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The cost of parasitism: High larval developmental mortality following attacks by a parasitoid fig wasp on a fig pollinating wasp

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Abstract

Parasitoids contribute to controlling phytophagous insect populations. Their action on a host is often measured by numbers of emerging adult parasitoids. However, parasitoid oviposition attempts may lead to host mortality and sometimes both host and parasitoid die during larval development. Therefore, establishing the effect of parasitoids on host populations requires estimating total effect of parasitoids.

The communities of wasps developing in figs (the closed inflorescences of *Ficus*) have become a model system to investigate micro-hymenopteran interaction networks. A galled ovule produces either a single galling wasp or a single parasitoid providing a simple way to measure costs. However, some galled flowers produce no wasps. We show that about one quarter of galled flowers fail to produce pollinator offspring in the absence of parasitoids. In the presence of parasitoids, the number of empty galls is increased. For each emerging parasitoid, 1.9 pollinator larvae were killed. Hence, host mortality induced by parasitoids is much larger than actual parasitoid production, a feature documented in some other host-parasitoid interactions and that may be pervasive in nature

Keywords: *Ficus racemosa*, parasitoid, demography

Introduction

Parasitoid hymenoptera represent the most diversified lineage of insects (Forbes et al., 2018). They can exert strong control of host populations (Godfray, 1994). As such, they provide natural ecological services (Losey and Vaughan, 2006) and they are largely used as biological control agents (Wang et al., 2019). The effect of parasitoids on a host may be measured as numbers of emerging parasitoids. However, actual parasitism levels may be much higher as joint mortality of host and parasitoid larva is increasingly documented, especially using nextgeneration sequencing (Sow et al., 2019). Other factors, such as parasitoid ovipositor probing, may also result in increased mortality (Abram et al., 2019). An extreme situation was observed for *Itopectis conquisitor* (Say) ovipositing on *Lymantria dispar*, with 200 hosts killed by oviposition attempts for one successfully developed parasitoid offspring (Campbell, 1963). Such mortality has mainly been investigated for some invasive host species and for some parasitoids that are bred for biological control (Abram et al., 2016). It is difficult to obtain a global vision on the prevalence of host mortality that does not lead to parasitoid production in natural host-parasitoid communities as they are generally complex with a diversity of more or less specialized parasitoids feeding on a set of hosts (Stone et al., 2012).

Fig trees and their host-specific associated communities of fig wasps constitute a tractable model system to investigate the ecology and evolution of wasp communities (Cook and Rasplus, 2003). Because fig wasps are fig specialists, it is possible to collect the complete regional diversity of fig wasps by collecting wasps on the whole set of *Ficus* species. Levels of host specificity can be established (Farache et al., 2018). Unique

insights may be obtained. For instance, observations throughout the range of a *Ficus* species has evidenced the presence of series of mutually exclusive parapatric sister species, demonstrating competition between species in a saturated community (Darwell and Cook, 2017).

Ficus are characterized by their enclosed urn-shaped inflorescence whose inside is lined by uniovulate pistillate flowers and some male flowers. Pollinating wasps enter figs and oviposit in the pistillate flowers. A pistillate flower will either give a seed or turn into a gall that will eventually produce one wasp. Usually, a *Ficus* species is pollinated locally by a single pollinating fig wasp species while it can host multiple non-pollinating fig wasps (Borges, 2015). Non-pollinating fig wasp (NPFW) communities include gallers, inquilines, kleptoparasites, parasitoids of the pollinators, parasitoids of other non-pollinating wasps, and hyperparasitoids and can be particularly diverse, with up to 30 or more species present on a single tree (Compton and Hawkins, 1992). As the pollinators, non-pollinating fig wasps oviposit into ovules and, whatever the species, a single non-pollinating wasp individual emerges from an ovule. Most non-pollinating wasp species have very long ovipositor that allow them to lay their eggs from outside the fig through the fig-wall. The timing of oviposition of the different species is scattered throughout the development of the fig (Wang and Qi, 2008).

Despite the interest for non-pollinating fig wasps biology, most studies are based on observations of timing of oviposition and correlations between the number of wasps of different species produced within a fig (Bronstein, 1991; Cardona et al., 2013; Kerdelhue and Rasplus, 1996; Krishnan and Borges, 2014; West et al., 1996). However, the results of correlation analysis can be very misleading as demonstrated by Raja et al. (2015): more productive figs produce more pollinators and more parasitoids resulting in a positive correlation between pollinator and parasitoid production (Raja et al., 2015). Lack of direct evidence for feeding regime may also obscure interpretations.

