

Comparison of reproductive strategies in two externally ovipositing non-pollinating fig wasps

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Abstract The reproductive strategies of *Walkerella* sp.1 associated with *Ficus curtipes* and *Walkerella* sp.2 associated with *Ficus benjamina* were investigated. Both species oviposited from outside the fig wall. *Walkerella* sp.1 was the first non-pollinating fig to oviposit on *Ficus curtipes* and began to do this ten days after figs syconia began to develop. The larvae of *Walkerella* sp.1 were only found in the most external ovary layer of the fig. *Walkerella* sp.2 starts ovipositing after several other non-pollinating fig wasps have already laid their eggs in *F. benjamina*. The progeny of *Walkerella* sp.2 are distributed in the external ovary layer, the middle ovary layer, and/or the inner ovary layer of the figs. However, more than a quarter of the offspring were found in the most external layer and only a few in the inner layer. Experimental studies proved that the two *Walkerella* species are gall formers. In both manipulated figs and in natural figs, the sex ratios of *Walkerella* sp.1 and *Walkerella* sp.2 were female-biased. In *Walkerella* sp.2, the overall sex ratio increased with the proportion of figs parasitized in a crop, but this was not the case for *Walkerella* sp.1. Females of both *Walkerella* species appear not to have information about the patches on which they

oviposit because sex ratios of both species decreased as brood sizes within individual figs increased and foundresses of both species were able to lay clutches containing a single male egg and several female eggs.

Keywords Reproductive strategies · Fig wasp · Larvae diet · Sex ratio

1 Introduction

Pollinating fig wasps (Hymenoptera, Agaonidae) are obligate mutualists with their *Ficus* (Fig tree) hosts (Galil 1977; Wiebes 1979; Cook and Power 1996; Peng et al. 2005a), but they are outnumbered by a diverse group of non-pollinating fig wasps (NPFW) that also develop within figs (Hawkins and Compton 1992; West and Herre 1994; Kerdelhué and Rasplus 1996). Pollinating fig wasps have been studied extensively, whereas much less is known about the biology of NPFW (West et al. 1996).

Some NPFW, like pollinators, have foundresses that enter the figs to oviposit, however, they are unable to transport pollen efficiently for fig trees (Kerdelhué and Rasplus 1996). Unlike pollinating fig wasp, most NPFW lay their eggs through the fig wall from the outside and do not transfer pollen (Kerdelhué and Rasplus 1996). Regardless of the way they oviposit, NPFW are directly or indirectly dependent on the fig-pollinating wasp mutualism for their survival (Bronstein 1991; Kerdelhué and Rasplus 1996). NPFW include species that gall *Ficus* ovaries, that are inquiline, or that are parasitoids (Compton and van Noort 1992; Kerdelhué and Rasplus 1996). Gallers and inquiline are phytophagous, while parasitoids are carnivorous. The larval diet of NPFW can be assessed by looking for correlations between parasite presence, pollinator wasp and

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viable seed production (West and Herre 1994; Kerdelhué and Rasplus 1996; Kerdelhué et al. 2000). However, determining the larval diets of NPFW this way may yield inconclusive results (Bronstein 1991; West and Herre 1994).

How cooperation is maintained in the face of cheating is a central problem for evolutionary biology (Yu 2001; Douglas 2010). The NPFW also appear to be species-specific to single fig species as is the case of pollinating fig wasps, however, a single species of fig tree may be host several non-pollinating fig wasp species (West et al. 1996). Jusselin et al. (2008) found that the *Galoglychia* fig wasp community is highly dependent on the codiversification of wasps and their host figs, suggesting that all pollinating fig wasps and non-pollinating fig wasps studied are specialized to their host. Niche Partitioning may lead to NPFW and pollinating fig wasps coexisting in the fig. In some monoecious fig species, the external ovary layer of a fig contains galler progeny while the inner ovary layer contains pollinators (Kerdelhué and Rasplus 1996; Cook and Power 1996; Yu 2001). However, in other fig species, galls and pollinators can both occur in the inner ovary layer (West and Herre 1994; West et al. 1996; Kerdelhué and Rasplus 1996).

