

## Costs of inflorescence longevity for an Asian fig tree and its pollinator

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**Abstract** In ecological situations where interactions between two species are to their mutual benefit, traits are expected to evolve to maximise the value of the timing of their encounters. Plants that depend on animals for pollination vary in the longevity of their flowers and also in how the quality of the rewards they offer varies in flowers of different ages. However, costs of floral longevity are rarely studied. Using field experiments with *Ficus semicordata*, a SE Asian dioecious fig tree, we examined sexual differences in syconium ageing, how the reproductive success of the plant and its pollinator change with syconium age and whether these changes are reflected in pollinator preferences. Un-pollinated syconia remained receptive to their host-specific pollinators for long periods, but eventually abort. Compared with male syconia, un-pollinated female syconia aborted more quickly and lost their ability to attract pollinators more quickly. Older pollinated female syconia were also more likely to abort. Further, declines in productivity with syconium age were also more apparent in female syconia, though older male syconia also produced fewer, smaller wasp offspring. The longevity costs are reflected in pollinator preferences. This suggests that sexual differences in duration of receptivity may be adaptive and a component of the reproductive strategies. It also indicates that placing fig wasps onto older syconia over-estimates their likelihood of being pollinated under natural conditions and prolonged receptivity increases the likelihood of pollination at the cost of reduced productivity with syconium age. This opens interesting perspectives on the co-evolution of this inter-specific interaction.

**Keywords** Ageing · *Ficus* · Fig wasp · Mutualism · Pollination · Receptivity

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## Introduction

In animal-pollinated plants, floral longevity (the length of time a flower has viable pollen and receptive stigmas) equates with the maximum period for which a flower can wait for a pollinator to arrive (Petanidou et al. 2001; Celedón-Neghme et al. 2007). Floral longevity can vary from hours to weeks in different plant species and reflects a balance between the benefits of increased pollinator visits and the costs of continued flower maintenance (Primack 1985; Ashman and Schoen 1994; Yasaka and Nishiwaki 1998; Abe 2001; Rathcke 2003). For pollinators, the rewards on offer may decline or increase as the flowers get older (Zimmerman and Pyke 1986; Fenster et al. 2006; Ollerton et al. 2007).

The interaction between fig wasps and their host fig trees (*Ficus* spp.) is a striking example of an obligate pollination mutualism (Janzen 1979; Weiblen 2002) that has broader ecological consequences because of the large numbers of animals that feed on syconia (fig fruits—the inflorescences of *Ficus* species) once they are mature (Shanahan et al. 2001). The syconium is urn-shaped and lined with numerous tiny uniovulate female flowers. Species-specific fig wasp females (Agaonidae: Hymenoptera) carry pollen from their natal syconia into receptive syconia, entering through a narrow bract-lined ostiole. Once inside the foundresses actively or passively pollinate the flowers, some of which can also be galled and have eggs laid in them (Ramirez 1970; Wiebes 1979; Weiblen 2002; Herre et al. 2008). After mating, the winged female wasps of the next generation emerge through the exit hole created by the males and fly in search of a syconium at an earlier stage of development, which is usually on another tree (Ware and Compton 1994a). Whether the wasps oviposit depends on the breeding system of the host *Ficus*. If it is a monoecious species then each syconium produces seeds and pollinator offspring, but in dioecious fig trees there is reproductive specialization, with male trees producing only pollinator offspring and no seeds, and female trees producing only seeds (Herre et al. 2008).

Successful pollination of fig trees depends on a specific species of fig wasp managing to find receptive syconia of the correct host plant. Receptive syconia display several traits that increase the likelihood of successful visitation by pollinators. These include (1) emitting species-specific volatile chemicals to attract their pollinators (van Noort et al. 1989; Ware and Compton 1994b; Grison-Pigé et al. 2002); (2) closing the ostiole at varying rates after pollinator entry depending on foundress number, thereby balancing the needs of individual syconia with the total number of syconia that can be entered by a given number of fig wasps (Verkerke 1989; Hu et al. 2010) and (3) prolonging the duration of the receptive period of un-pollinated individual syconia (Anstett et al. 1995; Khadari et al. 1995). In *Ficus* species, the length of the receptive period during which unpollinated syconia are attractive to pollinators appears to vary from a few 5 days to several weeks (Newton and Lomo 1979; Khadari et al. 1995; Bronstein and Hossaert-McKey 1996; Patel 1996). After pollinator entry, receptivity is lost quickly (Ramirez 1970; Janzen 1979), though some syconia can extend their receptive period if visited by only a single pollinator (Khadari et al. 1995). Extended receptivity following the entry of the first pollinators clearly influences the total number of wasps that are likely to enter. Too few foundresses can reduce the efficiency of reproduction (because more female flowers remain un-utilized), but the value of additional foundresses declines as more of them are present. This is because of mutual interference and eventual saturation of the flowers that are available for pollination or oviposition. Additional foundresses also increase the risk of diseases being carried into a fig (Herre 1993). The duration of receptivity not only influences the

probability that a syconium will be pollinated, but also the local dynamics of fig wasp populations and their likelihood of local extinction (Anstett et al. 1995).

