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POLLINATOR AND NON-POLLINATOR FIG WASP RELATIONSHIP IN SYCONIA OF *FICUS EXASPERATA*

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ABSTRACT

Ficus species are pollinated only by species specific wasps of the subfamily Agaoninae (Hymenoptera: Agaonidae). Hence, figs have an intimate relationship with its pollinating fig wasps that oviposit within fig ovaries and the resulting larvae feed on the developing seeds. Figs are also associated with non-pollinator wasps of the family Agaonidae that either oviposit within fig ovaries thereby resulting in galls, or parasitize the larvae of pollinator wasps thereby affecting the fig-pollinator relationship. The present study identifies the fig wasps associated with the dioecious fig, *Ficus exasperata*, a common fig in Sri Lanka and investigates the relationship between the pollinator and non-pollinator wasps. During the fig off season in December 2007, 50 syconia collected from a single hermaphroditic tree of *F. exasperata* located in the Peradeniya University Park were subjected to this study. From these figs emerged the pollinator wasp *Karadibia gestroi* and the non-pollinator parasitoid wasp *Philotrypesis quadrisetosa*. Emergent pollinator fig wasps were the most abundant with a mean of 213.50 wasps per fig in comparison to the non-pollinator parasitoid wasps that ranged from 0-67 per fig. There was no significant relationship (r = -0.168) between the numbers of pollinator and non-pollinator wasps that emerged from a fig. The sex ratio of the pollinator wasp, *K. gestroi* that emerged from figs was strongly female biased (0.20) inferring that the offsprings are from a single or few mothers.

Keywords: dioecious fig, syconia, parasitoid, parasitism

INTRODUCTION

The genus *Ficus* (Moraceae) comprises about 900 fig species (Janzen, 1979) of which 750 species (Berg, 1989) constitute the most distinctive of the wide spread genera of tropical plants. Figs produce a characteristic inverted inflorescence termed syconium bearing many flowers around a centrally hollow sphere. The syconium opens to the outside through a tiny opening termed the ostiole. Half the number of *Ficus* species in the world is monoecious and the others are termed gynodioecious. All of gynodioecious *Ficus* species are Old World species (Janzen, 1979). Monoecious figs have both male and female flowers within the same syconium. In gynodioecious figs each species produces two types of trees: hermaphroditic and female trees. The hermaphroditic trees produce syconia that contain both male and female flowers while female trees produce syconia with only female flowers having comparatively long styles.

Wasps (Hymenoptera: Agaonidae: Agaoninae) that pollinate figs have an intimate relationship with fig trees. Each species of fig is known to have its species specific wasp species. Pollen bearing female fig wasps enter a receptive fig syconium through the ostiole and pollinate the female flowers while moving inside searching for fig ovaries in which to lay eggs. Female fig wasps lay a single egg in each of the many fig ovaries. In *Ficus exasperata* which is an actively pollinated fig, at each time a female fig wasp enters a fig to lay eggs, it also discharges some pollen grains stored in its mesothoracic pollen pockets, with the help of its fore legs (Frank, 1984). Females die inside the syconium after oviposition. The fig wasp larvae that hatch from the eggs develop inside, and feed on the developing fig seed. On completion of development, male fig wasps are the first to emerge and they are wingless. These males mate with female wasps which are still inside the fig ovaries. During this stage male flowers in the syconium dehisce releasing pollen. In *Ficus exasperata*, the newly emerged pollinator females collect pollen with their forelegs and pack it into the mesothoracic pollen pockets with the help of their fore coxae (Kjellberg *et. al*,. 2001). The mated females that emerge from the ovaries get packed with pollen (Galil and Eisikowitch, 1969; Ramirez, 1969)

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and come out of the syconium through holes cut by the males that emerge first but die inside the natal syconium. The pollen bearing female fig wasps that come out of the syconium disperse in search of new receptive fig trees of the same species to continue their life cycle.