According to local mate competition theory (LMC), female-biased sex ratios are favoured when one or a small number of foundresses contribute progeny to a combined brood, and optimal sex ratios should increase as the number of females contributing offspring to a patch increases (Hamilton 1967; Hardy and Mayhew 1998). Reflecting this, the sex ratios of pollinators are typically female biased and vary according to foundress number (Raja et al. 2008). In many non-pollinating fig wasp species, some mating also occurs away from the natal patch (termed partial LMC) and if this is the case, selection will favour less female-biased sex ratios (West and Herre 1998).

Foundress numbers can be estimated directly in some pollinating fig wasps by calculating the remains of foundresses in the fig (Herre 1985, 1987; Fellowes et al. 1999). However, most non-pollinating wasps lay their eggs through the fig wall from the outside (Cook et al. 1997; Fellowes et al. 1999). In such cases, foundress number can not be estimated directly but West and Herre (1998) developed a model to estimate fig wasp foundress numbers indirectly. This model showed that the proportion of figs parasitized by a given NPFW species positively correlated with the average number of foundresses of a given species ovipositing in a fig. Furthermore, the proportion of figs in which a given NPFW species occurred also positively correlated with the overall sex ratio of the given species. Greeff (1997) developed models that showed that externally ovipositing non-pollinating fig wasps should optimally either lay a single male egg, or a larger clutch consisting of female eggs except one that should be male. This is

irrespective of the knowledge they have of laying order or population density. When females “know” their arrival order the sex ratio per fig was predicted to increase with brood size and the crop sex ratio should increase with population density. When females had no information on their arrival order or on the population density, the patch sex ratio should show no trends with brood size nor with population density. If females do not know their arrival order, but can detect population density, then the sex ratio should not increase with brood size within crops, but should increase with crop density.

In the present study, we compared the reproductive strategies of two *Walkerella* species and addressed the following questions. (i) Does the ovipositing timing and behaviour differ between species? (ii) What is the larval diet of the two species? (iii) How do wasp progeny distribute in the ovary layers? (iv) Is proportion of figs parasitized positively correlated with the overall sex ratio of the *Walkerella* species? (v) Do brood sex ratios of *Walkerella* sp.1 or *Walkerella* sp.2 vary with brood size in individual figs?

2 Materials and methods

2.1 Study site and species

The study was carried out in 2008 at the Xishuangbanna Tropical Botanical Garden (XTBG) (101°15'E, 21°55'N), located in south-west China at the northern margin of tropical South-east Asia. *Ficus curtipes* (subsection *Conosycea*) is a large free standing monoecious fig tree (5–10 m in height) native to Xishuangbanna (Zhang and Yang 2009), with each fig usually producing both seeds and fig wasps. *F. curtipes* produces figs throughout the year in synchronous crops but there is asynchrony between trees which bear several thousands of figs in each crop. The mature figs are dark red to purplish red, measure 15.52 ± 0.75 mm in diameter (mean \pm S.E., $n=47$) (Zhang and Yang 2009).

Walkerella sp. 1. (Otitesellinae) is one of 11 non-pollinating fig wasps which together with the pollinator *Eupristina* sp., develop in the figs of *Ficus curtipes* at the Xishuangbanna Tropical Botanical Garden. *Walkerella* sp1. foundresses oviposit from the outside of the figs and the males are wingless.

