RESEARCH ACCOUNT

Pollinators for a syconium: How do wasps choose among syconia?

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Female agonid wasps, pollinators of monoecious figs, on entering a syconium (foundresses) are trapped in it and are committed to share the limited resources (flowers) with other foundresses. Hence, foundresses need to ensure that they choose the most suitable syconium. In three fig–wasp associations, we analysed if foundresses could indeed discriminate among syconia of different resource levels. In *Ficus benghalensis*, *F. microcarpa* and *F. racemosa*, the foundress wasps could easily discriminate between the empty and wasp-laden syconia and preferred to enter the former than the latter. Further, in two of these species (*F. benghalensis* and *F. microcarpa*), the species-specific foundresses were also capable of quantitatively assessing loads of the foundresses in the syconia on the basis of wings left behind at and around the ostiole. The wings load on the ostiole was strongly correlated to the foundresses loads. Foundresses preferred entering those syconia from which the wings were removed to those on which the wings were retained. The extent to which the foundresses preferred to enter the syconia was found to be influenced by the density of wings at and around the ostiole. Adding wings artificially to the empty syconia also deterred the foundresses from entering them, suggesting that these residual wings serve as negative feedback regulators for the preference and entry of foundresses. Thus, we show that pollinator wasps of fig–wasp associations choose the most suitable syconia to enter as long as they have opportunity.

Keywords: *Ficus*, fig–wasps, foundress, optimization, syconia.

FIG trees and their pollinating wasps exhibit one of the best known instances of insect–plant co-evolution, where the partners exhibit an obligate dependence on each other for their reproduction[1–7]. Every species of *Ficus* (Moraceae) is pollinated by a specific species of the female agonid wasp (Hymenoptera: Chalcidoidea: Agaonidae). These specific wasps (called foundress wasps), which on entering the syconium bring about pollination of flowers and also lay eggs in to a proportion of the flowers. Thus, flowers in the syconium constitute the resource patches for the foundresses to rear their offspring[8], with more foundresses entering a syconium, the available resources (flowers) per foundress decreases affecting their reproductive success. On entering the syconium, the foundresses are committed to share the available resources within the syconium with other foundresses. Thus, foundresses need to ensure that they choose to enter the most suitable syconium and this decision by the foundresses plays a crucial role in their ability to garner resources for their offspring and hence in shaping their reproductive success. It is therefore likely that foundresses have evolved the ability to discriminate among the syconia with different wasps loads in them. In this study, we have examined three questions in this context: (i) Are foundresses capable of assessing the wasp load of a syconium? (ii) Are they accordingly capable of choosing, and hence preferring, the most suitable syconium to enter? and (iii) if so, what clues do they use for assessing the foundresses load of a syconium?

Material and methods

The experiment was designed in the laboratory, as it is very difficult to track and regulate pollinators in the natural system. Three monoecious fig species, namely *F. benghalensis* L., *F. microcarpa* L. and *F. racemosa* L., were selected for the study as they are available in abundance around the study site (University of Agricultural Sciences, GKVK Campus, Bangalore, India).

D-phase syconia[9,10] of *F. benghalensis* were collected in the early morning hours before sunrise and kept in a 10 glass chamber to collect the species-specific pollinator *Eupristina* (*Eupristina*) *masoni Saunders*. Similarly, *E.* (*parapristina*) *verticillata* (Waterstone) and *Ceratosolen* (*C*) *fusciceps* (Mayr) were collected from *F. microcarpa* and *F. racemosa* respectively. B-phase syconia[9,10] of each species were also collected from different trees which were located at more than 5 km distance from the trees of D-phase syconia. A set of young syconia (A phase) were bagged using muslin cloth to prevent the entry of pollinators a week prior to the harvest for testing the entry of pollinators. The samples were collected early in the morning before sunrise and were well maintained to retain freshness to attract pollinators.

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Table 1. Details of average number of foundresses per syconium in natural conditions, sampling intervals and sample sizes in three species. The time at which the fresh set of 'unoccupied' syconia were introduced (hours after exposing the first set; first column) and their numbers (in parenthesis), the total period of sampling (hours) and, intervals at which the samples were drawn (hours) are provided. The sample size drawn at each interval is also given (parenthesis, column four)

Fig species	Pollinator wasps species	Number of foundresses per syconium in natural conditions *N* = 300 (5 trees)	Time of introduction	Total sampling period	Sampling interval
Ficus benghalensis	*Eupristina* (*Eupristina*) *masoni* Saunders	7.94 ± 3.71	2 (90)	8	2 (30)
Ficus microcarpa	*Eupristina* (*parapristina*) *verticillata* (Waterstone)	1.71 ± 0.90	1 (90)	4	1 (30)
Ficus racemosa	*Ceratosolen* (*C*) *fusciceps* (Mayr)	21.72 ± 6.75	4 (80)	8	1 (10)

N, Number of syconia sampled from five trees.

