Confirmation of the parasitoid feeding habit in *Sycoscapter*, and their impact on pollinator abundance in *Ficus formosana*

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Abstract

Blastophaga taiwanensis Chen & Chou (Chalcidoidea: Agaonidae) is the pollinator of *Ficus formosana* Maxim. (Moraceae) at the Guandaushi Forest Station, Taiwan. It co-exists with two non-pollinating species of *Sycoscapter* Saunders (Chalcidoidea: Pteromalidae). This study of the ecology of two *Sycoscapter* species provides the first evidence of their parasitoid role and also demonstrates their impact on abundance of *B. tawanensis* in *F. formosana* in relation to season. Females of the two *Sycoscapter* species are differentiated by their different ovipositor lengths. The species with the longer ovipositor was more abundant overall, but less so than the species with the shorter ovipositor in the winter crop. There was no obvious difference in the timing of oviposition between the two species, with females of both species appearing on male syconia 1–6 weeks after pollination. Females oviposited externally and their larvae fed on the *B. tawanensis* larvae. The two *Sycoscapter* species reduced the abundance of *B. tawanensis* larvae by 62% within parasitized syconia, and by 54% for all syconia. There was a seasonal variation both in the abundance of wasps and in correlation relationships between pollinators and parasitoids, i.e. parasitoid proportions were much higher and the correlations were mainly significant in the winter and spring crops. We suggest the pollinator and the fig exerts two levels of control on the rate of parasitism by *Sycoscapter*, and this may help to maintain a balanced symbiotic relationship between the three organisms.

Keywords: *Ficus formosana*, *Blastophasga taiwanensis*, *Sycoscapter*, parasitoid, mutualism, Guandaushi Forest Station

1. Introduction

There are more than 750 fig species (*Ficus*, Moraceae) globally (Berg, 1989), each of which is pollinated by highly specific fig wasp species (Agaonidae, Agaoninae) (Wiebes, 1979). *Ficus* and their pollinating fig wasp present a striking example of mutualism. The fig provides habitat (galls) for the wasps' offspring to develop, whereas the agaonine wasps provide a pollination service for the fig. Figs are also exploited by a large community of chalcidoid wasps that develop within the syconia but do not transfer

pollen (Compton et al., 1994; Weiblen et al., 2001, but see Jousselin et al., 2001). Non-pollinating wasps can be roughly divided into two groups (Kerdelhué and Rasplus, 1996b). Some are gall-makers, who either enter the fig cavity at the same time as the pollinator or oviposit through the syconium wall, whereas others are inquilines or parasitoids of gall making wasps and always oviposit through the syconium wall. In contrast to the pollinators, the taxonomy and life history of the non-pollinators is very poorly known. Parasitoids or inquilines, are usually identified based on negative correlations between pollinator and non-pollinator abundances (Chen, 1994; Compton et al., 1994; Weiblen et al., 2001; Peng et al., 2005).

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The monophyly and subfamilial classification of the Agaonidae remains controversial. Bouček (1988) classified Agaoninae and five other subfamilies, of which Sycoryctinae was one, of non-pollinating wasps in the Agaonidae. However, based on molecular evidence, Rasplus et al. (1998) classified Sycoryctinae in Pteromalidae and restricted Agaonidae to the pollinating fig wasps, i.e., Agaoninae.

Species of *Sycoscapter* Saunders (Pteromalidae, Sycoryctinae) oviposit from outside the syconium, and have previously been considered to be parasitoids or inquilines (Chen, 1994; Compton et al., 1994; Kerdelhué and Rasplus, 1996a; Weiblen et al., 2001). However, there is no direct evidence of their larval feeding habits.

Ficus formosana Maxim. (section *Ficus*) is a functionally dioecious, small evergreen to semi-deciduous understory shrub, 0.5–3 m in height (Tzeng, 2004). Both genders of fig trees produce one to three crops annually. Post-pollination development of figs is significantly longer in winter than in summer (Tzeng et al., 2005b). The syconia production of female trees is earlier than male trees and show a greater seasonality (Tzeng et al., 2005a, b). *Ficus formosana* is pollinated by *Blastophaga taiwanensis* Chen & Chou (Agaonidae) (Chen and Chou, 1997; Tseng, 1999), and two unidentified species of *Sycoscapter* are associated with the syconia (personal communication with Dr. Rasplus, with the voucher specimens deposited at his laboratory). The aim of the present study was to confirm the role of the *Sycoscapter* species as parasitoids or inquilines, and to assess their impact on *B. taiwanensis* Chen & Chou.