Ficus benjamina Linn. (Section *Conosycea*) is another large free-standing monoecious fig tree, native to Xishuangbanna, that produced figs containing both seeds and fig wasps (Bai et al. 2008). *F. benjamina* produces figs throughout the year in synchronous crops, again trees fruit at different times. Crops consist of several thousand figs which at maturity are subglobose, yellow and measure 12–25 mm in diameter (Bai et al. 2008). Each fig contains around 700

flowers (mean±S.E.=614.71±18.61 female flowers and 59.29±2.16 male flowers, $n=24$ figs). In addition to the pollinator fig wasp *Eupristina koningsbergeri*, *F. benjamina* supports 14 NPFW at the Botanical Garden. One of these is *Walkerella* sp.2 (Otitesellinae). *Walkerella* sp.2 which oviposit from the outside of the figs, piercing the fig wall with their ovipositors to lay eggs in the ovules. *Walkerella* sp.2 males are wingless.

2.2 Oviposition behaviour

Thirty pre A-phase figs of *F. curtipes* and thirty pre A-phase figs of *F. benjamina* were respectively marked in 2008. The figs were observed once a day. When the two *Walkerella* species arrived and started ovipositing, we recorded the oviposition behaviour of foundresses in detail.

2.3 Spacial distribution in figs

Fifteen early D phase figs from *F. curtipes* and fifteen early D phase figs from *F. benjamina* were collected in 2008. The figs were sliced open and the pedicels of gall containing *Walkerella* sp.1 or *Walkerella* sp.2 were measured under OLYMPAS (SZX12-3141) anatomical lens.

2.4 Natural populations

We collected late C and early D phase figs from 2006 to 2008 (before any exit holes were present) from both *F. curtipes* (four crops) and *F. benjamina* (nine crops). The figs were sliced open and placed in emergence bags to allow the wasps to emerge. The numbers of male and female *Walkerella* were then recorded.

2.5 Experimental manipulation of foundress numbers

Pre-female-phase figs from *F. curtipes* and *F. benjamina* were enclosed in fine-mesh nylon bags to prevent any female fig wasps from utilizing them. We waited for *Walkerella* females to start laying eggs in adjacent figs at the same developmental stage and then released a single foundress reared from figs collected on other trees into each bag. When the figs matured, they were removed and cut open. Then, the wasps present were recorded. Twelve figs containing *Walkerella* sp.1 and 16 figs containing *Walkerella* sp.2 were successfully oviposited upon and then the progeny studied.

2.6 Data analysis

We used generalized linear models (GLMs) to analyse the data on relationship between (1) the proportion of figs parasitized and the sex ratio of *Walkerella* species with

binomial distribution, (2) the relationship between brood sex ratio of *Walkerella* species and brood size in individual figs with binomial distribution, and (3) the relationship between proportion of figs parasitized and brood size with quasipoisson distribution. An independent sample t-test was used to compare the sex ratios or body size of the two *Walkerella* species using the same foundress number. Sex ratios that did not have a normal distribution were arcsine transformed before the test. All analyses were carried out with R (version 2.5.1) software.

3 Results

3.1 Oviposition behaviour

Walkerella sp.1 was the first fig wasp species to oviposit on *F. curtipes*. Foundresses started ovipositing ten days after syconia began to develop by which time the figs were 5.75 mm (S.E.=0.09 mm, $n=39$). From 1 to 7 foundresses were observed simultaneously ovipositing on the same fig. When foundresses arrived at a suitable fig, they began to search for an oviposition site by tapping repeatedly on the fig wall with their antenna. When a foundress found a suitable ovipositing site, it took one or several steps which allowed the end of the ovipositor to rest on the ovipositing site. The foundress then lifts its abdomen up and stretches out the ovipositor to penetrate the fig wall. After most of the ovipositor has entered the fig, the foundress lowers her abdomen and begins to lay eggs in the flowers. The average ovipositing time was 49 min (S.E.=6.89 min, $n=16$), ranging from 7 min to 132 min. After oviposition, a foundress withdraws its ovipositor and continues to search for another suitable ovipositing site on the fig or flies away to find a second fig at the proper stage for oviposition.