All the experiments were conducted in plexi-glass insect cabins of size 18 × 18 × 18 inches and were provided with a door on one side for handling the samples and ventilated with a 0.25 mm size nylon mesh on the other two opposite sides. The activity of most of the pollinators of monoecious figs are diurnal[11], the experiments were set up in such a way that there was a uniform spread of light throughout the cabin and room temperature was maintained inside the cabin.

Testing the choice between 'occupied' and 'unoccupied' syconia

A set of 120 receptive B-phase syconia were exposed to a large number of foundresses in the insect cabin, for 2 h. Although we did not count the wasps in the chamber, we attempted to maintain consistency in their numbers by using a defined number of equal-sized D-phase syconia as source of foundresses in each species. On an average, each of these yielded 50–70 foundresses per syconium in *F. benghalensis*, 48–60 in *F. racemosa* and 26–38 in *F. microcarpa*. Thus, we ensured that there are about 4000 foundresses in the chamber.

During the exposure, foundresses entered the syconia and hence they were termed 'occupied'. About 30 syconia from these 'occupied' set were randomly selected and cut open to estimate the number of foundresses in them at the end of 2 h. At this time, a new set of fresh 'unoccupied' syconia, comparable in their freshness to the 'occupied' set, were introduced into the same insect chamber containing pollinators. The base of the insect cabin was divided into a matrix (18 rows × 18 columns) of small grids of approximately 4 sq. cm, such that without marking, we could identify the position of each syconium. The 'occupied' and 'unoccupied' syconia were randomly distributed on this matrix of grids and the positions of each of the category noted for further sampling. These two categories of syconia thus exposed to foundresses were randomly sampled at regular intervals. The time and number of 'unoccupied' syconia introduced, the number and time intervals of sampling and total time exposed to wasps differed among species (Table 1) because of differences in the rate of entry of foundresses (see results). After sampling, the average number of foundresses entering 'unoccupied' syconia in a given sampling interval was compared with those entering 'occupied' sets in the corresponding time period by Student's *t*-test using Proc *t* test SAS (SAS Institute, Version 9.2).

Identification of physical cues used by the foundresses

When foundresses enter the syconia, their wings are left behind generally on, in and around the ostiolar opening[12]. We tested if these wings could serve as cues for the wasps to discriminate the 'occupied' and 'unoccupied' syconia. A set of pollinated syconia (C phase) was collected from each species (n = 30 for all the species), wings around the ostiole of the syconium were counted and then these syconia were cut open to estimate the number of foundress wasps inside the syconium. The wings and the foundresses loads were correlated.

Testing for wings as cues for foundresses

A set of 350 receptive (B-phase) syconia of *F. benghalensis* was kept inside the insect cabin along with a sufficient number (approximately 4000; see above) of foundress wasps obtained from healthy D-phase syconia. After 2 h of exposure, about 50 syconia were randomly sampled and cut open to estimate the number of foundresses. The remaining 300 syconia were divided into two equal subsets. For one set, the area around ostiole was gently brushed using a camel hair brush to remove the wings attached to them at every 2 h interval up to 14 h. Thus, this pool of syconia represented 'occupied' but 'wings removed' (OW–). The other set was retained as such and hence represented 'occupied' with 'wings retained' (OW+). The two sets were arranged in random, but in a known pattern in the insect cabin.

The two sets were exposed again to foundresses for 4 h and 25 syconia from each set were sampled at 2 h intervals to count the number of foundresses in them. After every sampling, the OW– syconia were brushed, their wings were removed and exposed to foundresses. The same procedure was followed for *F. microcarpa* (with approximately 2000 wasps in the insect chamber) and *F. racemosa* (approximately 8000) except that the syconia were sampled every 1 h for 18 and 10 h respectively. The number of wasps entering the two sets was compared by Student's *t*-test.

In another experiment, a fresh set of 475 B-phase syconia from *F. benghalensis* was exposed to foundresses in an insect cabin. About 25 syconia were randomly sampled after 2 h to estimate the number of foundresses per syconium. The remaining syconia were divided equally into three sets, and were re-exposed to foundresses. In one set, the control group, wings were retained (OW+); in the second set, wings were removed partially (about half; OW–p) and in the third set, wings were completely removed by brushing gently (OW–) after every 2 h up to 14 h. This experiment was repeated with 400 B-phase syconia of *F. microcarpa*, brushing the syconia after every 2 h up to 10 h. The mean numbers of foundresses in the three sets were compared by *F* test using PROC GLM SAS (SAS Institute, version 9.2).

To test if wings serve as overriding cues, four sets of B-phase figs of *F. benghalensis*, namely A, B, C and D with 60 syconia in each were taken. Set A syconia were already occupied by the wasps and their ostioles were surrounded with wings. Set B was also occupied with wasps, but their ostioles were brushed to remove the wings present. In set C syconia, four pairs of wings were artificially placed around the ostiole. This was done by dissecting out the wings of wasps and placing them carefully on the ostiole using a fine insect needle with the help of stereomicroscope. Set D syconia were empty. All the sets were exposed to sufficient number of wasps for 8 h in an insect cabin. Two samplings were done at 4 h intervals. The syconia were cut open and the number of wasps in them was counted after 4 and 8 h. The different sets were compared for both 4 and 8 h; significant differences were graphically represented by diffogram using PROC GLM SAS (SAS Institute, version 9.2).