Gynodioecious fig species have both hermaphroditic trees and female trees. In the hermaphroditic trees (termed gall figs) male flowers in the syconia produce pollen, while in their female flowers, pollinator wasps develop following oviposition. In the female trees, the female fig wasps that enter a syconium fail to lay eggs within the ovaries of female flowers as their long styles make the ovaries inaccessible to the wasps (Janzen, 1979; Weiblen, 2002). Therefore, female trees produce only seeds hence are termed seed figs. Female fig wasps searching for figs to oviposit cannot discriminate between the two types of trees (gall figs and seed figs) before entering the "tomb blossom" (Patel *et. al.,* 1995; Anstett *et. al*., 1998). However, the seed figs benefit by being pollinated by the pollen bearing female wasps. Much attention has been paid to this species-specific fig–fig wasp interaction considering it a remarkable example of co-evolution (Kjellberg *et. al.,* 1987; Lachaise 1994).

Sex ratios of pollinator wasps are important in predicting local mate competition within figs. This has largely been studied using monoecious fig species where both male and female flowers occur in the same syconium. In haplodiploid inbreeding systems daughters are considered to be genetically more valuable to their mothers than sons (Hamilton, 1967) driving mothers to produce more daughters than sons. Mating in fig wasps is not panmictic (not random-mating), but takes place within a fig where brothers compete with each other to mate with their sisters. As a result mothers tend to invest more in daughters and less in sons to obtain more daughters to mate with (Taylor, 1981) her sons which takes place within the fig. This is referred to as local mate competition (LMC) (Hamilton, 1967). The extent of LMC among brothers depends on how many mothers lay eggs within a particular fig. The sex ratio becomes more female biased as inbreeding and the LMC increases (Herre, 1985). As the number of ovipositing mothers increases, LMC decreases resulting in less female biased sex ratios (Frank, 1985). Sex ratios of monoecious fig pollinators with one or two foundresses are female biased rarely rising above 0.30 (Patel, 1998). In dioecious figs, pollinator sex ratios are known to range between 0.20 and 0.28 (Abdurahiman and Joseph, 1976; Nair and Abdurahiman 1984; Godfray, 1988).

In every fig species several other wasp species termed non-pollinating wasps (Hymenoptera: Agaonidae) also lay eggs and develop within ovaries of the syconium. These wasps belong to the subfamilies Epichrysomallinae, Otitesellinae, Sycoecinae, Sycophaginae, Sycoryctinae, Eurytomidae, Torymidae, Braconidae, Orymidae and Pteromalidae (Weiblen, 2002). Non-pollinating fig wasps representing the first five subfamilies have been recorded from many species of figs distributed in Kerala, India (Priyadarsanan, 2000). These non-pollinating wasps are also specific to a particular fig species (Bronstein, 1991). Non-pollinator fig wasps also oviposit in fig ovaries and may also lay eggs in ovaries already oviposited by a pollinator wasps. Its larvae feed on the pollinator wasp larva while developing inside the ovaries and hence are known as parasitoids. Other non pollinator wasp species may lay eggs in ovaries not oviposited by pollinator fig wasps. Such ovaries develop into galls and hence the wasps are termed gall formers. Thus non-pollinator fig wasps reduce the number of pollinator wasps produced in a syconium through direct parasitism, or by competition for oviposition sites, and thereby affect pollen dispersal (Kuttamathiathu, 1959; Compton *et. al.,* 1994; West and Herre, 1994; West *et. al.,* 1996). These non-pollinator fig wasps thus may affect the mutualistic relationship between the pollinator fig wasps and the fig tree, if a large number of non-pollinator wasps are produced per syconium in comparison to pollinator fig wasps. Studies reveal that dioecy in figs has reduced the level of parasitism through which both the pollinator and its host benefit (Kerdelhue and Rasplus, 1996; Patel, 1998).