Prolonging the duration of receptivity may maximize the number of encounters, but the optimal numbers of pollinator visits for female function may be different from what is optimal for male function (Celedón-Neghme et al. 2007; Khadari et al. 1995). This difference is most readily visualized in dioecious plants. Around half the 800 or so species of fig trees have a dioecious breeding system, where female trees produce seeds and male trees produce pollen-carrying fig wasp offspring (Herre et al. 2008). This is achieved because the pollinating wasps do not avoid female syconia despite their total failure to reproduce there, and because they continue to effect pollination once they are inside (Raja et al. 2008). Mutual mimicry between the sexes is responsible for this deception (Grafen and Godfray 1991; Weiblen et al. 2001), but some differences between the sexes are nonetheless evident. Receptivity of female flowers lasts longer on male trees than on female trees of *Ficus carica* (Khadari et al. 1995), whereas female syconia of *Ficus montana* maintain receptivity for longer than male syconia (Suleman et al. 2011). Varying temperatures (Khadari et al. 1995), asynchronous within-tree fruiting patterns (Suleman et al. 2011), and seasonal variation in the timing of fruiting (Patel and Hossaert-Mckey 2000) have been linked to these differences, which may also reflect different selection pressures acting on male and female function. One potential selection pressure is different costs of inflorescence longevity in male and female *Ficus*.

In this study we conducted controlled experiments using an Asian dioecious *Ficus* species with synchronized fruiting to examine whether the sexes differ in floral traits and to quantify the costs of inflorescence longevity. We asked: how long is the period that male and female syconia remain receptive in the absence of pollinators and after entry of their first pollinator? What is the effect of prolonging receptivity on seed production in female syconia and the reproductive success of the pollinators in male syconia (as measured by the numbers and size of their progeny)? Based on these results we were also able to determine whether the placement of female fig wasps at the ostioles of syconia (the standard technique for determining whether or not a syconium is receptive) over-estimates the likelihood of a fig being pollinated under natural conditions.

## Materials and methods

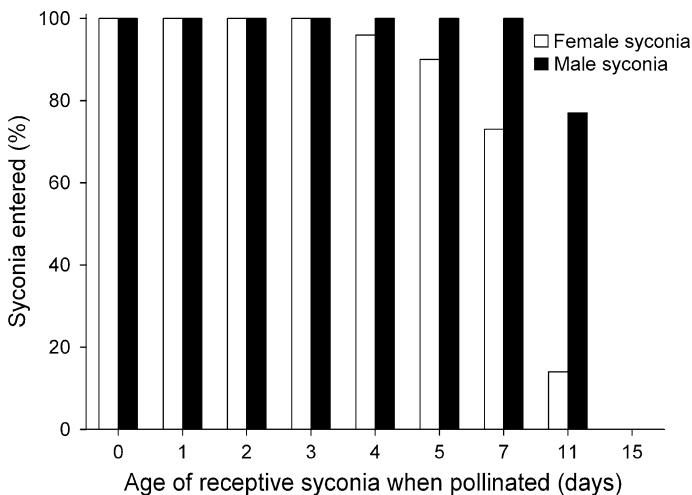
### Study species and sites

*Ficus semicordata* Buch.-Ham. ex J. E. Sm. (section *Hemicardia*, subgenus *Sycomorus*) has a wide distribution across SE Asia. At our Xishuangbanna Tropical Botanical Garden (XTBG) study site in SW China it is pollinated by *Ceratosolen graveleyi* Grandi. The tree grows to a height of up to 10 m and produces its syconia on long, slender branches that hang down near to the ground. Syconia are produced in two or three synchronous crops annually, with different trees fruiting at different times. The diameter of syconia on the first day of receptivity varies from 12 to 16 mm. One female syconium contains  $1,631 \pm 16$  female flowers (mean  $\pm$  SE;  $n = 116$ ), and a male syconium has  $1,573 \pm 14$  female flowers ( $n = 133$ ). Under natural conditions, the syconia are entered by between one and nine foundresses, with a significantly higher number of foundresses entering female figs (mean  $\pm$  SE pollinators per syconium =  $1.96 \pm 0.08$ ,  $n = 234$  for female syconia;  $1.67 \pm 0.08$ ,  $n = 182$  for male syconia; Wilcoxon test:  $W = 98,553$ ,  $P < 0.001$ ). Foundresses have not been observed to re-emerge from syconia after entry. Receptive syconia of