Results

Foundresses discrimination between 'occupied' and 'unoccupied' syconia

The number of pollinator wasps (foundresses) per syconium under natural conditions was determined by counting the foundresses inside C-phase syconia of five trees of each species. In *F. benghalensis*, the average number of foundresses per syconium was 8 ± 3.7 ($n = 300$). There were no significant differences among five trees for number of foundresses per syconium ($F_{4,295} = 1.02$; $P = 0.397$). Similarly, the average number of foundresses was 1.7 ± 0.90 with $F_{4,295} = 1.63$; $p = 0.168$ and 21.7 ± 6.75 with $F_{4,295} = 0.83$; $p = 0.5107$ for *F. microcarpa* and *F. racemosa* respectively (Table 1). There were no significant differences among the five trees of three species for number of foundresses per syconium.

On exposing of fresh syconia to the foundresses in the insect cabin, an average of 4.50 ± 2.39 ($n = 30$; for 2 h) foundresses entered the syconia in *F. benghalensis*, 0.6 ± 0.5 ($n = 30$; for 1 h) in *F. microcarpa* and 4.4 ± 2.1 ($n = 10$; for 1 h) in *F. racemosa*. When this 'occupied' set was further exposed to foundresses along with the 'unoccupied' syconia, the former received significantly lesser number of foundresses than the latter. In *F. benghalensis*, an average of 3.6 additional foundresses entered the 'occupied' set whereas 6.5 ± 2.5 entered the 'unoccupied' syconia during the first interval of sampling. The two sets significantly differed in the number of foundresses entering only in the initial stages. The differences between the two sets persisted up to 6 h of sampling after which, the wasps preferred both the sets equally (Figure 1 *a*). In *F. microcarpa* also, fresh syconia received more foundresses than the 'occupied' although differences were significant towards the end of the sampling period (Figure 1 *b*). In *F. racemosa*, five additional foundresses entered the 'occupied' syconia compared to 6.2 ± 2.8 into the 'unoccupied' syconia. There was no significant differences between the two sets; the wasps equally preferred both the sets (Figure 1 *c*). However, in the other two *Ficus* spp., more foundresses entered the 'unoccupied' than 'occupied' syconia initially suggesting their ability to discriminate the two sets.

Wings as cues

When wasps wriggle through the ostiole, they leave behind their wings and these wings may obviously serve as an index of the level of occupancy of the syconium. The number of wings on the ostiole and the number of foundresses entered in B-phase syconium were significantly positively correlated in *F. benghalensis* ($r = 0.955$; $p < 0.0001$; $n = 30$) and *F. microcarpa* ($r = 0.853$; $p < 0.001$; $n = 30$), but not *F. racemosa* ($r = 0.18$; $p > 0.05$; $n = 30$) in natural condition. Therefore, we summarized that the wasps may use wings left behind as cues in *F. benghalensis* and *F. microcarpa*.

In *F. benghalensis*, an average of 3.8 ± 2.7 foundresses have entered in 2 h leaving wings on the ostiole. The samples of syconia were then divided into two equal sets where wings on the ostiole were brushed in set OW–, and wings were retained in another set OW+ syconia. The number of foundresses entering 'occupied' syconia on which wings were retained (OW+) stabilized at a very early stage but foundresses continued to enter syconia from which wings were brushed away (OW–) in all the sampling intervals. Consequently in *F. benghalensis*, the number of foundresses that entered syconia was significantly higher from second sampling itself (t_{28} = 2.16; p = 0.0362). After every brushing, the average number of foundresses entering 'OW–' syconia was significantly higher than that of 'OW+' syconia (Figure 2 *a* and *b*).

Similarly in *F. microcarpa*, an average of 0.5 ± 0.8 foundresses had entered in 1 h leaving wings on the ostiole. The samples of syconia were then divided into 'OW+' and 'OW–'sets. The mean of foundresses in OW+ set was 1.30 ± 0.75 and that of 'OW–' syconia was 2.5 ± 1.04 at fourth hour. These differences in means were found significant when Student's t test was conducted (t_{28} = 4.98; p = 0.0001; n = 30). Further, the additional number of foundresses entering the OW– set after every brushing was significantly higher than the 'OW+' syconia (Figure 3 *a* and *b*).

However in *F. racemosa*, the two sets did not differ throughout the sampling period despite the fact that the wings left on the ostiole were brushed continuously. In fact, after 5–6 h, in both the sets, the number of foundresses entering syconia reached a plateau at around 14–16 (Figure 4 *a* and *b*).

