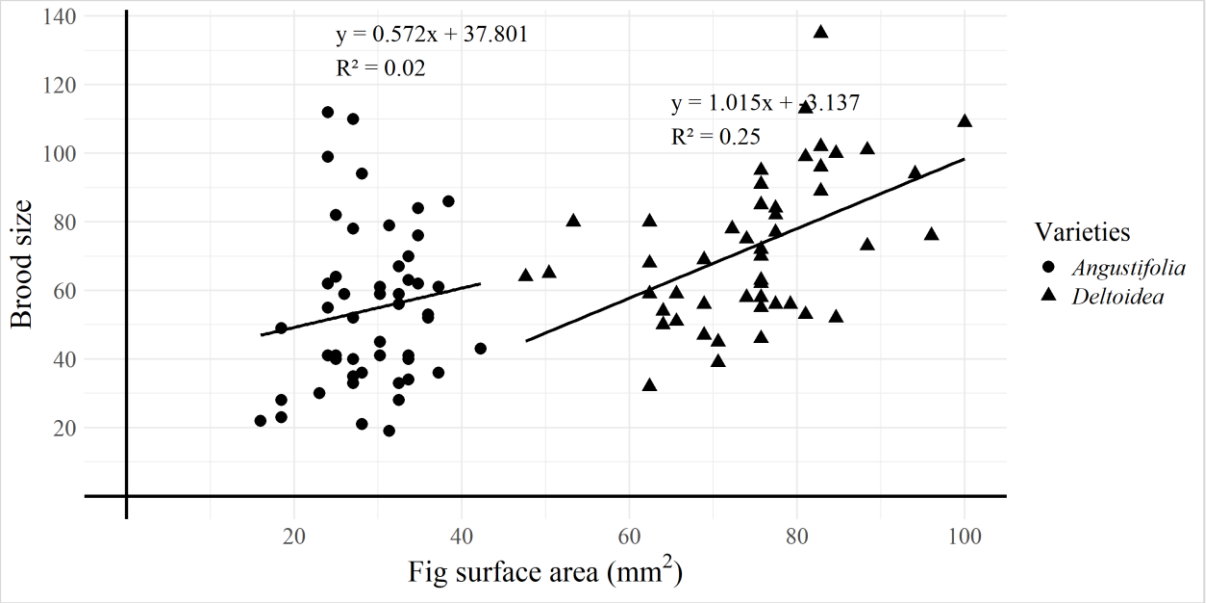

Figure 6. Relationships between the brood size and fig surfaces (mm2) per fig; (●) = var. *angustifolia*, (▲) = var. *deltoidea*. Each data point represents one fig

Wasp Gender Distribution

As illustrated in Figure 3, the female wasps were more abundant than male wasps in both host varieties. The evaluation of the gender composition revealed that 728 males and 1992 females have been recorded in var. *angustifolia*, while 944 males, and 2701 females in var. *deltoidea* (Figure 3). The imbalance of wasps frequency between the gender in each host was further supported by the Chi-square goodness-of-fit test, which confirmed that the gender distribution contrasted from expected 1:1 sex ratio. The Chi-square scored in var. *angustifolia* is $X^2(1) = 576.01$, $P<0.05$ and var *deltoidea* is $X^2(1) = 846.93$, $P<0.05$, indicating that a strong female-biased population in both host varieties are observed.

Sex Ratio and Its Relationship with the Wasp Brood Size

The mean sex ratio of *Blastophaga* wasp from var. *angustifolia* was 0.256 (SD = 0.145), ranging from 0.03 to 0.58. However, the mean sex ratio from var. *deltoidea* was 0.252 (SD = 0.146), ranging from 0.09 to 0.63. Given that the mean sex ratio from both host varieties was below 0.5 thus, this data indicates the frequency of female wasps outnumbered the male wasps among all the figs collected. The Shapiro-Wilk test revealed that the sex ratio from var. *angustifolia* was normally distributed ($P>0.05$) though, the sex ratio in var. *deltoidea* was not normally distributed. Therefore, the data of var. *angustifolia* was further tested through Pearson's correlation test and the data from var. *deltoidea* was tested through Spearman's correlation test. Both correlation tests showed positive linear trends however, the relationship were statistically insignificant (Figure 7). The correlation test for var. *angustifolia* scored ($r = 0.25$, n = 50, $P>0.05$) whereas var. *deltoidea* scored ($r = 0.27$, n = 50, $P>0.05$), indicating the relationship strength of the sex ratio and wasp brood in both host varieties are considered as weak correlated.