*F. semicordata* produce an unusually simple volatile blend to attract the pollinator, with 4-methylanisole comprising more than 90% of the total. Receptive male syconia are recorded as producing significantly more 4-methylanisole than female syconia, with production of this attractant declining after pollinators enter the syconia (Chen et al. 2009).

### Floral longevity in the absence of pollination

Between July and November 2008, young pre-receptive syconia were enclosed in netting bags on one tree of each sex to prevent oviposition by pollinators and other fig wasps. The onset of receptivity was determined on the basis of pollinator behavior: if freshly-emerged pollinators placed on a syconium succeeded in partially gaining entry within 5 min (at which point they were removed), the syconium was deemed receptive. If still pre-receptive the bag was replaced and the syconium was tested again in the same way the following day. The duration of the receptive period after the first day that pollinators were willing to enter was recorded at intervals by again placing females on the bagged syconia and recording whether or not they attempted to enter them. A syconium was deemed as losing receptivity if three different wasps were not willing to enter it. Syconia that pollinators entered were recorded. A total of 227 female syconia and 202 male syconia were investigated in this way (sample sizes for each syconium age group are listed in the legend for Fig. 1). In addition, 41 female syconia and 32 male syconia that were in the first day of receptivity were selected to observe syconium abortion rates (the ratio between aborted syconia and total syconia) of unpollinated syconia. They were bagged to prevent pollinator entry, and the numbers of aborted syconia were recorded at 5 day intervals, until they had all aborted.



**Fig. 1** Pollinator entry into male and female syconia that had been waiting for varying lengths of time since becoming receptive. Willingness to enter was tested by placing wasps near the ostiole. Sample sizes for female syconia of different ages = 28, 28, 28, 23, 23, 30, 26, 21, 20; for male syconia = 17, 18, 15, 18, 20, 16, 17, 61, 20

## Age-related differences in pollinator attraction

Age-related differences in pollinator attraction were also examined by exposing male and female syconia of different ages to free-flying fig wasps. From April to May 2010, pre-receptive syconia on adjacent male and female trees growing only 2 m apart, were bagged so as to allow un-pollinated syconia of different ages to be exposed to pollinators on the same day. All unbagged and potentially receptive syconia were removed from the trees. At 5:00 AM, 100 mature male syconia (collected the previous day) were placed on the ground about 5 m from the edge of the plants and receptive syconia of varying ages were exposed to allow pollinator entry. The syconia were removed 7 h later and the numbers of pollinators inside was recorded. The experiment was carried out on a wind-free day. The nearest conspecific tree with receptive syconia was more than 300 m away. Totals of 266 female and 207 male syconia were investigated. Numbers of replicates for each syconium age group are listed in the legend of Fig. 2.

## Floral longevity after pollinator entry

The onset and duration of receptivity in one male tree and one female tree was detected as before, but on the first day of receptivity one, three or five pollinators were allowed to enter the syconia before the bags were replaced. Sample sizes for female syconia were 23, 24, 25, and for male syconia were 51, 19, 16 for one, three and five foundress treatments, respectively.