2. Materials and Methods

The study was conducted at the Guandaushi Forest Station of the Hue-Sun Experimental Forest Station (24 4'N 12°80'E, 500 to 800 m altitude), one of the Long-Term Ecological Research (LTER) sites in Central Taiwan. The mean annual rainfall, relative humidity, and yearly temperature during the study period were 2,597 mm 79%, and 21ºC, respectively. Most of the rainfall (96%) occurs mainly May through September during the rainy and typhoon seasons.

Syconia production was observed in 80 fig trees (42 males and 38 females) growing within a 5 ha area at 5–14 day intervals from 1996 to 1999 (for phenology see Tzeng et al., 2005a,b). The occurrence of pollinating and non-pollinating fig wasps on male syconia was recorded, and their oviposition behaviour was recorded.

To determine larval feeding habit of the non-pollinators, 2–5 recently pollinated syconia were collected weekly. These syconia, sometimes with non-pollinating wasp adults still attached to the fig surface, were fixed in 0.25% glutaradehyde 0.2 M phosphate buffer, or F.A.A. (Formalin: acetic acid: 50% alcohol = 5:5:90), and

dissected under a stereomicroscope. The galls were then dehydrated through an alcohol series from 50 to 100% and critical-point dried using CO_2. The preserved ovaries and fig wasps were attached to metal stubs using double-sided sticky tape, coated with gold-compounds, and studied under a scanning electron microscope (SEM) at 15 kV.

To investigate the species composition of wasps within syconia, 34 near-mature syconia from ten trees were collected during 1997 and 1998. The synconia were preserved in F.A.A., then dissected and the wasps counted under a stereomicroscope. Regression relationships between pollinators and non-pollinators were obtained using GLM program of SAS statistical software.

3. Results

Oviposition and larval development of Sycoscapter

Females of both species of *Sycoscapter* appeared 1–6 weeks after pollination by *B. taiwanensis*, and were often seen together on the syconia surfaces. There were usually 1–3 *Sycoscapter* foundresses ovipositing at any one time, but more than 5 females were observed when wasps were emerging nearby. Females of the two species varied in the length of their ovipositors (*Sycoscapter* sp. A = 1.8±0.19 mm min.–max. = 1.0– 2.5 mm, n=87; and *Sycoscapter* sp. B = 4.6±0.61 mm, min.–max. = 3.0–5.5 mm, n=163). Males of the two *Sycoscapter* species are wingless and we could not differentiate them to species.

There was no clear difference in the timing of oviposition between the two *Sycoscapter* species. We recorded the various developmental stages of the larvae of *B. taiwanensis* and the two *Sycoscapter* species based on dissection of more than 50 syconia. Females of *B. taiwanensis* laid their eggs in the ovary nucellus (Fig. 1a), and after 6 to 7 weeks the larva occupied more than one third of the galled ovary space. During this period, some gall ovaries were occupied by two grubs, one being the larger larva of *B. taiwanensis* and the other being a smaller larva of *Sycoscapter*, which was positioned on the back or side of the pollinator larva (Fig. 1b). Therefore, *Sycoscapter* larvae are parasitic on the larvae of *B. taiwanensis* rather than inquilines. The developmental period of *Sycoscapter* larvae was estimated as the time between oviposition to eclosion, and was about 5–11 weeks in summer and about 14–24 weeks in winter.

Impact of Sycoscapter *spp. on the pollinator*

Because we could not differentiate the *Sycoscapter* males, we used only females to examine the association between the two species of *Sycoscapter* and *B. taiwanensis* the pollinator. Of the 34 syconia sampled, 30 (88%) hosted at least one *Sycoscapter* species, whereas 4 (12%) had only

Table 1. Seasonal abundance of female florets and fig wasps, *Blastophaga taiwanensis* (pollinator) and *Sycoscapter* spp. (parasitoids) in the syconia of *Ficus fomosana* at Guandaushi Forest Station, Taiwan from 1997 to 1998.