Thus, pollinators of the two species, *F. benghalensis* and *F. microcarpa*, seem to assess the foundress loads in their respective host syconia on the basis of wings left behind at and around the ostiole; but the pollinators of *F. racemosa* do not seem capable of doing so. However, there was no critical discrimination between the two sets in the initial hours as represented by overlapping error bars (Figures 2 *a*, 3 *a* and 4 *a*). In later hours, the discrimination was more critical in both the species.

Assessing wasp loads in syconia

In both *F. benghalensis* and *F. microcarpa*, the number of wasps entering syconia was found to be influenced by the density of wings on and around the ostiole. Syconia

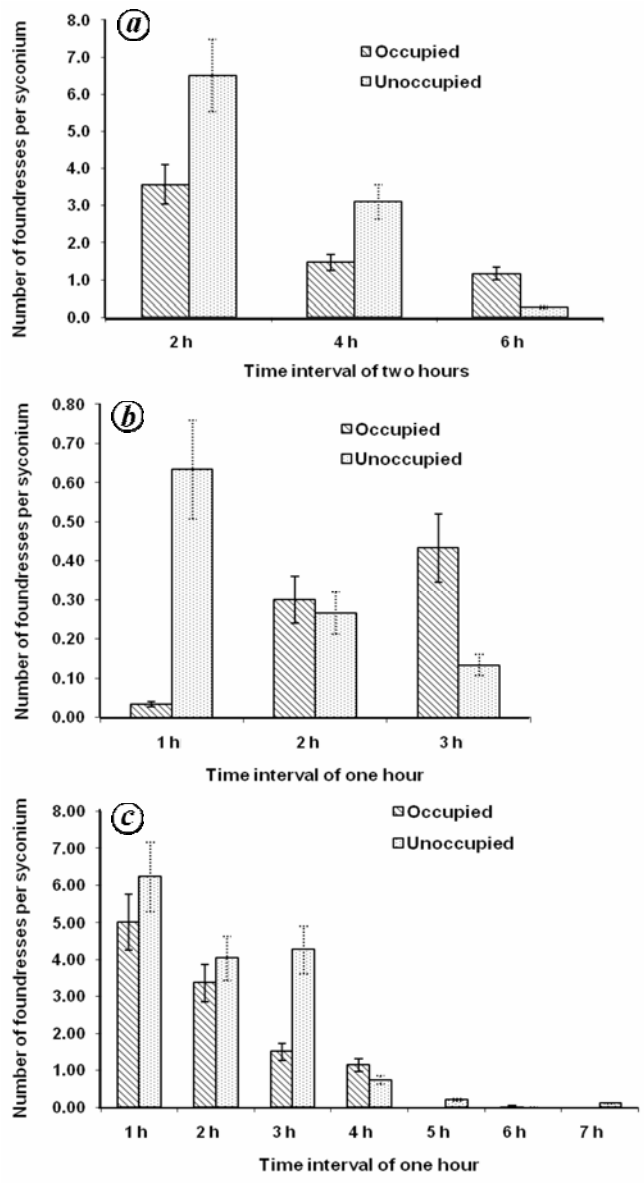

Figure 1. Average number of foundresses per syconium in 'occupied' and 'unoccupied' sets entering afresh at different time intervals. ***a***, *F. benghalensis*, Sample size (n) = 30; ***b***, *F. microcarpa*, n = 30; ***c***, *F. racemosa*, n = 10.

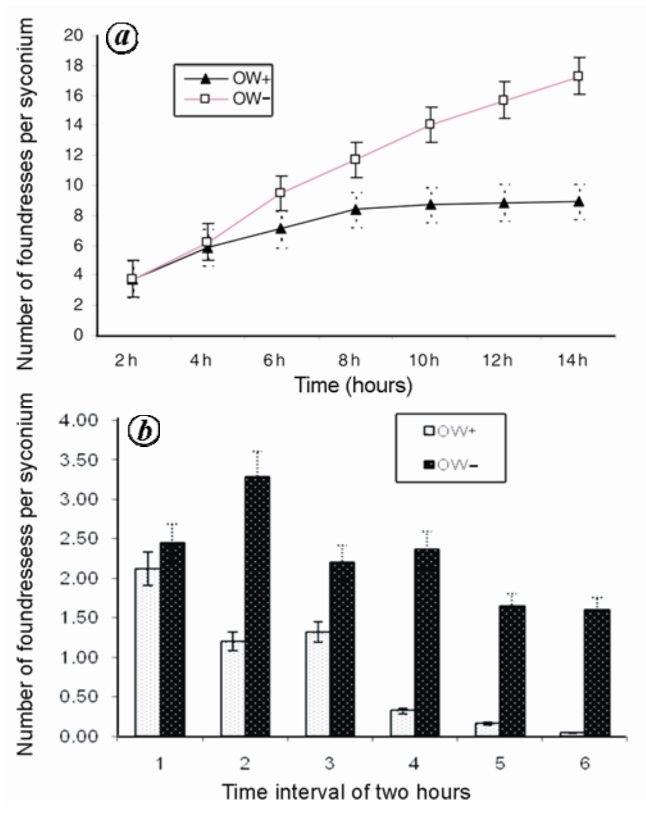

Figure 2. Number of foundresses in 'wings retained' (OW+; solid triangles) and 'wings removed' (OW–; open squares) syconia in *F. benghalensis* with sample size (n) = 25. ***a***, Average number of foundresses per syconium at every 2 h time interval. ***b***, Number of pollinators entering afresh in 'wings retained' (OW+; dotted bar) and 'wings removed' (OW–; shaded and dotted bar) after brushing the ostiole at every interval.