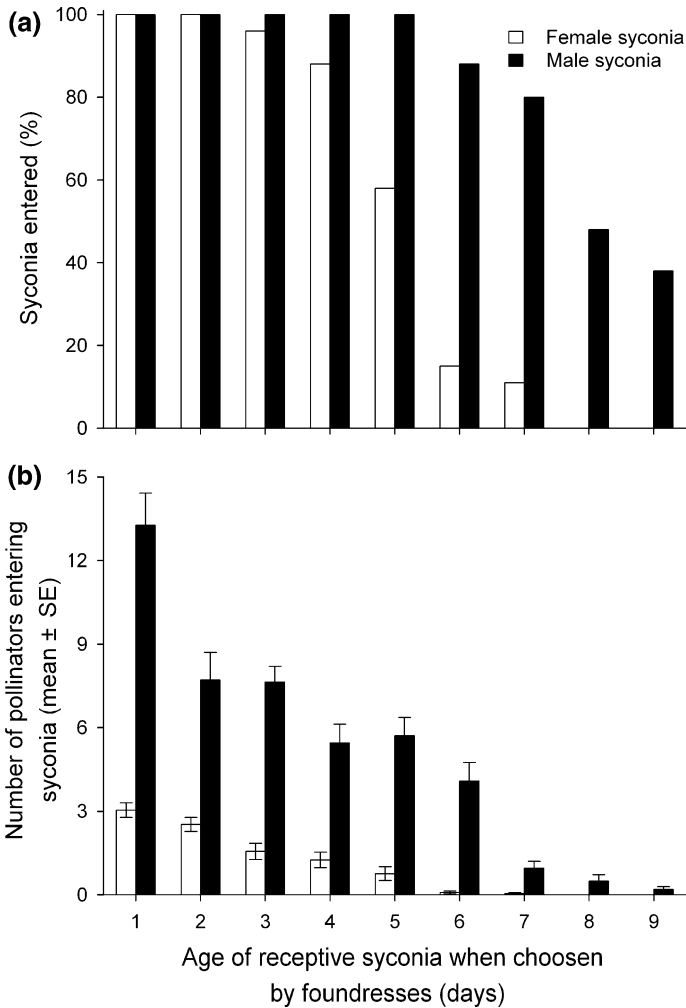
## The reproductive success of syconia entered at different ages

Detection of the onset of receptivity and prevention of unwanted pollination were achieved as before. Single recently emerged pollinators were then allowed entry into male and female syconia of known age and the bags were replaced for the duration of floral development, which takes several weeks. The timing of any subsequent abortions of syconia was recorded and those syconia that reached maturity were then removed and their contents recorded. We recorded the total number of female flowers in each syconium, the numbers of seeds in female syconia and numbers of pollinator progeny and empty galls ('bladders') in male syconia. Sample sizes for female and male syconia of different age groups are given in the legends of Figs. 4, 5.

Body size is one measure of the quality of the fig wasp offspring produced in syconia that were pollinated at different ages. Ten female fig wasps from each of five syconia in each age group were stored in 80% ethanol with added glycerine before their overall length of the head plus body (excluding ovipositor) was measured using an eyepiece graticule mounted on an Olympus SZX12 binocular microscope (see Dunn et al. 2008 for details). A total of 400 wasps were measured, with sample sizes of 50 wasps for each syconium age group.

## Data analysis

We used General linear models (GLM) to compare the proportions of un-pollinated syconia that pollinators were willing to enter. GLMs were also used to analyze the effect of syconium age on biological variables, including abortion rates of pollinated syconia, seed and wasp production, pollination efficiency (proportion of female flowers developed into seeds), wasp reproductive efficiency (proportion of female flowers utilized for wasp



**Fig. 2** **a** The relationship between fig age and likelihood of pollinator entry under ‘free flight’ conditions. **b** The numbers of pollinators that entered the syconia. Sample sizes for female syconia of different ages = 28, 32, 27, 24, 38, 26, 27, 35, 29; for male syconia = 19, 21, 22, 31, 31, 26, 20, 21, 16

offspring developing), and the proportion of empty galls (‘bladders’) in pollinated syconia. Syconium age (length of time a fig had been waiting to be pollinated) and fig gender were included as covariates for above analysis. We used binomial errors where data was proportional (proportions of un-pollinated syconia that pollinator were willing to enter, abortion rates of pollinated syconia, pollination and reproductive efficiency and empty galls), and Poisson errors for count data (seed and fig wasp offspring production). We used Gaussian errors (LM) to analyze the relationship between the age of syconia and body sizes of the pollinator progeny they produced.

Fisher’s exact test was used to analyze differences in syconium receptivity and differences between sexes after different numbers of pollinators had been introduced.

Wilcoxon's rank-sum tests were used to compare the length of time that un-pollinated male and female syconia that were protected from pollinator entry were retained on the trees. All analyses were conducted using R software package (R Development Core Team 2007).