Ficus racemosa is one of the rare species for which the feeding regimes of the associated community of wasps is well described (Wang and Qi, 2008; Yadav and Borges, 2018). Using the pollinator of *F. racemosa*, *Ceratosolen fusciceps* and its single parasitoid, *Sycophaga agragensis*, we addressed the following questions: i) do we have evidence for larval mortality in *Ceratosolen fusciceps* in the absence of parasitism; ii) do we have evidence for reduced total wasp production in the presence of parasitoids iii) and is increased pollinator mortality affecting equally male and female pollinating wasps?

Material and method

The work was carried out in and around the Xishuangbanna Tropical Botanic Garden (21°41' N, 101°25' E), Yunnan province, China. The altitude is approximately 600 m and the climate includes a wet and dry season. In Xishuangbanna, the wet season lasts from May to October.

A single crop on a single tree was used for the experimentation in order to reduce sources of variation. Indeed, our aim was to demonstrate the presence of an effect. We did not try to quantify the consequences of this effect on wasp population dynamics, as this will require much larger experimentation. The experiment consisted of two treatments. In one, we introduced 5 pollinating fig wasps per fig, and in the other treatment we introduced 5 pollinating wasps and then we exposed the fig to 10–20 parasitoid wasps.

We located trees that presented a crop of pre-receptive figs and enclosed randomly selected figs in nylon bags in order to prevent natural wasp colonization. The figs were monitored every three days. When the figs were close to the receptive stage (the stage at which pollinators are attracted and enter the figs), they were checked daily. When the figs were receptive, we deposited 5 pollinating wasps on each fig and let them enter. We used pollinating wasps that had emerged naturally from other trees. The figs were then enclosed individually in nylon bags to prevent further pollinator entries or uncontrolled parasitism by non-pollinating fig wasps. When the figs were ready for parasitoid oviposition (8–10 days after pollinator oviposition), we replaced the nylon bag enclosing the fig by a bag containing 10–20 parasitoid wasps and let the parasitoids

oviposit. Several days later, when the parasitoid wasps had ceased oviposition, we replaced the bag with a new empty protective bag. After pollinating wasp introductions, we let the treated figs develop to maturity and collected the figs just after the wasps had emerged from the figs into the bag. Wasps and fig were then preserved in alcohol.

Each fig was longitudinally bisected twice along the ostiole–peduncle axis, so that the wasps still inside the fig cavity, the empty galls from which wasps had emerged, and galls containing dead wasps could be counted. We also counted the number of “bladders”. These are empty, unperforated galls (bladders) similar in size and form to normal galls but lacking insects (Galil and Eisikowitch, 1971). They are generally interpreted as having been galled by ovipositing wasps but have become hollow due to early mortality of the wasp egg or embryo, (Galil and Eisikowitch, 1971; Jansen-González et al., 2012; Verkerke, 1989). Total gall numbers were calculated by summing numbers of exited galls, bladders, and those containing dead, non-emerged wasps.

2.1. Data analysis

We used the Shapiro-Wilk test to test the normality of the data of two treatments. The number of galls, wasps, and the sex ratio of pollinator offspring for the two treatments were normally distributed. Therefore, we used Student independent sample *t*-tests comparing gall numbers, pollinating wasp numbers and sex ratio of pollinating wasp between the two treatments. To analyze the relationship between the total number of wasps and the number of galls, two linear models in which the total number of wasps was set as explanatory variable and the gall number as the variable to be explained were used separately for the two treatments. Three other linear regression models were used to explore the quantitative effects of the presence of *Sycophaga agraeensis* in this study. One linear model in which total gall number was set as explanatory variable and the number of *Sycophaga agraeensis* as the variable to be explained was used to explore whether the number of offspring *Sycophaga agraeensis* increases with gall number. To determine the effect of *Sycophaga agraeensis* on the probability that a gall would give a wasp, we used a linear model in which the proportion of galls that produced a *Sycophaga agraeensis* in each fig was set as explanatory variable and the proportion of the galls in which a wasp developed to become adult as the variable to be explained variable. To describe the relationship between offspring number of *Sycophaga agraeensis* and pollinator, a linear model in which number of *Sycophaga agraeensis* was set as independent variable and pollinator offspring number as dependent variable was used. The statistics were carried out with R 3.5.3.