from which wings were completely removed (OW–) continued to receive more foundresses for a longer period of time and hence eventually had more foundress loads than those from which wings were partially removed (OW–p). In *F. benghalensis*, wasp loads were stabilized at around eight in the control group (OW+); whereas in partially (OW–p) and completely removed (OW–) syconia, foundresses continued to enter even up to 14 h when the wasp loads were 10 and 12 respectively (Figure 5). The three sets differed significantly for mean number of foundresses after 10 h ($F_{2,72} = 6.85$, $p = 0.0019$). In *F. microcarpa*, the number of wasps entering OW– and OW–p was significantly higher than OW+ at every brushing. But the entry got stabilized after the eighth hour in all the three sets with different wasps loads (Figure 6). The three sets differed significantly after 4 h ($F_{2,72} = 3.21$, $p = 0.046$).

Wings as overriding cues

Exposure of 90 syconia for 2 h resulted in an average of 3.6 ± 1.6 ($n = 30$) foundresses per syconium. The remaining syconia were divided into two sets, set A and set B. At the fourth hour in set A, when the syconia were occupied and wings were present on the ostiole, an average of 6.2 ± 3.2 wasps was found; whereas in set B (occupied; wings removed) 9.8 ± 3.8 wasps had entered. In contrast, set C (unoccupied syconia on which wings were artificially placed) received 2.6 ± 2.25 wasps. Set D (unoccupied syconia without any wings on the ostiole) received 8.5 ± 3.01 wasps after 4 h of exposure (Figure 7). The sets differed significantly for number of foundresses per syconium (ANOVA $F_{3,116} = 30.52$; $p < 0.0001$). Set D received maximum number of foundresses as it was unoccupied and free from wings but set B was already occupied by an average of 3.6 wasps and received an additional 6.2. Sets B and D were not significantly different because the wasps entered syconia in which wings were not present. However, the other sets differed significantly from each other which is presented in the diffograms (Figure 8 *a*).

Similarly, after 8 h different loads of foundresses entered the four sets. After the second sampling at eighth hour there were 4.9 additional wasps in set A, 6 in set B, 5 wasps in set C and 3.7 in set D (Figure 7). The ostiole of set B was brushed during the first sampling after 4 h. Set B received more number of foundresses compared to other sets, indicating that foundresses preferred to enter the syconia on which wings were absent. Sets B and C were not significantly different as the wasp load and

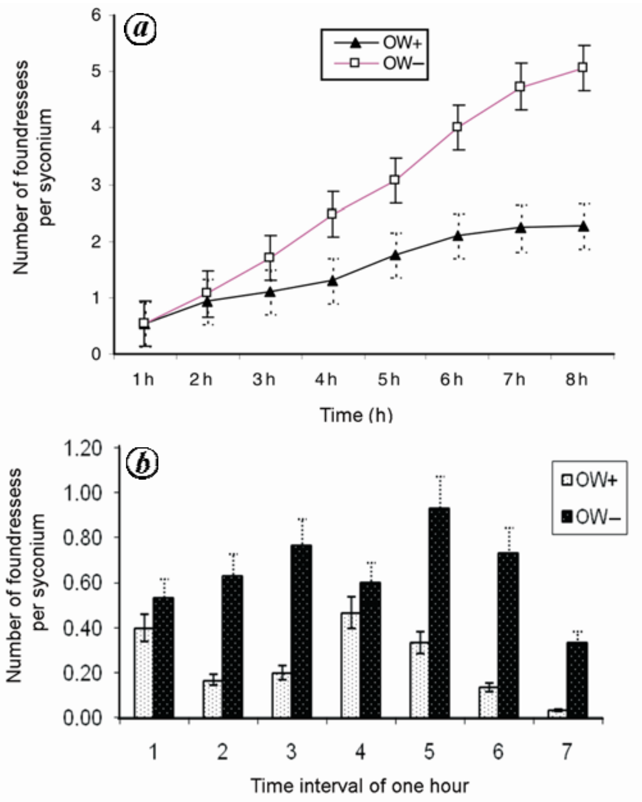

Figure 3. Number of foundresses in 'wings retained' (OW+; solid triangles) and 'wings removed' (OW–; open squares) syconia in *F. microcarpa* with sample size (n) = 30. ***a***, Average number of foundresses per syconium at every 1 h time interval. ***b***, Number of pollinators entering afresh in 'wings retained' (OW+; dotted bar) and 'wings removed' (OW–; shaded and dotted bar) after brushing the ostiole at every interval.