Female florets	Total wasps	Ovule hosted ratio (%)	No. of *B. taiwanesis*	No. of *Sycoscapter*	*Sycoscapter* (%)	No. of female *Sycoscapter* sp. A	No. of female *Sycoscapter* sp. B
Winter crop (N=9)							
299.4±136.0[a]	179.4±87.2[a]	63.0±22.7[a]	47.2±44.5[b]	132.2±46.4[a]	78.3±14.1[a]	57.9±[a]	35.0±[ab]
Spring crop (N=10)							
355.7±82.7[a]	140.3±107.5[a]	38.1±19.6[bc]	51.6±71.2[b]	88.7±56.8[b]	71.1±27.9[a]	4.7±[b]	58.1±[a]
Summer–fall crop (N=12)							
376.2±102.8[a]	186.1±91.0[a]	52.0±22.2[ab]	155.3±100.8[a]	30.8±28.0[c]	20.2±19.0[b]	4.8±[b]	14.8±[b]
Total average (N=34*)							
341.3±109.0	161.1±94.2	49.0±23.0	85.0±90.3	76.1±59.0	54.3±34.8**	19.1±29.1	33.8±36.7

Means in the same column followed by the same letter are not significantly (*p*=0.05) different according to the Waller Duncan test. Mean±standard error. *There were 3 syconia that lost their dating tags, and cannot be traced back to seasonal crops. **For *Sycoscapter* parasitized syconia, the rate was 61.5±29.7% (n=30).
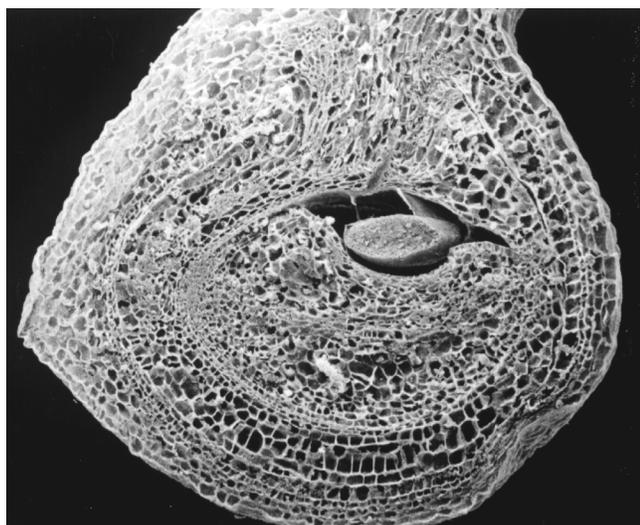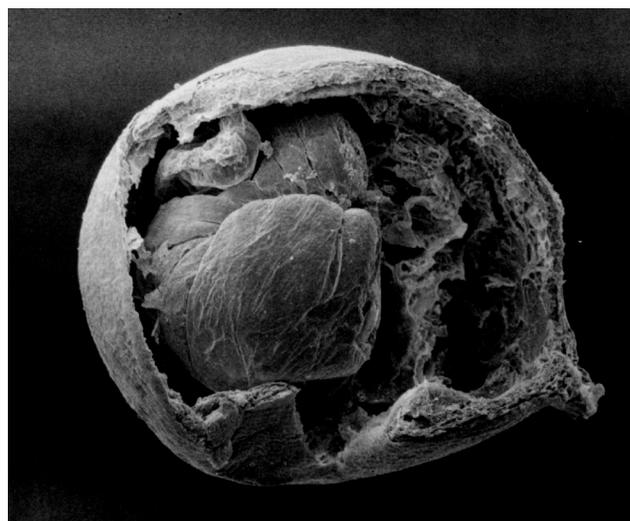
(a)   **(b)**

Figure 1. The relationship of *Blastophaga taiwanensis* (pollinator) to *Sycoscapter* spp. (parasitoid) on *Ficus formosana* in Taiwan. (a) *B. taiwanensis* egg (=e) in the ovary of a female floret (scale bar=100 μm), and (b) a larva of *B. taiwanensis* (=bl) being parasitized by a *Sycoscapter* larva (=sl) (scale bar=200 μm).

B. taiwanensis. Three of these syconia (75%) with only *B. taiwanensis* occurred in summer–fall crops, and the other occurred in the spring crop. Of the 30 syconia in which *Sycoscapter* were present, 18 hosted both species, 3 had only females having the shorter ovipositor, and 8 had only females with the longer ovipositor. When females of both species occurred in the same syconia, those with the longer ovipositor were significantly more abundant (t=1.740, *p*=0.043, n=18), comprising 64% of the total number of female *Sycoscapter* wasps. However, the number of *Sycoscapter* females with the shorter ovipositor was somewhat greater than those with the longer ovipositor in winter, whereas the reverse was true during other seasons (Table 1).