## Results

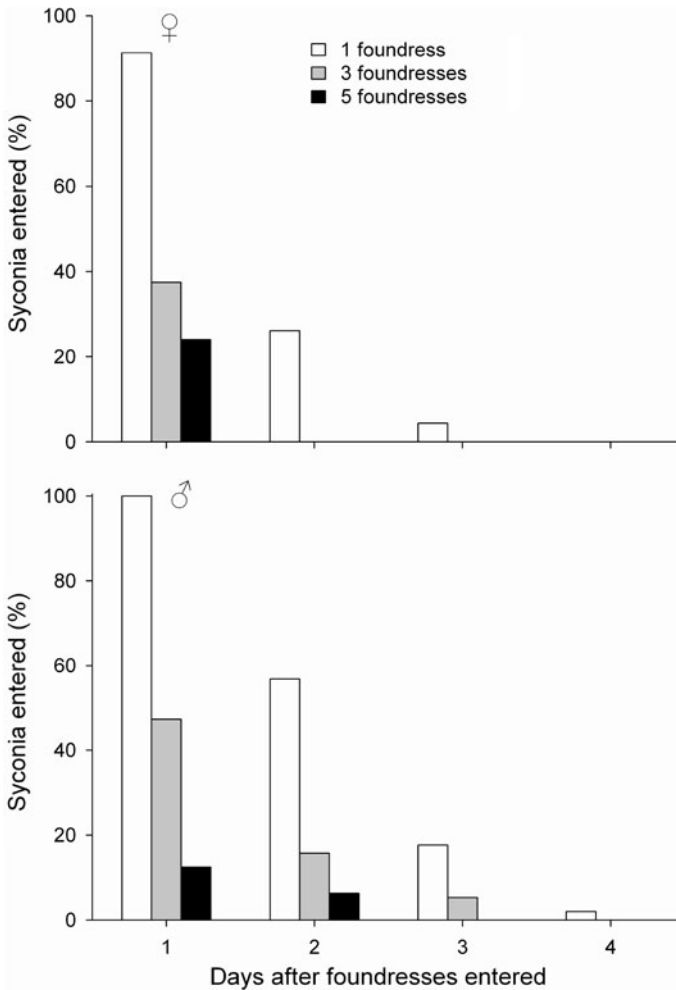
### Duration of syconium receptivity in the absence of pollinators

Based on tests where pollinator females were placed at their ostioles, most syconia that had been protected from pollinator entry were still receptive after 7 days, but a week later they were no longer receptive (Fig. 1). Male and female syconia were equally likely to be entered (GLM,  $Z = -0.83$ ,  $P = 0.41$ ), although female syconia displayed a more rapid decline in receptivity with age than male syconia (Fig. 1). Reflecting this, the effect of syconium age (up to day 11) on syconium entry was only significant for female syconia (GLM,  $\beta \pm SE = -0.11 \pm 0.04$ ,  $Z = -2.87$ ,  $P < 0.01$ ), not for male syconia (GLM,  $Z = -1.00$ ,  $P = 0.32$ ).

The decline in attractivity with syconium age was much more rapid under 'free choice' conditions, where female fig wasps were given the choice of syconia of different ages to fly to and enter (Fig. 2a). Syconia started to fail to attract pollinators after only 3 days (females) or 6 days (males) and no female syconia remained attractive after 8 days. Consequently, the proportion entered by pollinators declined significantly with syconium age in both sexes (GLM,  $\beta \pm SE = -0.09 \pm 0.05$ ,  $Z = -2.07$ ,  $P < 0.05$  and  $\beta \pm SE = -0.40 \pm 0.06$ ,  $Z = -7.27$ ,  $P < 0.01$  for male and female syconia, respectively). Overall, male syconia were more likely to be entered than female syconia (GLM,  $Z = -2.36$ ,  $P < 0.05$ ) (Fig. 2). Male syconia of all age classes were also entered by more pollinators than female syconia of equivalent age and overall the male syconia were entered by larger numbers of pollinators than female syconia (GLM,  $Z = 5.88$ ,  $P < 0.001$ ) (Fig. 2b). The numbers of pollinators entering the syconia of both sexes declined rapidly with syconium age (GLM,  $\beta \pm SE = -0.32 \pm 0.01$ ,  $Z = -21.14$ ,  $P < 0.001$  and  $\beta \pm SE = -0.51 \pm 0.04$ ,  $Z = -14.43$ ,  $P < 0.001$  for male and female syconia, respectively).