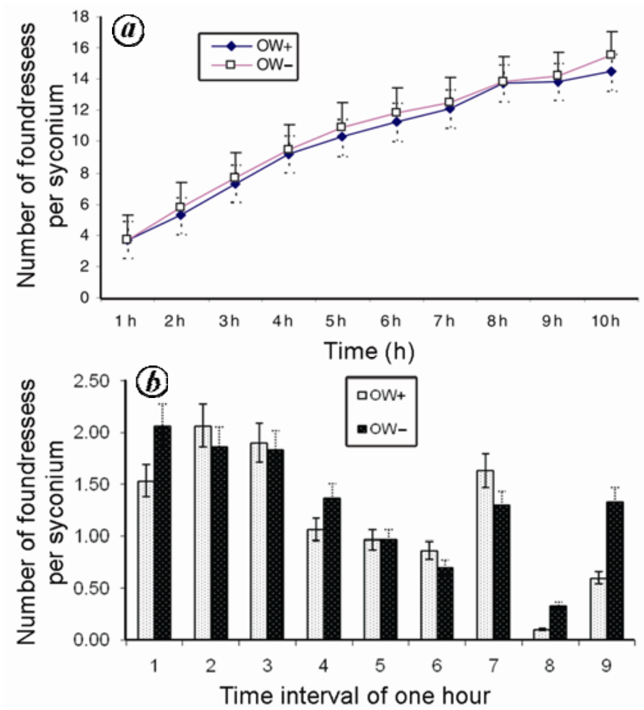

Figure 4. Number of foundresses in 'wings retained' (OW+; solid triangles) and 'wings removed' (OW–; open squares) syconia in *F. racemosa* with sample size (n) = 30. ***a***, Average number of foundresses per syconium at every 1 h time interval. ***b***, Number of pollinators entering afresh in 'wings retained' (OW+; dotted bar) and 'wings removed' (OW–; shaded and dotted bar) after brushing the ostiole at every interval.

wings on the syconia of sets C were relatively low compared to set A and set D (Figure 8 *b*).

Discussion

The results show that 'unoccupied' syconia received significantly more foundress wasps than the 'occupied' syconia in all the three species. Even in *F. microcarpa*, where the number of foundresses entering the syconia plateaus off at around 1 or 2, its pollinator distinctly exhibited this ability. Thus fig pollinators appear capable of discriminating fresh or 'unoccupied' syconia from the 'occupied'. This discrimination was strong at early hours, persisted for sometime through the experiment but the number of additional foundresses entering syconia of both the sets continued to decrease as both sets eventually became 'occupied'. At this stage, wasps did not discriminate the two sets probably because it is not profitable any longer to choose among the syconia than to simply enter any syconium they encounter; time spent in choosing would increase the risk of their reproductive failure[1,13] and also decrease receptivity in figs in later stages[14,15].

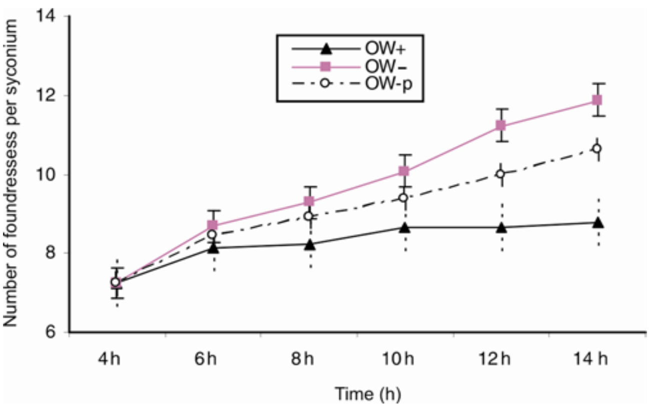

Figure 5. Number of foundresses entering the syconium with wings completely removed (OW–; shaded squares), wings retained (OW+; shaded triangles) and wings partially removed (OW–p; open circles) in *F. benghalensis*, Sample size (*n*) = 25.

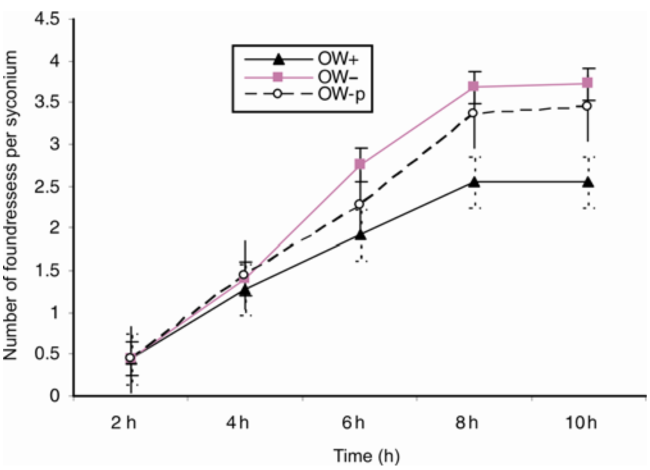

Figure 6. Number of foundresses entering the syconium with wings completely removed (OW–; shaded squares), wings retained (OW+; shaded triangles) and wings partially removed (OW–p; open circles) in *F. microcarpa*, Sample size (*n*) = 25.