The objectives of the present study were to (i) identify the pollinator and non-pollinator wasps in a hermaphroditic tree of the dioecious fig, *Ficus exasperata*, (ii) investigate whether there is a relationship between the number of pollinator wasps and non-pollinator wasps produced per syconium and to (iii) determine whether the sex ratio of pollinator wasps is highly female biased. The fig species, *Ficus exasperata* (S: Bu-thediya, Sewan-Mediya) selected for the study is a very common native tree in lowlands (up to 1000 m) of Sri Lanka. It also occurs in East Africa, Arabia and Central

and South India. It is a medium size deciduous tree with stout hairy leaves. The tree produces solitary hairy figs that turn yellow on ripening (Dassanayake and Fosberg, 1981). This fig species which is actively pollinated (Kjellberg *et. al.*, 2001) by its pollinator fig wasps has been studied in India by Patel (1998) and Priyadarsanan (2000).

MATERIALS AND METHODS

This preliminary study was carried out during December, 2007 which is considered the off season for figs in its range of distribution. A hermaphroditic tree of *Ficus exasperata* (Plate 1) in fruit, located in the University of Peradeniya was selected as the study tree to obtain syconia. Fifty syconia that were soft and with no exit holes were plucked randomly from the tree on 3 consecutive days. In the laboratory, syconia were placed separately in plastic cups and covered with a piece of fine mesh cloth to collect any emerging wasps. Wasps that emerged from individual figs were separately preserved in 70% alcohol. Wasps were separated as pollinators and non-pollinators based on the length of the ovipositor and the characteristics of the mandibles. Thereafter, they were sexed and counted. Pollinator fig wasps were identified using keys and descriptions of Wiebes (1994) and the non-pollinator fig wasps using Priyadarsanan (2000). Data on the pollinator and non-pollinator wasp species that emerged from the 50 syconia were analyzed using MINITAB (Version 14).

Plate 1. *Ficus exasperata*, branch of a hermaphroditic tree showing hairy leaves.

RESULTS

Two species of wasps emerged from the field collected figs of *F. exasperata* held in the laboratory. The pollinator fig wasp was identified as *Karadibia gestroi* (Grandi, 1916) (Agaoninae) (Plate 2) and the non-pollinator fig wasp as *Philotrypesis quadrisetosa* (Westwood, 1883) (Sycorictinae) (Plate 3). In the field on close observation, the non-pollinator female wasps were seen to insert their ovipositor through the wall of the syconia (Plate 4).

Plate 2. Female pollinator wasp, *Karadibia gestroi.*

Plate 3. Female non-pollinator wasp, *Philotrypesis quadrisetosa.*

Plate 4. Non-pollinator wasp, *Philotrypesis quadrisetosa* inserting the ovipositor through the fig wall.

The number of pollinator fig wasps that emerged per syconium ranged from 42 - 413 individuals with a mean of 213.50 (n=50) (Table 1). The number of non-pollinator fig wasps that emerged per syconium gave a mean of 22.76 individuals and ranged from 0-69 (*n*=36). Non-pollinator wasps did not emerge from 14 (8%) of the collected figs. The sex ratio of pollinator wasps that emerged from 50 syconia was 0.20 (2160/10673) and that of the non-pollinator wasps that emerged from 36 syconia was 0.39 (445/1138) (Table 1).

The number of pollinator wasps that emerged per fig gave a normal distribution (Fig. 1a). In contrast, the non-pollinator wasps showed a distribution skewed to the left (Fig. 1b), where 40% of the figs yielded less than 10 non-pollinator wasps per fig and 14 of the figs (8 %) did not yield any non-pollinator wasps. However, during field observations non-pollinator wasps were seen exploring almost all the mature syconia in the selected tree, and at a given time more than five individuals were present on a syconium (Plate 4).

There was no significant relationship (Pearson Correlation coefficient r = -0.168, P = 0.245) between the total number of pollinator wasps and non-pollinator parasitoid wasps that emerged per fig of *F. exasperata* (Fig. 2).

Table 1. Descriptive statistics of pollinator and non-pollinator fig wasps that emerged from syconia of *Ficus exasperata*.