Walkerella sp.2 started ovipositing on *F. benjamina* 16 days after syconia began to develop by which time the figs were 6.54 mm (S.E.=0.18 mm, $n=21$). From 1 to 10 foundresses were observed simultaneous laying eggs on the same fig. *Walkerella* sp.2 foundresses also searched for an oviposition site by tapping on the fig wall with their antenna. When a suitable ovipositing site was located, the foundress stretched out ovipositor and penetrated the fig wall to oviposite. The average oviposition time was 31.07 min (S.E.=3.07 min, $n=15$), ranging from 11 min to 52 min. After oviposition, the foundress withdrew her ovipositor. About 10-94% of sampled figs contained *Walkerella* wasps, and a fig produced about 2-15 individuals (Table 1).

3.2 Larval diet and male character

Both *Walkerella* sp.1 and *Walkerella* sp.2 can develop in figs in the absence of other fig wasps, suggesting that the two *Walkerella* species are herbivorous gallers (Table 2).

Table 1 Brood size and sex ratio of two *Walkerella* species in natural figs

Fig wasp species	Crops	Sample size	Combined brood size (mean±S.E.)	Proportion parasitized fig	Sex ratios
<i>Walkerella</i> sp.1	1	28	3.44±0.80	0.33	0.30
	2	28	3.40±0.54	0.55	0.39
	3	28	6.00±1.34	0.46	0.24
	4	28	6.91±0.91	0.92	0.25
<i>Walkerella</i> sp.2	1	31	6.50±1.88	0.29	0.31
	2	30	2.00±1.00	0.10	0.36
	3	30	4.80±1.25	0.17	0.21
	4	19	6.00±4.50	0.16	0.17
	5	24	15.31±1.86	0.92	0.48
	6	29	1.67±0.67	0.10	0.20
	7	28	6.61±1.45	0.64	0.38
	8	34	6.63±1.82	0.24	0.29
	9	31	11.57±1.62	0.94	0.37

After maturing, *Walkerella* sp.1 can leave the fig via a hole on the fig wall bitten out by males of this species. Males of *Walkerella* sp.2 are not able to make a hole on the fig wall and so have to leave the fig through a hole bitten by pollinating fig wasp males. Males of both *Walkerella* species disperse from their natal figs and mate outside the figs.

3.3 Spatial distribution

The pedicels of each gall containing *Walkerella* sp.1 was 0 mm, suggesting that all the *Walkerella* sp.1 larvae are distributed in the most external layer of the fig. In contrast, the pedicels of galls containing *Walkerella* sp.2 were from 0 mm to 3.34 mm, which indicated that larvae of this wasp can develop in the inner ovary layer, the middle ovary layer and the external ovary layer of figs. However, nearly a quarter of *Walkerella* sp.2 larvae were in most external layer where the galls did not have pedicels. Only a few larvae were distributed in the innermost layer where the galls have the longest pedicels (Fig. 1).

3.4 Sex ratios and brood size

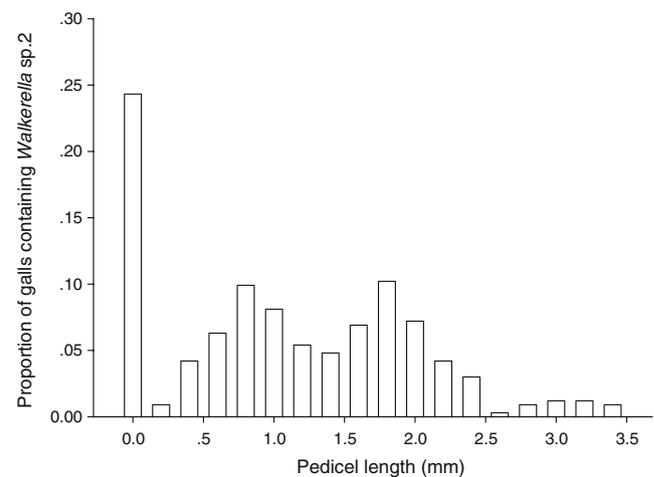
In Table 1, we show the characteristics of the two *Walkerella* species. In each crop, the overall sex ratio (proportion of males) of the two species was female biased. For *Walkerella*