As pollinators enter the syconium, wings are left behind in, on and around the ostiole and these remnants are suggested to serve as indicators[12] or negative feedback regulators for wasps outside the syconium. The remnant wings on the ostiole and number of foundresses in the syconium was significantly correlated in *F. benghalensis* and *F. microcarpa* but not so in *F. racemosa*. Thus, the wings can be expected to serve as indicators of foundress wasp loads in syconia only in the former two fig species but not in the latter. This was also borne out by our results. Syconia free from remnant wings received more wasps than those that had them in *F. benghalensis* and *F. microcarpa*, but not in *F. racemosa*. It has been suggested that pollinators locate trees with B-phase figs from a distance, based on the volatile compounds emitted by receptive figs[16].

However, their ability to find receptive figs and their decision on whether to enter the syconia or not is based on the details they gather at a close range of the syconia[17]. Our results suggest that in some species, foundress wasps use the wings on the ostiole as an important cue to assess the resource quality of the syconium. Discrimination during initial hours is less critical in both the species owing to density of wings on the ostiole, which could merely serve as physical barriers.

In fact, pollinators also exhibited their ability to quantitatively assess the foundresses load in the syconium based on the number of wings left on and around the ostiole. The number of pollinators entering the syconia was found

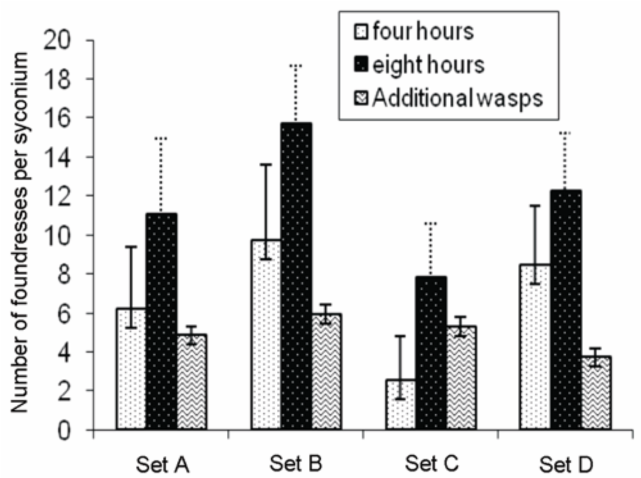

Figure 7. Number of foundresses entering different sets of *F. benghalensis* into set A (occupied, wings removed), set B (occupied, wings retained), set C (unoccupied, wings artificially placed on the ostiole) and set D (unoccupied syconia) at 4 h and 8 h sampling with *n* = 30. The wasps entering during the interval of 4 h between fourth and eight hour are presented in bars with zigzag lines.

to be a function of the density of wings at and around the ostiole; syconia from which wings were completely brushed away and hence appeared as good resource patches, received more pollinator wasps than those on which a proportion of wings was retained; control set of syconia where wings were completely retained received the least number of wasps. Thus, pollinators of *F. benghalensis* and *F. microcarpa* choose to enter those syconia in which they can avoid overcrowding of egg layers (and pollinators).