	Mean (Wasps per fig)	S.E.M.	Range	Sex ratio (male/total)	Sample size (*n*=50)
Pollinator wasp - *K. gestroi*	213.50	11.40	42 - 413	0.20	(*n* = 50)
Non-pollinator wasp - (Parasitoid) *P. quadrisetosa*	22.76	2.85	0 - 69	0.39	(*n* = 36)

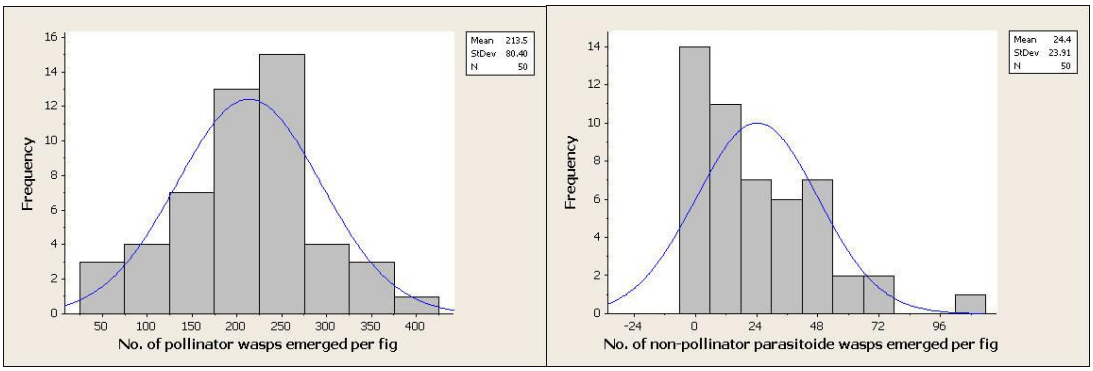

Figure 1. Distribution of (a) pollinator and (b) parasitoid wasps emerged per syconium.

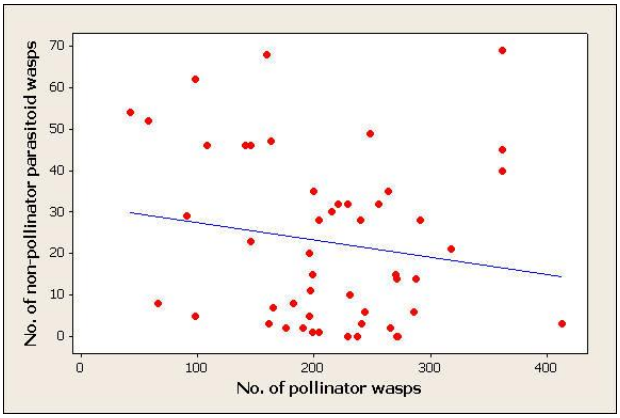

Figure 2. Relationship between the number of pollinator wasps and non-pollinator parasitoid wasps produced per fig.

DISCUSSION

The pollinator wasp, *Karadibia gestroi* recorded during this study was first described from *Ficus exasperata* in Africa in 1916. This is the first record of the genus *Karadibia* and of the species *K. gestroi* in Sri Lanka. This genus exclusively includes pollinators of figs in the old world.

The non-pollinator, parasitoid fig wasp, *Philotrypesis quadrisetosa* recorded during the study had been reported from Sri Lanka in 1883 (Westwood, 1883) from *Ficus exasperata*. Thus, although the non-pollinator parasitoid wasp has been recorded from Sri Lanka previously, its host and the pollinator wasp, *Karadibia gestroi* had not been reported previously from Sri Lanka (fig-web-http://www.figweb.org). Through this study, the relationship between the fig tree species and its pollinator wasp and non-pollinator parasitoid wasp and its host, the pollinator fig wasp has been established for Sri Lanka.