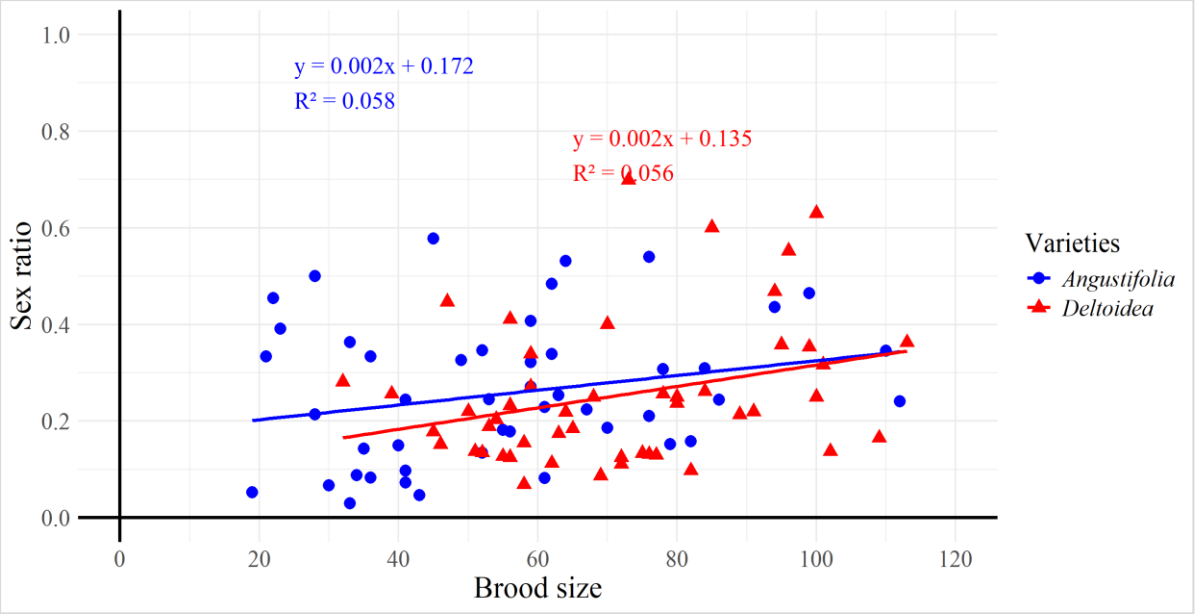

Figure 7. Relationships between the sex ratio and the wasp brood size per fig; (●) = var. *angustifolia*, (▲) = var. *deltoidea*. Each data point represents one fig

DISCUSSION

This study revealed significant differences in *Blastophaga* wasp brood size between *F. deltoidea* var. *angustifolia* and var. *deltoidea*. This result suggests that, although they are classified under a same fig species, the two varieties may differ in the capacity to support wasp reproduction, potentially due to variation in traits that influence the number of flowers, and foundresses abundance in a shared fig (Dunn 2020; Suleman et al. 2013b; West et al. 1997). However, a previous study determined that there was no significant different in the female flower's quantity between var. *angustifolia* and var. *deltoidea*, despite the significant different in their fig surface area (Hatta 2019). This suggests that variation in brood size between the host varieties may not be completely explained by the flower quantity only, though other factor such as foundresses abundance potentially contribute. Nevertheless, the foundress abundance could not accurately be quantified in this study because not all foundresses remained in the oviposited hosts.

Subsequent analysis determined the significant different in the fig surface area between the two host varieties. This result suggests that even in fig of closely-related species exhibit distinct and identifiable morphology. The character not only applies in the fig size (fig surface area), but it also exhibits in structures of leaf, inflorescence, ostiole, volatile organic compound, and qualitative trait such as colour of the fig (Cope et al. 2012; Deng et al. 2022; Lanzes et al. 2026; Zulkifli et al. 2026). Similar variation was reported by Hatta (2019) in multiple varieties of *F. deltoidea*, suggesting the different character was due to cope with the co-evolution with the species-specific pollinator (Machado et al. 2005; Molbo et al. 2003). The different geographic location between these host varieties may attribute to the variation in fig surface area as well (Cerezini et al. 2024). However, data such as soil and rainfall measurement was not included in this study.