Results

The number of galls did not differ between the two treatments (with and without parasitoid wasp) (893.82 ± 45.97 versus 939.82 ± 45.91 (Mean \pm SE), $t = 0.696$, $df = 37$, $P = 0.491$), while fewer wasps developed in parasitized figs than in figs into which only pollinators oviposited (720.94 ± 36.55 versus 893.82 ± 31.88 (Mean \pm SE), $t = 3.239$, $df = 37$, $P < 0.01$). The proportion of galls that produced a wasp was reduced in figs exposed to *Sycophaga agraeensis* (0.63 ± 0.02 versus 0.77 ± 0.02 (Mean \pm SE), $t = 0.379$, $df = 37$, $P < 0.001$). The sex ratio (number of males divided by total number of pollinating wasps) of pollinating wasps did not differ between the two treatments (0.291 ± 0.012 versus 0.286 ± 0.008 (Mean \pm SE), $t = 0.311$, $df = 37$, $P = 0.758$).

The number of pollinator offspring that developed in figs exposed to *Sycophaga agraeensis* was reduced by one third (472.18 ± 29.99 versus 720.94 ± 36.55 (Mean \pm SE), $t = 5.309$, $df = 37$, $P < 0.001$; Fig. 3). Both female pollinator offspring (338.73 ± 22.84 versus 513.00 ± 28.75 (Mean \pm SE), $t = 4.811$, $df = 37$, $P < 0.001$; Fig. 3) and male pollinator offspring numbers declined in figs exposed to *S. agraeensis* (133.45 ± 8.16 versus 207.94 ± 12.65 (Mean \pm SE), $t = 5.147$, $df = 37$, $P < 0.001$; Fig. 3). The

number of empty galls (bladders) was much higher in figs exposed to parasitoids (329.82 ± 23.60 versus 218.88 ± 19.18 (Mean \pm SE), $t = -3.495$, $df = 37$, $P < 0.01$).

The total number of wasp offspring produced per fig correlated strongly with the total number of galls in both treatments, but the regressions were significantly different between the two treatments (*Sycophaga agragensis* absent: $y = 0.7297x + 35$, $N = 17$, $R^2 = 0.84$ $p < 0.001$; *S. agragensis* present: $y = 0.6087x + 20$, $N = 22$, $R^2 = 0.7703$, $p < 0.001$; test of difference between the two regressions, $F_{2,35} = 16.6$, $P < 10^{-4}$; Fig. 1). For the two correlations, the intercepts were not significantly different from zero.

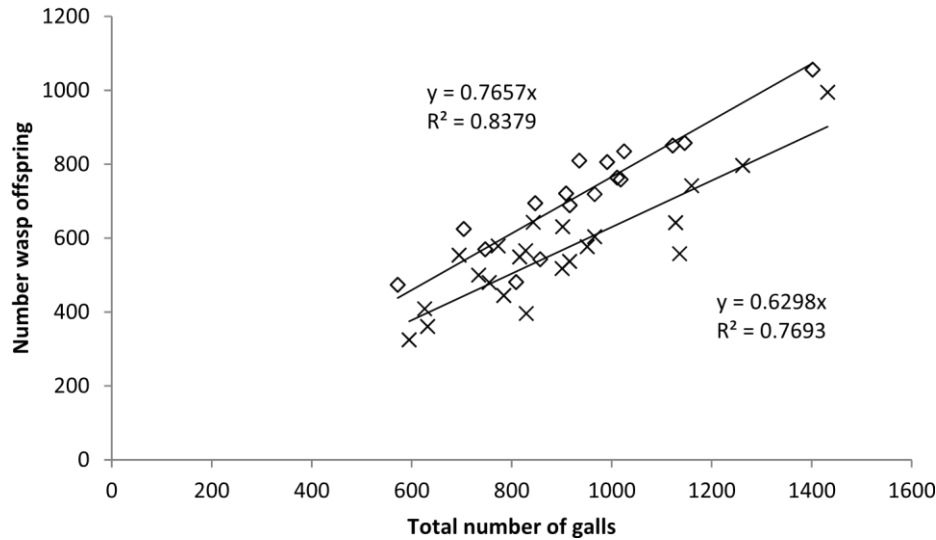


Fig. 1. Linear regression forcing the intercept to zero between the number of wasp offspring and the total number of galls when *Sycophaga agragensis* is absent or present. Open diamonds: *S. agragensis* absent; crosses: *S. agragensis* present

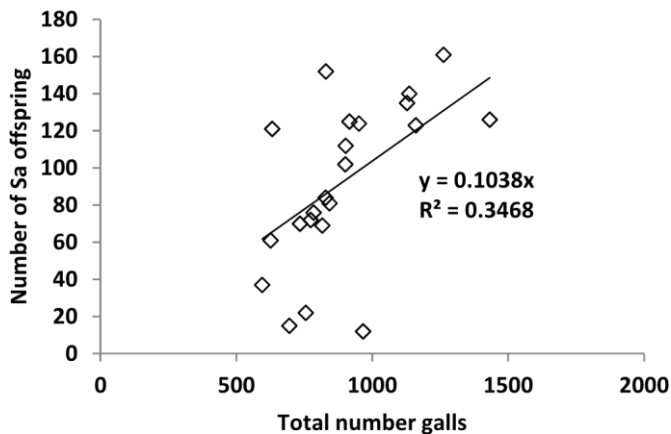


Fig. 2. Linear regression forcing the intercept to zero between the number of *Sycophaga agragensis* offspring and the total number of galls when *S. agragensis* is present.

