

ORIGINAL ARTICLE

Pollinating fig wasp *Ceratosolen solmsi* adjusts the offspring sex ratio to other foundressesHao-Yuan Hu¹, Zhong-Zheng Chen¹, Zi-Feng Jiang², Da-Wei Huang^{3,4}, Li-Ming Niu⁵
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Abstract Local mate competition theory predicts that offspring sex ratio in pollinating fig wasps is female-biased when there is only one foundress, and increased foundress density results in increased offspring sex ratio. Information of other foundresses and clutch size have been suggested to be the main proximate explanations for sex ratio adjustment under local mate competition. Our focus was to show the mechanism of sex ratio adjustment in a pollinating fig wasp, *Ceratosolen solmsi* Mayr, an obligate pollinator of the functionally dioecious fig, *Ficus hispida* Linn., with controlled experiments in the field. First, we obtained offspring from one pollinator and offspring at different oviposition sequences, and found that offspring sex ratio decreased with clutch size, and pollinators produced most of their male offspring at the start of bouts, followed by mostly females. Second, we found that offspring sex ratio increased with foundress density, and pollinators did adjust their offspring sex ratio to other females in the oviposition patches. We suggest that when oviposition sites are not limited, pollinators will mainly adjust their offspring sex ratio to other foundresses independent of clutch size changes, whereas adjusting clutch size may be used to adjust sex ratio when oviposition sites are limited.

Key words behavior, co-evolution, local mate competition, mutualism, pollinating fig wasp, sex ratio adjustment

Introduction

Sex ratio in a local environment has been taken as a model of sex ratio theory (Hamilton, 1967; Frank, 1985; Herre, 1985, 1987; West *et al.*, 2000; Steiner & Ruther, 2009; West, 2009) and a case study of adaptation in evolutionary biology (Fellowes *et al.*, 1999). In a random-mating populations of infinite size, natural selection favors equal investment in both sexes, and an equal sex ratio is an evolutionary stable result (Fisher, 1930). However, in a

highly structured population, such as mating only between full siblings, evolutionary stable strategy models predict a female-biased sex ratio (Hamilton, 1967; Maynard Smith, 1976). In haplodiploid hymenoptera, with haploid males (developed from unfertilized eggs) and diploid females (developed from fertilized eggs), the primary sex ratio is determined by the mothers' control of fertilization at the time of oviposition (Charnov, 1982).

There may be natural selection on foundresses to adjust their offspring sex ratio because of local mate competition (LMC) (Charnov, 1982; West *et al.*, 2005). When patches are founded by one female and all mating occurs between siblings, brothers may compete locally with each other for mating with their sisters. Such LMC selects for fewer male offspring (Sheldon & West, 2002). If offspring in a

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patch originate from two foundresses, the value of sons increases because sons have the potential to mate with the daughters of other foundresses, and a less female-biased offspring sex ratio is preferred (Hamilton, 1967, 1979; Herre, 1985, 1987; Werren, 1987). Sex ratios increase with foundress number, as LMC models predict, in many parasitoid wasps (reviewed in King, 1993) and some fig wasps (e.g., Raja *et al.*, 2008).

The proximate explanations for such sex ratio adjustment under LMC may differ among species (Moore *et al.*, 2005). Some reports have argued that clutch size might be one of the main explanations when more parasitoid wasps or fig wasps oviposit in a limited patch (Kjellberg *et al.*, 2005; Moore *et al.*, 2005; Raja *et al.*, 2008). When multiple foundresses oviposit in figs, oviposition site limitation would lead to reduction of offspring reproduction (Moore & Greeff, 2003). Limited clutch size and the oviposition order of fertilized and unfertilized eggs may lead to a less female-biased sex ratio (Kjellberg *et al.*, 2005; Moore *et al.*, 2005; Raja *et al.*, 2008; Sun *et al.*, 2009). Another explanation of sex ratio adjustment under LMC is foundress density affecting probability of ovipositing a son and that probability being independent of order. Foundresses may adjust their offspring sex ratios by the information of other foundresses or of oviposition in a patch left by other foundresses (Hamilton, 1967, 1979; Herre, 1985, 1987; Kinoshita *et al.*, 2002; Moore *et al.*, 2002; Pereira & Prado, 2006; Herre *et al.*, 2008; Abe *et al.*, 2009; Somjee *et al.*, 2011).