A similar study on fig pollinators of *Ficus exaperata* conducted in Western Ghats, India by Patel (1998) recorded *Sycoscapter longipalpus* (Joseph, 1953) (Agaonidae: Sycoryctinae) as yet another wasp that develop in the syconia. It has been established as another non-pollinator parasitoid of the pollinator wasp, *K gestroi* of *Ficus exasperata*. Priyadarsanan (2000) working on the same fig species in Kerala, India has identified yet another fig wasp species *Sycoscapteridea longipalpus* Joseph, 1956 (Agaonidae: Sycoryctinae). However, this wasp species is now considered a synonym of *Sycoscapter longipalpus* (Universal Chalcidoidea Database - http://www.nhm.ac.uk/jdsml/research-curation/research/projects/chalcidoids). Thus, presence of two non-pollinator parasitoid fig wasp species, *P. quadrisetosa* and *S. longipalpus* has been established in India for *F. exasperata*. Hence, it is likely that the latter species also occurs in Sri Lanka. The failure to record this species during the present study may be due to the off season effect on fig production. Therefore, studies are being continued into the fig season (January- August) to check for the presence of any other wasp species associated with *F. exasperata*. However, initial observations made during the fig season in early 2009 yielded only the same non-pollinator wasp species. The non-pollinator parasitoid wasp was found to have a low prevalence in comparison to the pollinator wasp. According to the study carried out by Patel (1998) in Western Ghats, India, of the two parasitoid wasps that emerged the number of *P. quadrisetosa* that emerged per syconium ranged from 0-19 (with a mean of 2±) wasps (n=37) and that of *S. longipalpus* ranged from 0-20 (with a mean of 3±) wasps (n=43). The failure to record *S. longipalpus* from *F. exasperata* syconia is difficult to explain. In the present study as only limited number of syconia were examined (n=50), it is likely that a larger sample may yield *S. longipalpus* or perhaps this species is not present in Sri Lanka. Further work covering the distribution range of *Ficus exasperata* may shed light as to the presence of this species and any other in Sri Lanka.

The female biased sex ratio of 0.20 of the pollinator wasp of the fig *F. exasperata* recorded during the study agrees with the pollinator sex ratios for other species of dioecious figs in the world. A study conducted in Western Ghats, India (Patel, 1998) during the peak fig production season has recorded a slightly higher sex ratio of 0.16 for the pollinator of *Ficus exasperata*, which is female biased, than recorded during the present study. The female biased sex ratio of the pollinator wasp in the study system suggests that the offspring produced in a syconium of *Ficus exasperata* may be from only one or two foundress (egg laying) females that has also been observed by Patel (1998).

The pollinator wasps that emerged per fig showed a normal distribution inferring that the natural populations of the pollinator wasp are also normally distributed. However, the distribution of non-pollinator parasitoid wasps that emerged per fig was skewed to the left inferring that there are more un-parasitized and less parasitized figs in the sample. This may result from the low abundance and patchy distribution of the parasitoid or due to the difficulty in locating syconia that contain pollinator eggs in the fig ovaries. It may also be a result of the parasitoid avoiding syconia already oviposited. Yet another likely reason for the low incidence of parasitism in *F. exasperata* is the presence of fewer ovary layers in dioecious figs compared to monoecious figs as documented by Kerdelhue and Rasplus (1996). Furthermore, female trees of dioecious fig species bearing flowers with long styles are similarly visited by non-pollinator wasps, thus wasting their time and energy in search of oviposition sites (Weiblen *et al.*, 2001).

The study reveals that there is no significant relationship between the pollinator and non-pollinator parasitoid wasps produced per syconium, even though each parasitoid wasp emerges at the expense of a pollinator larva, during its development. The non-pollinator parasitoid wasp could affect the pollinator wasps by destroying the larvae of the fig pollinator wasp through parasitism. However, the low abundance of non-pollinator parasitoid wasps per fig in comparison to the fig pollinator wasp as reported in this study suggest that the pollinator-non pollinator relationship is not significantly affecting the relationship between the pollinator and the *Ficus* tree. Thus, the relationship of the fig tree and its pollinator and the non pollinator parasitoid wasp have evolved with the least detrimental effect to this system. Reduction of parasitism through dioecy is advantageous to the pollinator fig wasps and as well as to the fig tree, particularly during the off season when the production of syconia is low.

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