Table 2 Single foundress brood size and sex ratios of two *Walkerella* species

Fig wasp species	Sample size	Brood size (mean±S.E.)	Sex ratios
<i>Walkerella</i> sp.1	12	12.92±1.93	0.25
<i>Walkerella</i> sp.2	16	7.75±0.77	0.29

sp.1, overall sex ratios were not significantly correlated with the proportion of figs occupied in a crop (GLM: $\beta \pm \text{S.E.} = -0.31 \pm 0.50$, $P=0.52$). For *Walkerella* sp.2, however, the overall sex ratios significantly increased with the proportion of figs parasitized in a crop (GLM: $\beta \pm \text{S.E.} = 0.60 \pm 0.25$, $P < 0.05$). The progeny sex ratio of *Walkerella* sp.1 did not decrease significantly as brood size increased (GLM: $\beta \pm \text{S.E.} = -0.06 \pm 0.05$, $P=0.21$). Similarly, progeny sex ratios of *Walkerella* sp.2 did not decrease as brood size increased (GLM: $\beta \pm \text{S.E.} = -0.01 \pm 0.01$, $P=0.26$).

After controlling for foundress number, we found both species had female biased sex ratios. Single foundress sex ratios of the two *Walkerella* species did not significantly differ (t-test: $t_{26} = -0.87$, $P=0.36$), but single foundress brood size of *Walkerella* sp.1 is significantly more than that of *Walkerella* sp.2 (t-test: $t_{26} = 2.77$, $P < 0.05$). In addition, 4 (33.33%) of the 12 figs experimentally manipulated using *Walkerella* sp.1 contained clutches with one male eggs and

**Fig. 1** Spatial distribution in figs of *Walkerella* sp.2

several female egg, and 6 (37.50%) of the 16 figs experimentally manipulated using *Walkerella* sp.2 contained clutches with one male egg and several female eggs.

4 Discussion

Walkerella sp.1 and *Walkerella* sp.2 are both externally ovipositing NPFW. The process of oviposition of the two species generally included searching for oviposition sites, penetrating the fig wall, oviposition and withdrawing the ovipositor in a similar way to other NPFW (Zhen et al. 2005).

Our results showed that the larvae of both *Walkerella* sp.1 and *Walkerella* sp.2 can develop in figs without any other fig wasps confirming that both species are gallers. For gallers, oviposition timing in figs is very important because space constraints probably prohibit later oviposition (Elias et al. 2008). Some studies indicate that the largest wasps oviposit well before receptivity which enables the galls to grow larger (Elias et al. 2008). Both *Walkerella* sp.1 and *Walkerella* sp.2 oviposited in A-phase figs and induce large galls, but their ovipositing sequence is different. Joussetin et al. (2006) found that *Otitesella longicauda* and *O. rotunda* associated with *Ficus ingens* differ in ovipositor lengths and assumed this difference might lead to a different timing of oviposition. In our study, however, the two *Walkerella* species inhabit two different species of fig tree. A difference in ovipositor length therefore cannot be used to explain the different timing of oviposition. *Walkerella* sp.1 was the first NPFW to oviposit in *F. curtipes*, which means that *Walkerella* sp. 1 does not compete with any other fig wasp for reproductive resources. In contrast, *Walkerella* sp.2 oviposited in *F. benjamina* after several other NPFW had already oviposited in the fig. As a result, *Walkerella* sp.2 can only use the reproductive resource left by other NPFW foundresses. This different ovipositing sequence would seem to provide *Walkerella* sp.1 with an advantage over *Walkerella* sp.2 in terms of competing for reproductive resource with other fig wasps. Besides oviposition timing, the characteristics of males are different in the two *Walkerella* species. While both *Walkerella* sp.1 and *Walkerella* sp.2 can develop in figs that have not been pollinated, males of the former can chew their way out of the figs, while the latter cannot and must rely on the exit holes provided by pollinator males. The *Otitesella* wasps observed by J.M. Greeff can also develop in figs without the pollinator's presence, but none of them can find their own way out like *Walkerella* sp.1 (J.M. Greeff, *personal observation*). This suggests that chewing their way out of the figs is not common in the subfamily Otitesellinae.