In some pollinating fig wasps, clutch size would be the major explanation to sex ratio adjustment under LMC (Kjellberg *et al.*, 2005; Moore *et al.*, 2005; Raja *et al.*, 2008; Sun *et al.*, 2009). The effect of sex adjustment to other foundresses has been called in to question (Kjellberg *et al.*, 2005). But oviposition sites would not be always limited when only several foundresses lay eggs in a patch. When oviposition sites in a patch are sufficient, clutch size should be unaffected by foundress density. Given this, we predict that the effect of clutch size on sex ratio adjustment should be weak when oviposition sites are rarely limited, as in some figs with plenty of florets, where oviposition sites are always enough. We test this with *Ceratosolen solmsi* Mayr, an obligate pollinator of the functionally dioecious fig, *Ficus hispida* Linn.

Materials and methods

Study species and site

Experiments on *Ficus hispida* Linn. – *Ceratosolen solmsi* Mayr mutualism were conducted at the Chinese

Academy of Tropical Agricultural Sciences (CATAS), Danzhou, Hainan province, China (19°30.410'S, 109°29.340'E). Hainan Island is located south of the China mainland separated by the Qiongzhou Strait, approximately 40 km wide. The climate includes well-defined dry (November–April) and rainy (May–October) seasons, and the annual mean temperature is 24.3°C, with the lowest mean temperature in February (18.2°C) and the highest in July (29.6°C).

Ficus hispida is a functionally dioecious and free-standing tree, with inter-sexually synchronously flowering phenologies. Most fruits grow on fruit branches, and can be kept away from pollinators using specially made securing nylon bags during fig receptivity. Pollinators can be collected from mature male fruits in mesh-lidded pots just before wasp emergence (Hu *et al.*, 2009, 2010).

Offspring sex ratio and clutch size

To investigate the effect of clutch size on offspring sex ratio, we obtained offspring from one-foundress figs. Female pollinators were collected as above and immediately introduced into the protected receptive figs with a soft brush. One pollinator was allowed to enter each fig, and then the figs were re-bagged individually; 241 one-foundress figs were obtained from seven male *F. hispida* trees from January to December in 2007.

Small clutch size can be obtained by ceasing oviposition after the pollinator's entry. Pollinators oviposit inside figs, and it is hard to cease the oviposition and keep development of the figs at the same time. Recent research has used poisons such as insecticide pyrethrum (Raja *et al.*, 2008) and ether (Sun *et al.*, 2009) to cease the oviposition. Patino *et al.* (1994) showed that when figs reach temperatures higher than 8°C above the ambient temperature in full sunlight, pollinators inside figs would be killed. Warm water has been used to kill pollinators inside figs (Hu *et al.*, 2009). In this article, warm water (36–40°C), 8°C above ambient temperature, was injected into a plastic bag (≈ 2 L), and the figs were put into the bag to kill pollinators *in situ*. One-foundress figs were opened at 2-min intervals after the figs were put into warm water to examine whether the foundress was dead or not. Ten minutes were selected because foundresses inside large and small figs were all dead then. Twenty one-foundress figs warmed at 4 h after pollinator entry were protected from entry by other foundresses with nylon bags, and 13 treated figs matured normally. Previous research has shown that *C. solmsi* could only live in figs for less than 24 h, and the duration of oviposition lasts less than 9 h (Yang *et al.*, 2002). Thus, three treatments were designed: one without

warming, the other two with 2- and 4-h intervals (from pollinator entering to warming) respectively. More than 50 one-foundress figs were used in each treatment on two male *F. hispida* trees in September 2007 and August 2008, respectively.

Offspring sex ratio and foundress density

To investigate the effect of foundress density on the offspring sex ratio, the following experiments were conducted. Five treatments were designed with 1–5 foundresses respectively, and more than 30 figs were used in each treatment. Female pollinators were collected as above and immediately introduced into the protected receptive figs. Wasps introduced to multiple-foundress figs were from mature figs on different fig trees, which ensured that the wasps were non-siblings. In the multiple-foundress figs, foundresses were allowed to enter each fig at 20-min intervals so the earlier entrants could finish crawling through most of the ostiolar bracts. The experiments were conducted on five male *F. hispida* trees from January to December in 2007.

Oviposition sites would not be limited in multiple-foundress figs if the entered foundresses were killed and oviposition inside figs ceased. One-foundress and three-foundress figs were obtained. Two hours after the first foundresses were introduced into figs, the figs were warmed and oviposition inside figs ceased with the methods as above. More than 30 figs were used in each treatment on a male *F. hispida* tree in August 2008.