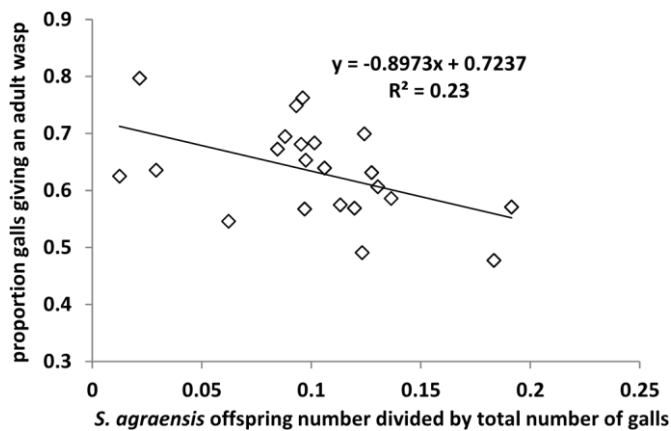


Fig. 3. Linear regression between overall development ratio and the relative number of *Sycophaga agraeensis* offspring when it is present. The number of pollinator offspring produced was independent of the number of *Sycophaga* produced ($y = 0.0156x + 84.46$, $N = 22$, $R^2 = 0.0024$, $P = 0.83$; Fig. 4).

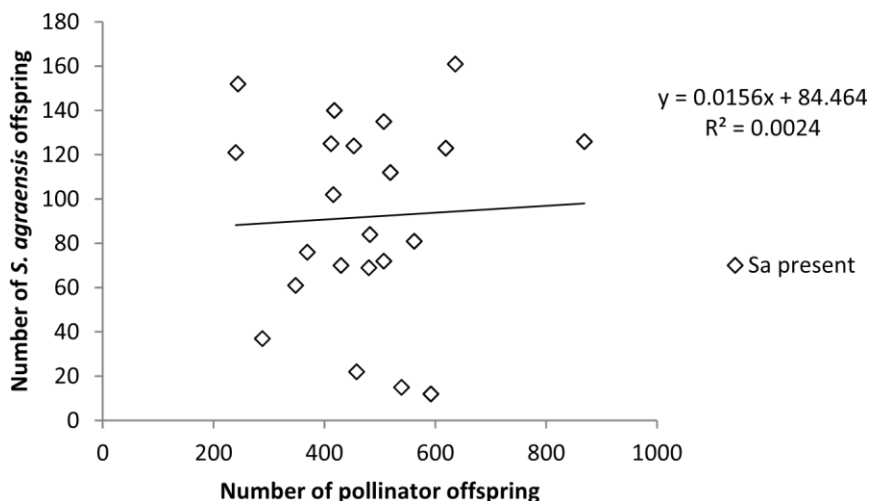


Fig. 4. Lack of correlation between number of pollinator offspring and number of *Sycophaga agraeensis* offspring.

The number of *Sycophaga agraeensis* produced correlates positively with the total number of galls: more productive figs produced more parasites ($y = 0.1224x - 17.595$, $N = 22$, $R^2 = 0.3555$, $p < 0.01$, intercept was not significantly different from zero, Fig. 2). The proportion of galls producing an insect correlated negatively with the ratio number of *Sycophaga agraeensis* divided by total number of galls ($y = -0.897x + 0.725$, $N = 22$, $R^2 = 0.23$ $p < 0.05$; Fig. 3). The intercept (0.725) is the proportion of galls giving a wasp in the absence of parasitism. The slope gives the decrease in the proportion of galls giving a wasp as a function of the abundance of *Sycophaga agraeensis*. For each additional *Sycophaga*, the total number of emerging wasps decreases by 0.897, and hence the number of emerging pollinating wasps decreases by 1.897.

In summary, figs without the parasitoid produced on average, 721 pollinators, 219 bladders, for a total of 940 galls while figs with parasitoids produced on average, 472 pollinators, 92 parasitoids, 330 bladders, for a total of 894 galls.