### Duration of post-pollination receptivity in syconia entered by different numbers of foundresses

The syconia rapidly became less attractive to pollinators once a pollinator had entered (Fig. 3). Based on the behavior of pollinators placed at the ostiole, the length of receptivity after the entry of one or more foundresses did not differ between the sexes (Fisher's exact tests,  $P = 0.26$ ;  $P = 0.30$  and  $P = 0.34$  for 1, 3 and 5 foundresses, respectively). When only one foundress had been introduced the mean receptive periods were  $2.76 \pm 0.11$  days (male syconia) and  $2.17 \pm 0.15$  days (female syconia). This was significantly longer than after entry of three and five foundresses (Fisher's exact test,  $P < 0.01$  for male syconia;  $P < 0.01$  for female syconia). There was no difference in duration of receptivity between three- and five-founderess syconia (Fisher's exact tests,  $P = 0.25$  for male syconia;  $P = 0.56$  for female syconia).



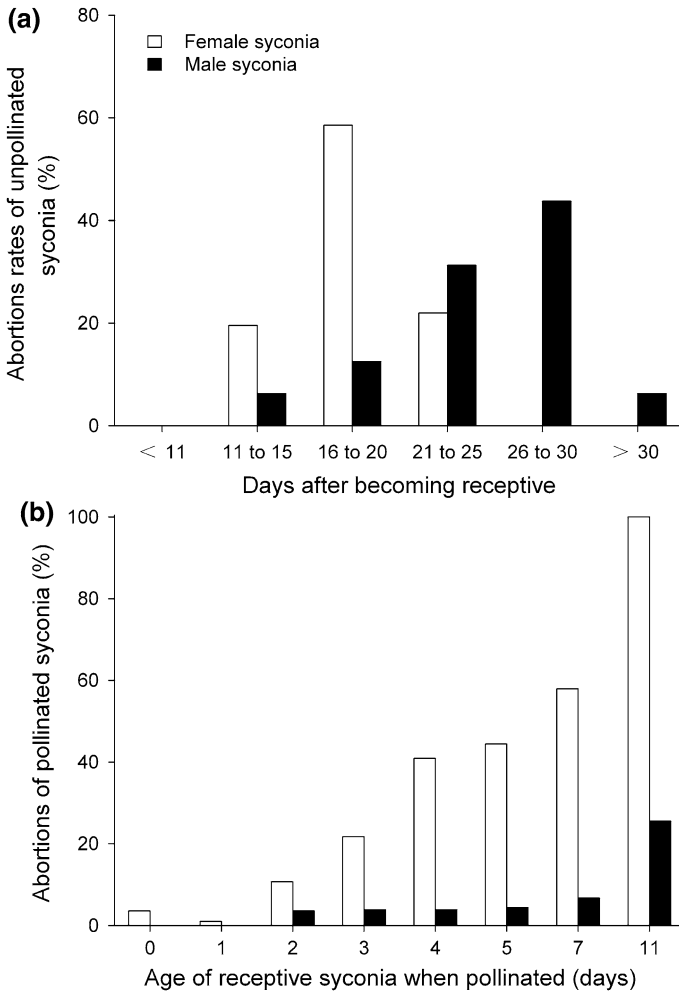
**Fig. 3** The duration of receptivity of syconia after entry by varying numbers of pollinators

#### Abortion rates of unpollinated syconia and Abortions among syconia entered at different ages

The speed at which abortions occurred among syconia that were protected from pollinator entry differed between the sexes with retention times of female syconia significantly shorter than those of male syconia (female syconia =  $18.17 \pm 0.57$  days, male syconia  $24.70 \pm 1.23$  days; Wilcoxon test,  $W = 5329$ ,  $P < 0.001$ ) (Fig. 4a). Male and female syconia both began to abort after day 8, but the peak rates of abortion in female syconia was on days 15–21 after they became receptive, whereas the peak rate of abortion among male syconia was after day 21.

Overall abortion rates among pollinated female syconia were significantly higher than those of male syconia (GLM,  $Z = -5.35$ ,  $P < 0.001$ ) (Fig. 4b). Sample sizes among the oldest syconia are small because few wasps were willing to enter them, but female





**Fig. 4** **a** Abortion rates among un-entered syconia waiting for wasps. Sample sizes were 32, 41 for male and female respectively. **b** Abortions among syconia that had been entered by a single pollinator at different ages since becoming receptive. Sample sizes for female syconia = 28, 28, 28, 23, 22, 27, 19, 3; for male syconia = 17, 18, 15, 18, 20, 16, 17, 47