Data analyses

When the figs matured, female and male wasps, galls, and total female flowers in each fig were counted. Total female flowers were counted from a quarter part of the fig. The proportional data, such as sex ratio, often have non-normally distributed errors and are difficult to analyze with traditional analysis of variance (ANOVA) techniques (Hardy, 2002). To avoid these problems, we first analyzed the sex ratio data using generalized linear model (GLM) analysis of deviance, assuming binomial errors, and a logit link function in R2.6.1 (Ihaka & Gentleman, 1996; Crawley, 2007). The number of male wasps in a fig was used as the response variable, and the total offspring number in a fig was used as the binomial denominator. We calculated a heterogeneity factor (HF), the ratio of residual deviance to the residual degrees of freedom, to examine the data for overdispersion. However, HF in our analyses were all larger than 3, which means the data would not fit the assumption of binomial errors.

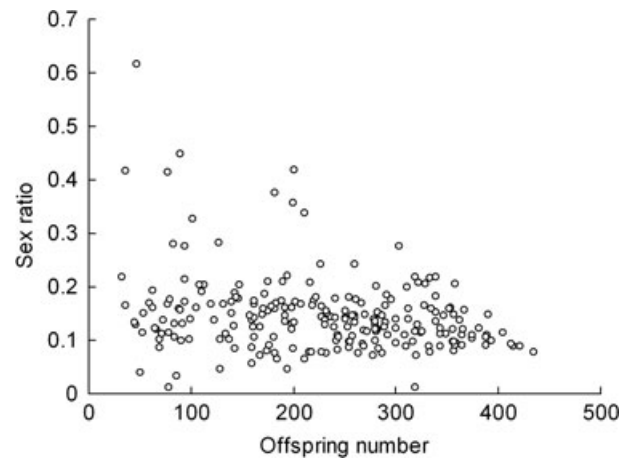


Fig. 1 Correlation between clutch size and sex ratio of *Ceratosolen solmsi* in one-foundress figs. Offspring sex ratio decreased with clutch size ($F_{1,230} = 13.45$, $P < 0.001$, $r = -0.24$).

The sex ratio data were arcsine square root transformed and used as the response variable in the analyses assuming normal errors (Flanagan *et al.*, 1998; Crawley, 2007). The other analyses were also finished in R2.6.1.

Results

Clutch size and offspring sex ratio in figs with one foundress

Of the 241 one-foundress figs, nine of them had only male offspring and were removed for further analyses. Mean numbers of female florets and galls (including empty galls) per fig were 1766.19 ± 300.66 and 312.96 ± 73.45 , respectively. Mean numbers of male and female offspring per fig were 31.14 ± 16.34 and 194.56 ± 89.47 , respectively. Thus, female florets were more than one foundress could use. Offspring sex ratios were highly female-biased and mean sex ratio (male/total offspring) was 0.15 ± 0.07 . Offspring sex ratio (arcsine square root transformed) decreased with clutch size ($F_{1,230} = 13.45$, $P < 0.001$, $r = -0.24$) (Fig. 1), which is consistent with the theoretical expectation that males are produced first.

To investigate the sex ratios at different oviposition sequences, we compared the offspring sex ratio at three time points: 2 h, 4 h and normal (life-long), and found that sex ratios (arcsine square root transformed) were not significantly different ($F_{2,102} = 1.46$, $P = 0.24$). The number of male and female offspring both significantly changed among treatments ($F_{2,102} = 15.76$, $P < 0.001$; $F_{2,102} = 38.43$, $P < 0.001$, respectively).

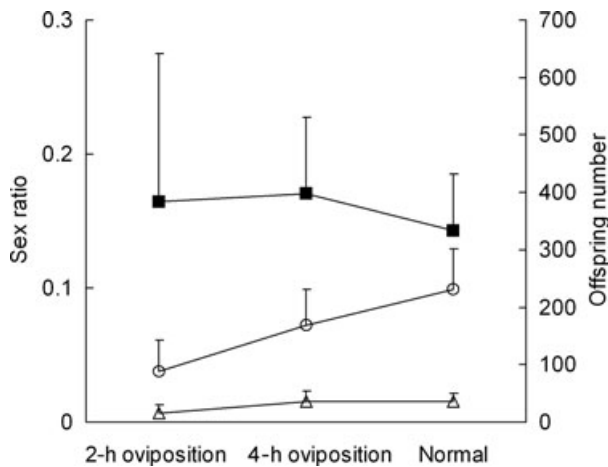


Fig. 2 Offspring sex ratio (square), male (triangle) and female (circle) *Ceratosolen solmsi* offspring (means \pm SD) in one-foundress figs with 2- and 4-h oviposition duration. Sex ratio was not significantly different ($F_{2,102} = 1.46$, $P = 0.24$), and pollinators tended to produce most male offspring at the start of bouts, followed by mostly females.