The mean numbers of female florets, numbers of *B. taiwanensis* pollinators, and non-pollinating *Sycoscapter* wasps for each seasonal crop are presented in Table 1. The average number of florets was 341±109, and the total number of wasp galls (original number of pollinators) was 161±94, which occupied 49±23% of florets. The correlation

between the total numbers of wasps and female florets was significant and positive ($\gamma^2=0.550$, $\rho=0.001$), even after the confounding effect of the syconium diameter was taken into account (the partial correlation is $\gamma^2=0.390$, $\rho=0.027$). *Sycoscapter* played a significant role in the wasp community inside the syconium, on average comprising $54\pm35\%$ (n=34) of the total number of wasps, or even $62\pm30\%$ of wasps when considering only the parasitized figs (n=30). Because each *Sycoscapter* larva consumes one *B. taiwanensis* larva, the total population of *Blastophaga* is likely to be reduced by 54% (=62% multiplied by 88% occupancy). There was a significant seasonal variation in the abundance of *Sycoscapter* (F=13.879, *p*<0.001), with the lowest being in the summer–fall crops, although the number of total florets and total fig wasps showed no significant seasonal difference (Table 1).
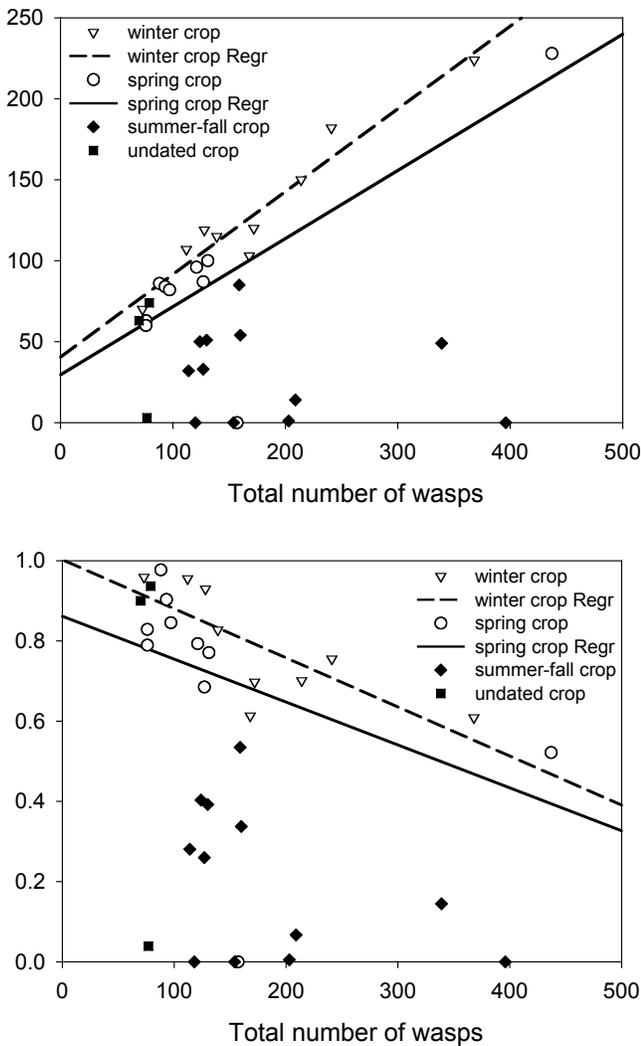

Figure 2. The relationship between the total number of wasps (combined pollinator and non-pollination wasps) and (a) the number of *Sycoscapter*, (b) parasitism rate during different seasons. Regr stands for regression.

Two seasonal patterns were revealed in correlation analysis between the abundance/parasitoidism rate of *Sycoscapter* and *Blastophaga* within the parasitized syconia (total n=27, with 3 parasitized syconia without dating). During the winter and spring seasons, there was a significant correlation between increasing numbers of *Sycoscapter* and increased pollinator abundance ($r^2=0.961$, *p*<0.001, n=9 in winter; and $r^2=0.990$, *p*<0.001, n=9 in spring, respectively) (Fig. 2a). In contrast, the percentage of parasitized galls (the rate of parasitoidism) showed a significantly negative correlation with pollinator abundance ($r^2=-0.759$, *p*=0.018, n=9 in winter; $r^2=-0.826$, *p*=0.006, n=9 in spring, respectively) (Fig. 2b). In other words, the abundance of parasitoids significantly increased with the increasing numbers of pollinator galls, but the increasing rate slowed down when the number of pollinator galls became larger. These correlations were not apparent during the summer–fall season, and none of the correlations was significant ($r^2=-0.115$, *p*=0.768, n=9 for the abundance of *Sycoscapter*; $r^2=-0.410$, *p*=0.273 for the parasitoidism rate).