Discussion

In the absence of parasitoids, 27% of the galled flowers became bladders. These bladders could result from larval mortality or from gall initiation without oviposition. In *Ficus montana*, counts of the proportion of flowers into which pollinators had oviposited have shown i) that bladders corresponded to flowers into which a pollinator had oviposited and ii) that in the absence of parasitoids over 1/3 of the flowers that had received a pollinator egg turned into bladders (Ghana et al., 2012). We therefore accept as a provisional working hypothesis that there is a 27% larval mortality in *Ceratosolen fusciceps*. Similarly, in *Ficus hirta* figs into which one or two foundresses had been introduced, over 25% of the galled flowers were bladders, suggesting high larval mortality (Yu et al., 2018). Hence, despite 70 Ma coevolution between *Ficus* and their pollinating agaonid wasps (Cruaud et al., 2012), and despite aligned interests of plant and insect (Anstett et al., 1997), it appears that larval mortality remains remarkably high.

In the presence of parasitoids, the proportion of bladders (empty galls) was increased. This suggests either an increase in wasp developmental mortality or the initiation of new galls by the parasitoids. Initiation of new galls is unlikely because female flowers wilt rapidly after fig visitation by pollinators. Therefore, when *Sycophaga agragensis* oviposits into figs, 1–2 weeks after pollinator entry (Yadav and Borges, 2018), female flowers can probably no longer be galled. Further, the total number of galls did not increase in the presence of parasitoids confirming that no additional galls were initiated. The regressions show that for each additional *Sycophaga* produced, 0.9 additional bladder was present in the fig. Hence, the development of one parasitoid results in 1.9 fewer pollinator offspring. In the literature it is often implicitly assumed that the impact of pollinator-sized NPFWs is equal to the number of occupied ovaries, a galler larva occupying a single ovary and each parasitoid/kleptoparasite larva developing at the expense of one host wasp larva (Conchou et al., 2014). Indeed, the weight of a female individual of *Sycophaga agragensis* is identical to that of an individual *Ceratosolen fusciceps*, confirming that this parasitoid feeds on a single host (Ghara and Borges, 2010). Nevertheless, the data presented here suggests high larval mortality, even in pollinators, and one parasitoid replacing two pollinator larvae. Hence, there is no simple proxy to determine the cost to the mutualism of the different non pollinating fig wasps involved.

While we show that the reduction in total wasp production due to parasitism should not be neglected, our result do not provide an estimate of induced mortality values in natural populations and of the factors influencing this mortality. This will require investigating variation among crops within trees and among trees. Nevertheless, a similar result was obtained in *Ficus sur*: figs protected against parasitoid oviposition produced 1.5 time more wasps than those that were exposed to parasitoids (Compton and Robertson, 1988). Hence the phenomenon described here is probably general in fig wasps.

The results also show that we cannot estimate a cost of parasitism simply correlating host and parasite production. Indeed, in our data, despite each parasitoid costing two pollinators, the correlation between number of parasitoids produced and number of pollinators produced was not significant. This is because figs that initially contained more pollinator larvae were more parasitized.

The sex ratio strategies of pollinating fig wasps have been extensively studied (Herre, 1985; Raja et al., 2008). Sex ratio adjustment is achieved by females beginning by laying many males, and progressively reducing the proportion of males throughout oviposition (Raja et al., 2008). Females are selected to lay a higher proportion of males at the beginning of an oviposition sequence if the pollinating wasps have incomplete control over the number of male and female offspring (Kjellberg et al., 2005). The large pollinator larval mortality documented here could be an important factor limiting this control. Asymmetric effect of parasitoids on male and female pollinator offspring mortality could also affect sex ratio. In *Ficus hirta*, male pollinator offspring have been shown to be less exposed to parasitoids than female offspring, probably because their galls are located further from the fig wall, a factor that may limit the risk of a fig containing insufficient numbers of males to ensure female fertilization (Yu and Compton, 2012). This was not the case

in our study and may relate to figs of *Ficus racemosa* generally containing many more wasp offspring than *F. hirta* figs. Larger broods automatically result in reduced sex ratio variance (Kjellberg et al., 2005), and hence reduced necessity to protect male offspring.

Conclusion

The study presented here confirms the necessity to take into account parasitoid effects on host mortality that do not simply result from the development of a parasitoid up to adult stage as suggested by (Abram et al., 2019). Neglecting these effects provides for a highly skewed vision of the effect of parasitoids on host populations.

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Role of authors

XWZ devised the experiments, did the experiments, analysed the data and co-wrote the paper. CC participated in the experiments. RWW devised the experiments, analysed the data and co-wrote the paper. FK contributed to data analysis and co-wrote the paper.

Declaration of competing interest

The authors declare that they have no competing interests.

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