Male offspring significantly differed between 2-h and 4-h treatments (least significant difference test [LSD], $P < 0.001$) but were similar between the 4-h treatment and normal (LSD, $P = 0.61$), and female offspring significantly differed between treatments (LSD, all $P < 0.001$). Pollinators tended to produce most of their male offspring at the start of bouts, followed by mostly females (Fig. 2).

Foundress density and offspring sex ratio

In the one-foundress and multi-foundress figs, floret numbers are similar ($F_{4,207} = 1.54$, $P = 0.19$). Offspring sex ratio (arcsine square root transformed) was significantly different among the five treatments ($F_{4,207} = 22.70$, $P < 0.001$), and significantly increased with foundress density ($F_{1,210} = 78.44$, $P < 0.001$, $r = 0.52$) (Fig. 3).

Offspring sex ratio in figs with one or more foundresses with similar total numbers of offspring in the fig were compared (Table 1). One-foundress figs usually had less than 400 offspring and only three multi-foundress figs had less than 150. Therefore, only figs with between 151–400 offspring were analyzed. Sex ratios (arcsine square root transformed) in multi-foundress figs were all significantly higher than that in one-foundress figs when the number of total offspring in the two types of figs were similar (Table 1).

In those three-foundress figs with 2-h oviposition duration, mean numbers of galls, and male and female offspring per fig were 259.92 ± 61.16 , 29.83 ± 11.82 , 94.75 ± 65.95 (all $n = 12$), respectively. Compared to

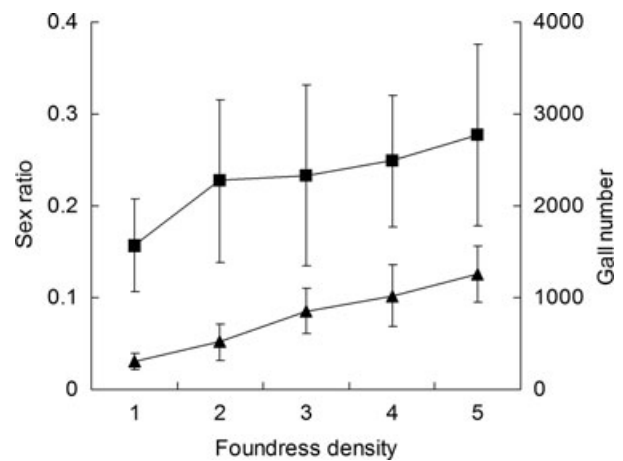


Fig. 3 Offspring sex ratio of *Ceratosolen solmsi* and gall number at different foundress densities. Offspring sex ratio (square) significantly increased with foundress density ($F_{1,210} = 78.44$, $P < 0.001$, $r = 0.52$).

one-foundress figs with 2-h oviposition, sex ratio (arcsine square root transformed) in three-foundress figs was significantly larger ($t_{19.89} = 2.55$, $P = 0.02$) (Fig. 4).

Discussion

Previous reports have shown that a female-biased sex ratio is expected when there is one foundress ovipositing in the fig cavity, and a lower female-biased sex ratio with increasing foundress density (Hamilton, 1967, 1979; Charnov, 1982; Herre, 1985, 1987; Werren, 1987). Our results show that offspring sex ratio significantly increases with foundress density, and sex ratio adjustment of the pollinator is in line with the theoretical prediction of LMC models. Clutch size has been suggested to be one of the proximate explanations for sex ratio adjustment under LMC (Kjellberg *et al.*, 2005; Moore *et al.*, 2005; Raja *et al.*, 2008; Sun *et al.*, 2009). Some pollinating fig wasps produce most male offspring at the beginning of oviposition (Moore *et al.*, 2005; Kjellberg *et al.*, 2005; Raja *et al.*, 2008; Sun *et al.*, 2009). If multiple foundresses oviposit in a fig, there should be a reduction in clutch size per foundress because of limited oviposition sites, and the LMC sex ratio increasing proportionately with foundress density would be expected (Kjellberg *et al.*, 2005; Moore *et al.*, 2005; Raja *et al.*, 2008; Sun *et al.*, 2009). In the present study, a significantly negative relationship between offspring sex ratio and clutch size was found in normal one-foundress figs. Pollinators tended to produce most of their male offspring at the start of bouts, followed by mostly females, which is similar to *Liporhopalum tentacularis* (Raja *et al.*, 2008). In *F. hispida*

Table 1 Comparisons of offspring sex ratio (means \pm SD) of pollinators between figs with one or more foundresses with similar clutch size.