In addition, the Pearson correlation test showed positive relationship between the fig surface area and wasp brood size, suggesting that larger fig surface area potentially produces

higher brood size. This interpretation is consistent with previous reports, which highlight that larger fig provides more oviposition sites and able to accommodate multiple foundresses with less competition for inflorescent resources and hence, the larger brood size (Dunn 2020; Dunn et al. 2025; Herre et al. 2008; Wang et al. 2009). However, the linear regression test then showed the fig surface area is a weak predictor which only contribute 2% and 25% of variance in wasp brood size in both host varieties, respectively. A study conducted by Dunn et al. (2025) stated this is where the host-symbiont association was conflicted. Although substantial number of flowers are available, the amount of egg to be oviposited; even by multiple foundresses, is considered disproportionate to the number of flowers (Frederickson 2017). This means that the ratio of egg-to-flower may be imbalanced, resulting in vast number of unexploited flowers and variation in brood productivity notwithstanding the large fig size (West et al. 2021).

The following analysis determined that the gender distribution of *Blastophaga* wasps from var. *angustifolia* and var. *deltoidea* is differ from 1:1 expected sex ratio which indicates these wasps are female-biased. This suggests that the reproductive strategy of pollinating wasps is consistent regardless of host varieties. The reproduction strategy such as selective oviposition of offspring gender is presumably to maximise the foundress's fitness through haplodiploid sex determination, given that, daughters are needed for pollination and oviposition, while sons only mate and create an exit path for females (Greeff & Kjellberg 2022; Li & Kokko 2019; Trochet et al. 2016). The female-biased ratio also suggested to be potentially enhanced due to inbreeding between the offspring in a shared fig and Local Mate Competition (LMC) which reduce male competitiveness and increase fertilisation opportunities (Greeff & Kjellberg 2022; Martel et al. 2016; Zhang et al. 2020). Therefore, female-biased in wasp brood are commonly observed in *Ficus* figs.

The Pearson and Spearman correlation tests indicated that the sex ratio and the wasp brood size among *F. deltoidea* varieties are positive correlated. Although the positive linear trends were observed in both host varieties where it was suggested that the wasp brood size influences the sex ratio, the relationship is considered as weak and statistically insignificant. The insignificant relationship was also observed in a previous study of *Syconia hodites* associated with *Ficus benjamina*, where it was suggested due to oviposition strategy involving the males-first rule (Felício & Pereira 2023). This strategy initiated with oviposition of male eggs in the first host then followed with continuous order in following host, meaning that the oviposition sequence will not reset upon entering a new fig (Suleman et al. 2013a; Zhang et al. 2020). The continuous oviposition strategy by foundresses in multiple hosts, resulting with variation in brood size and sex ratio (Chung et al. 2019; Hatta 2019). Therefore, the oviposition strategy involving male-first-rule and entrance of multiple foundresses in a shared fig potentially explain the insignificant relationship between the wasp brood size and the sex ratio.

CONCLUSION

In conclusion, this study reveals that the brood size of *Blastophaga* wasps and the fig surface area between *F. deltoidea* var. *angustifolia* and var. *deltoidea* are significantly different. However, fig surface area is a weak predictor for the wasp brood size of both host varieties which potentially due to several factors such as the flower quantity, abundance of foundresses, and host-symbiont conflict. In addition, this study also confirms the gender distribution of fig wasp in var. *angustifolia* and var. *deltoidea* is skewed towards female-biased. The potentially factor of this bias is due to inbreeding and LMC which enhance the fitness, pollination, and reproductive success of female fig wasps. Lastly, this study found that the sex ratio (male proportions from the brood size) is mainly less than 0.5 and sex ratio has no significant

relationship with the brood size, indicating females outnumbered the males and the brood size not significantly influence the sex ratio.

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AUTHORS DECLARATIONS

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.

Author Contributions
Qurratu' Aini Syasya Shamsuri wrote the first draft of the manuscript. Nur Badrina Mohammad Naser conducted the experiments and discussed the findings; Nur 'Aliyaa Nizam assisted in the practical aspects. Norashirene Mohamad Jamil co-wrote the manuscript. Siti Khairiyah Mohd Hatta designed the experiments, revised and refined the final manuscript.

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