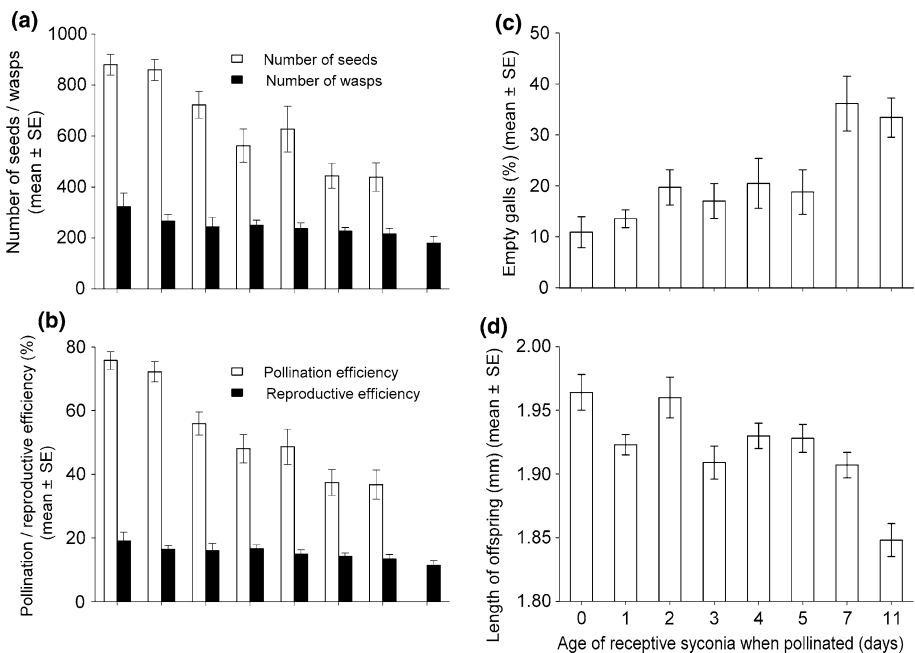
syconia that had waited longer to be entered were less likely to be retained (GLM,  $\beta \pm SE = -0.14 \pm 0.05$ ,  $Z = -2.67$ ,  $P < 0.01$ ). In males there was no significant effect of syconium age at time of pollinator entry on the proportion of aborted syconia (GLM,  $Z = -0.98$ ,  $P = 0.33$ ).

#### Seed and wasp production in syconia entered at different ages

Age-related changes in productivity were measured in syconia where a single female fig wasp was allowed entry. Female syconia produced more seeds than male syconia produced wasps, with the exception of the very oldest female syconia, where no seeds were produced

because all the syconia aborted (Fig. 5a). The syconia produced the highest number of seeds and wasps when entered on the first day they were receptive, with productivity then declining progressively with the length of time that the syconia had waited to be pollinated (GLM,  $\beta \pm SE = -0.12 \pm 0.002$ ,  $Z = -64.33$ ,  $P < 0.001$  and  $\beta \pm SE = -0.04 \pm 0.002$ ,  $Z = -23.93$ ,  $P < 0.001$  in female and male syconia respectively). Although productivity in both female and male syconia declined with age, declines in seed production were much more marked than the declines in wasp offspring numbers (Fig. 5a). Declines in pollination efficiency and wasp reproductive efficiency with syconium age were also evident if the total numbers of female flowers available in female and male syconia are taken into account (GLM,  $\beta \pm SE = -0.12 \pm 0.002$ ,  $Z = -52.94$ ,  $P < 0.001$ ;  $\beta \pm SE = -0.04 \pm 0.002$ ,  $Z = -23.30$ ,  $P < 0.001$ , respectively) (Fig. 5b).

The reduction in wasp progeny production with syconium age was reflected in an increase in the proportion of galled ovules that were empty and had failed to produce wasps (GLM,  $\beta \pm SE = 0.11 \pm 0.003$ ,  $Z = 31.79$ ,  $P < 0.001$ ) (Fig. 5c). This suggests that increasing numbers of wasp larvae were dying in older syconia. Further evidence for older male syconia offering poorer quality resources for pollinator development is provided by the sizes of the wasps that did manage to complete their development because adult female offspring that had developed in younger syconia were significantly larger than those from older syconia (LM,  $\beta \pm SE = -0.01 \pm 0.001$ ,  $t = -6.92$ ,  $P < 0.001$ ) (Fig. 5d).