4. Discussion

The present study is the first to report that *Sycoscapter* larvae feed directly on the larvae of *Blastophaga*, documented by SEM photographs of parasitism in a fig wasp. This confirms that *Sycoscapter* is a parasitoid. Our finding in part results from the uncomplicated composition of the wasp community on *F. formosana*, which consists only of *B. taiwanensis* and two *Sycoscapter* species.

The varying lengths of the ovipositors of the two co-existing parasitoid species may reflect a specialization of the two species for ovipositing into different layers of ovaries within the syconium. The *Sycoscapter* species with the longer ovipositor (Table 1, sp. B) comprised 64% of the total number *Sycoscapter*; however, the species with the shorter ovipositor (Table 1, sp. A) was more abundant in winter and much less abundant during the other seasons. The coexistence of these two *Sycoscapter* species may therefore also result from different physiological adaptations to climatic variability.

Sycoscatper species are undoubtedly critical factors affecting the reproductive success of *B. taiwanensis* and thus the host fig. The reduction of the pollinator population by *Sycoscapter* is estimated as 54% in our study. Many other non-pollinating fig wasps have been reported to affect negatively the production of pollinators (West et al., 1996; Kerdelhué and Rasplus, 1996a; Peng et al., 2005). In addition, the abundance of *Sycoscapter* showed a significant seasonality in our study. In the winter and spring seasons there was a significant positive correlation between the abundance of *Sycoscapter* and the total number of wasps in a syconium. However, the rate of parasitism was lower in syconia with a greater number of wasps. This

phenomenon is consistent with the host density-dependence phenomenon in Kerdelhué and Rasplus (1996a) and Weiblen et al. (2001). In other words, the parasitoids were numerically overwhelmed as the number of pollinators in syconia increased, leaving a larger proportion of pollinators free from parasitism. This could be a strategy of predator-satiation (Harrison and Yamamura, 2003).

No significant correlation between the abundance of *Sycoscapter* and the total number of wasps was apparent for the summer–fall crop, and there was no significant change in the rate of parasitism. The abundance of *Sycoscapter* was very low and consequently the production of pollinators much higher (about 80%). Several mechanisms may account for the low numbers of *Sycoscapter* in summer–fall, including seasonal variation in the abundance of syconia, differences in the survival of the *Sycoscapter* and *Blastophaga* adults relative to the changing climatic conditions, or a variation in the abundance of predators that attack the ovipositing *Sycoscapter*. Such predators include ants and spiders that may catch the parasitoid foundresses and decreases their egg-laying chances (Chou and Yeh, 1995; Weiblen et al., 2001). We do not think this mechanism plays a major role because we saw few predators at our field site. There is, however, a marked seasonality in the production of syconia (Tzeng et al., 2005a,b) so that a sharp peak (over ten-fold increase) in the availability of receptive syconia occurs in early summer. These syconia form the summer-fall crop. We believe that this sudden increase in the number of *F. formosana* syconia may effectively dilute the visiting of parasitoids, and leave a larger proportion of syconia free from parasitism. This hypothesis is supported by the big proportion (75%, although the sample size was quite small) of syconia containing only pollinator wasps occurred in the summer-fall crop.

In this study, we suggest that there are two levels of control on the rate of parasitism by *Sycoscapter*. The first level works within syconia. When relatively low numbers of syconia are available, syconia with higher numbers of pollinators have lower rates of parasitism, possibly because of predator-satiation. The key controlling factor at this level is the abundance of pollinators within the syconium. The second level of control depends on the availability of syconia. When there is a very high production of syconia, the visiting rate of parasitoids will be much decreased, and may even be zero (thus leave the syconia contained only pollinators). When this happens, the parasitoids tend to be randomly distributed, which leads to the non-significant correlations between the total numbers of wasps and parasitoid numbers/parasitism rate within syconia. This phenomenon allows many more pollinator offspring to escape from parasitism and results in much higher percentage of pollinator galls (80% for summer-fall crop, but 22–29% for the other two crops). The key controlling factor at the second level is the effect of season on fig production. Thus, both the pollinator and the fig can affect the rate of parasitism by *Sycoscapter at two levels and this* may help maintain a balanced symbiotic relationship between these three organisms.

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