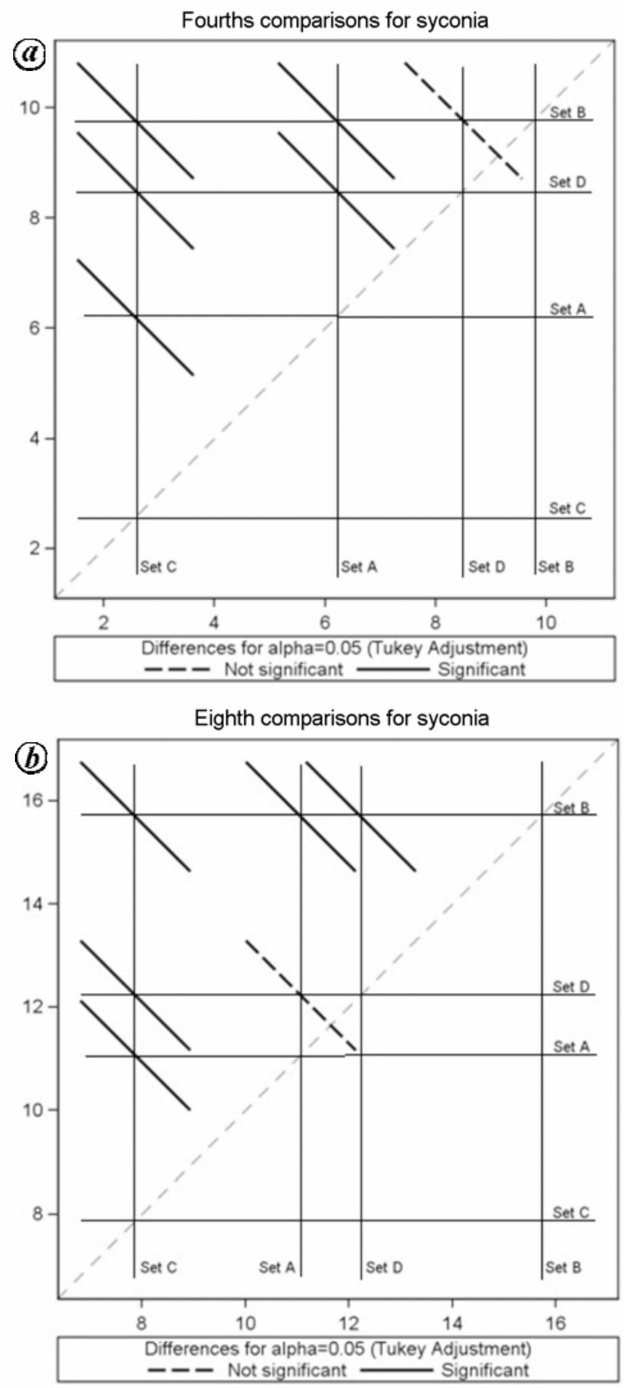

Figure 8. Diffograms showing significant differences among the sets A, B, C and D at (***a***) 4 h; (***b***) 8 h. Bold horizontal and vertical lines represent the four sets. The small lines passing through the squares diagonally represent nonsignificant or significant differences between the two corresponding sets.

It is not clear whether the feature of leaving behind the wings at and around the ostiole is an evolved adaptive trait or a mere consequence of weak wings. However, it may be in the interest of the wasp pollinators in general to have developed this behaviour because it serves as a negative feedback regulator for the foundress wasps arriving late such that those that have entered also reduce the competition for resources. However, it is shown that there is no special slit on wings[18] that facilitates this; perhaps it is likely that wings are broken up naturally, when they wriggle into the syconium. The wasps have selected this process for making decisions about entering the syconium.

We attempted to artificially place the wings around the ostiole without damaging the syconium. The pollinators choose to avoid entering these syconia and opted to enter unoccupied syconia and syconia on which wings were removed. This clearly shows that at initial entry, pollinators are capable of selecting the best place for egg laying. Thus, wings on the ostiole play a major role as physical barrier or an active clue for the pollinators entering the syconia.

In *F. racemosa*, pollinators do not use wings on the ostiole as cues for discriminating the syconium. The cues used by these pollinators are still unknown although the latex exuded at the ostiole as the wasps wriggle through the syconium may serve as a physical hurdle for further entry of wasps[5]. Chemical signals and floral scent could serve as cues to locate the host plants in *F. racemosa* by its pollinating and also non-pollinating wasps[19].

It may be argued that the wings serve more as physical barriers than as cues for the newly entering foundress wasps. Although both the mechanisms serve the purpose of controlling indiscriminate entry of wasps into syconia, we tested these two possibilities by artificially placing the wings around the ostiole so that they do not serve as physical barriers to the entry of foundress wasps. The number of foundress wasps entering the syconia without wings was significantly higher than that entering syconia with artificially placed wings and occupied wings retained. This was true for both the ‘unoccupied’ and ‘occupied but wings removed’ sets. Thus wings serve as an index rather than as a hurdle for the foundress wasps to assess the loads inside the syconia. The number of foundresses entering syconium (unmanipulated) reaches a plateau and this corresponds to wasp loads in the natural conditions. Incidentally, wasps seem capable of quantitatively assessing the loads of syconia before this limit is reached. It is tempting to hypothesize that wasps have evolved to assess the wasp loads in the syconia until an optima is reached. Studies at our laboratory have shown that the predicted optima of pollinators is at or slightly lesser than average loads in the natural conditions. Thus, it appears that discriminating ability of pollinator wasps disappears once the syconia have received more foundress wasps than the optima of pollinators.

Conclusion

The fig–wasp mutualism, resolving the conflict between the partners is studied differently by different groups. Our study in the first of its kind and includes laboratory techniques to study the entry behaviour of foundresses into the syconium. As it is difficult to study this behavioural regulation in natural condition, we attempted to develop various laboratory experiments. Although many studies have indicated that the foundresses are attracted by the chemical cues of the figs while selecting the fig species, very few studies have been attempted to know whether wasps can distinguish the different syconia within an individual fig tree to overcome the competition among foundresses and to get distributed within the resource patches. In this study, the foundresses are capable of discriminating between the fresh syconium versus the syconium in which wasps are already present. There could be different factors by which wasps can discriminate. One such factor studied was wings on the ostiole. The foundresses exhibited the capacity to quantify the wing load on the ostiole. When syconia without wings on the ostiole were available, the wasps avoided entering the ones on which wings were present. This clearly shows that the foundresses distribute themselves within the fig tree to avoid competition and interference to maintain the balance of mutualism.

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