Range of clutch size	Figs with one foundress	Figs with more than one foundress	<i>t</i> -test for means of clutch size	<i>t</i> -test for sex ratio (arcsine square root transformed)
151–200	0.16 \pm 0.03 (20)	0.24 \pm 0.07 (11)	$t_{17.23} = 0.74$, NS	$t_{13.67} = 3.73^{**}$
201–250	0.16 \pm 0.04 (10)	0.26 \pm 0.14 (13)	$t_{19.28} = 0.41$, NS	$t_{15.69} = 2.67^*$
251–300	0.13 \pm 0.03 (19)	0.23 \pm 0.09 (9)	$t_{18.21} = 0.46$, NS	$t_{9.03} = 3.22^*$
301–350	0.15 \pm 0.07 (7)	0.30 \pm 0.11 (10)	$t_{14.47} = 0.35$, NS	$t_{14.06} = 3.56^{**}$
351–400	0.13 \pm 0.04 (9)	0.23 \pm 0.09 (6)	$t_{13} = 2.07$, NS	$t_{6.44} = 2.55^*$

The number in parentheses means sample size. NS, not significant at $P > 0.05$. * $P < 0.05$, ** $P < 0.01$.

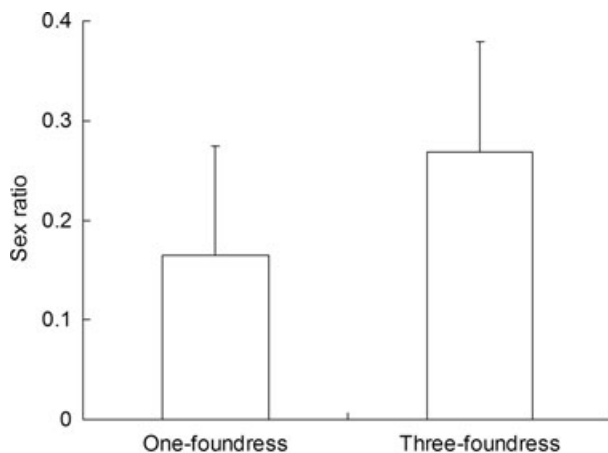


Fig. 4 Offspring sex ratio of *Ceratosolen solmsi* in one-foundress and three-foundress figs with 2-h oviposition duration. Sex ratio was significantly larger in three-foundress figs ($t_{19.89} = 2.55$, $P = 0.02$).

figs, there are enough florets, and oviposition site limitation would be weak when only a few foundresses oviposit in the figs, in which case clutch size changes are unlikely to provide a proximate mechanism for increased sex ratios in response to other mothers. However, we suggest that changes in clutch size as a mechanism for sex ratio adjustment under LMC of the pollinator would work when far more foundresses enter into the fig cavity, because then oviposition sites would be limited.

Alternatively, foundresses may adjust their offspring sex ratio in regard to other foundresses or in regard to oviposition in a patch left by other foundresses independently of order and clutch size (Hamilton, 1967, 1979; Herre, 1985, 1987; Werren, 1987; Kinoshita *et al.*, 2002; Abe *et al.*, 2009; Somjee *et al.*, 2011). Given another foundress in a short interval (0.5 h), Kinoshita *et al.* (2002) found contacting another foundress would cause a less female-biased sex ratio, which indicates pollinating fig wasps could adjust the offspring sex ratio in re-

gard to other foundresses. After clutches from different foundresses have been distinguished quantitatively, Greeff & Newman (2011) illustrated that the pollinating fig wasp *Platyscapa awekei* simultaneously uses its own clutch size as well as the other females in allocating sex, and especially, the wasp mostly adjusts its sex ratio in response to total foundresses and their clutch sizes. Our results show that those multi-foundress figs, with similar clutch size to one-foundress figs, had significantly higher offspring sex ratio, which suggests that foundress density significantly affected offspring sex ratio, even independent of clutch size. When oviposition only lasted for 2 h by experimental design, there was significantly higher sex ratio in three-foundress figs than in one-foundress figs, which indicates that the explanation to the sex ratio adjustment under LMC should mainly be in regard to other foundresses.

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Disclosure

The authors declare that they have no conflict of interest.

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