Our result also show that *Walkerella* sp.1 and *Walkerella* sp.2 exhibit different spatial distributions in figs. All

Walkerella sp.1 are distributed in the most external layer, while *Walkerella* sp.2 can also occur in the external, middle or inner ovary layer. Pollinating fig wasp females reproduce by inserting their ovipositors into the styles of fig flowers. One study found NPFW use their ovipositor to penetrate the ovary directly and lay their eggs in it (Peng et al. 2005b). We assume that both *Walkerella* sp.1 and *Walkerella* sp.2 also oviposit by directly penetrating the ovary. As *Walkerella* sp.1 was the first fig wasp to oviposit in *F. curtipes*, all the flowers are potentially available for them and this may be the reason why foundresses only oviposited in the most external layer which is easier to reach and thus saves reproduction costs. In the case of *Walkerella* sp.2, several NPFW have already oviposited in *F. benjamina* before it began to oviposit. As a result there may not be enough external-layer flowers for the foundresses to lay all their eggs in. Our results indicated that more than a quarter of *Walkerella* sp.2 progeny were distributed in the most external layer and the progeny number decreased with increasing gall pedicels. This suggests that *Walkerella* sp.2 foundresses use the resource by first accessing the flowers that are easiest to reach, but alternatively use flowers in other layers if the flowers in external layer are occupied. In contrast to our results, Moore et al. (2004) found that in both *Otitesella longicauda* and *O. rotunda* wasps, the eggs that are laid near the center of the fig result in larger galls. This suggests that *Otitesella* foundresses adjust spatial allocation of their offspring according to progeny body size. A comparison of spatial allocation within figs between *Walkerella* and *Otitesella* indicates that the two genera adopt different reproductive strategies, even though they belong to the same subfamily Otitesellinae.

Our data suggest that single foundresses of both *Walkerella* species produce female-biased sex ratios in situations where competition between males is at a low level. Fellowes et al. (1999) found sex ratios of several externally ovipositing NPFW were not extremely female-biased or were even male biased in nature. The sex ratios of the two *Walkerella* species studied here were also not extremely female-biased in all the natural crops. Males of both species have the ability to disperse and mate outside the figs. This engaging in non-local mating may explain why sex ratios of both species are not extremely female-biased. West and Herre (1998) show a positive correlation between sex ratios of NPFW species and the proportion of figs parasitized by a given species. Fellowes et al. (1999) found this positive correlation only across wingless male species, but not across winged male species. The overall sex ratio of *Walkerella* sp.2 increased with the proportion of figs parasitized in a crop. However, in the case of *Walkerella* sp.1, the correlation was not significant. We collected more than 10 crops of *F. curtipes* figs, but *Walkerella* sp.1 was only found in four crops which may not have been enough to assess whether the overall sex ratio

of *Walkerella* sp.1 varied with the proportion of figs attacked. Comparing these data to Greeff (1997) suggest that *Walkerella* sp. 1 can detect population density and take it into account while allocating sex. We found no sex ratio trends with brood size suggesting that females of both *Walkerella* species have no information about the patches on which they oviposit. Conversely, Pienaar and Greeff (2003) found that females of three species belonging to *Otitessella* genus respond to population densities at the level of individual figs. In addition, Pienaar and Greeff (2006) confirmed that foundresses of *Otitessella pseudoserrata* do have knowledge as to whether they were the first to arrive for oviposition. We conclude that foundresses of some species of non-pollinating fig wasps have knowledge of their oviposition site, while those of others do not.

The fact that females of both species produce clutches consisting of female eggs except for one male egg supports Greeff's (1997) predictions.

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