**Fig. 5** **a** Seed and wasp production and **b** pollination/reproductive efficiency (the percentage of female flowers that produced seeds or pollinator offspring) in female and male syconia that had been waiting for different lengths of time for foundress fig wasps to enter. **c** The relationship between the age of male syconia at the time they were entered by a single foundress and the proportion of female flowers that were galled but failed to produce pollinator offspring ('empty bladders'). Sample sizes for female syconia = 18, 22, 22, 16, 12, 15, 11, 0; for male syconia = 9, 18, 15, 18, 20, 16, 17, 20. **d** The sizes of adult female pollinator offspring that had developed in syconia that had been waiting for different lengths of time to be entered by pollinator fig wasps

## Discussion

Un-pollinated syconia of *Ficus semicordata* remained receptive to their host-specific pollinators for 2 week after first becoming receptive and syconia entered by a single wasp were still receptive for 2–3 days or more. A long duration of receptivity is probably the norm among *Ficus* species, but the extent of longevity varies among species, with *Ficus aurea* and *Ficus carica* remaining receptive 2–3 weeks (Khadari et al. 1995), and floral receptivity of *Ficus hispida* around 1 week (Patel and Mckey 1998). Floral longevity also varies within species, depending on physical conditions such as temperature (Yasaka and Nishiwaki 1998) and as syconium development is slower in colder seasons (Peng et al. 2010), it is likely that syconia can remain receptive for longer during colder periods.

Encounters between receptive syconia and their pollinators in natural environments are made more difficult by low densities of many fig tree populations (Hubbell and Foster 1986; Mawdsley et al. 1998), the short life spans of their pollinators (Kjellberg et al. 1988; Herre et al. 2008), a commonly synchronous fruiting phenology that forces pollinators to disperse between trees (Ware and Compton 1994a), and the variable and unpredictable numbers of receptive syconia on different trees (Patel and Mckey 1998). The extended duration of receptivity seen in *F. semicordata* can be interpreted as a response to the possibility of pollinator shortages that these factors generate, thereby increasing the reproductive success of the plants and benefitting the fig–fig wasp mutualism in general. As in other flowering plants, floral longevity reflects a balance between benefits and costs (Celedón-Neghme et al. 2007; Castro et al. 2008). The maintenance costs of retaining syconia are unknown, but in *F. semicordata* the syconia become less attractive and less likely to be pollinated as they become older and so are less efficient. Even if they do attract a pollinator, older syconia are also more likely to abort, thereby wasting pollinators that could have entered younger figs on the same trees. Moreover, among syconia that completed their development, the highest numbers of seeds and wasps were produced when syconia were entered on the first day that they were receptive and productivity then declined progressively with the length of time that the syconia had waited for wasp entry. When seed and pollinator production on the first and last days of receptivity are compared, seed production was reduced by 50% and pollinator production was reduced by 44%. The size (and likely fecundity) of the pollinators also declined in older syconia. Possible reasons for the decline in reproductive success of older syconia include the loss of gamete viability with flower age (Ashman and Schoen 1994) and that the metabolic investment required to prolong receptivity becomes too great (Pyke 1991), but these explanations remain speculative.

Our experiments also demonstrated that male and female syconia of *F. semicordata* differ in their ability to continue attracting pollinators once they become receptive, with male syconia persisting longer than females. Receptivity of un-pollinated female syconia lasted about 18 days, and male syconia 24 days. The effective floral longevity (the period when wasp entry results in the successful production of seeds or wasp offspring) was 8 days for female syconia and 12 days for male syconia. This implies that the receptive period of syconia, when they attract pollinators and allow them entry, does not necessarily equate with effective floral longevity. Syconia that had waited longer to be entered were more likely to subsequently abort.

Under ‘free choice’ conditions, where female fig wasps were given the choice of syconia of different ages on adjacent trees to fly to and enter, the female syconia attracted pollinators for 7 days and male syconia for 9 days, with more wasps preferring to enter male than female syconia. The reason that male syconia were more attractive than female

syconia in *Ficus semicordata* may be simply because the produce more of the volatile attractant 4-methylanisole than do female syconia (Chen et al. 2009). This difference is achieved despite male and female syconia of *Ficus semicordata* having similar numbers of female flowers—the likely source of the volatiles (van Noort et al. 1989). Volatile production may be a significant contributor to the overall energetic costs of extending syconial longevity and the higher levels of production of 4-methylanisole in male figs may reflect a need to attract more foundresses to maximize productivity per fig. Foundresses pollinate female flowers more efficiently than they lay eggs in them (a factor that may help enhance the stability of the mutualism) with female syconia entered by foundresses producing seeds in about 80% of the flowers, compared with only 20% of flowers producing wasps in male syconia. This implies that foundress limitation on plant reproductive success is more likely to occur in male than female syconia—the former need more foundresses in order to take advantage of the flowers that are on offer.

The greater longevity and ability to attract pollinators displayed by male syconia of *F. semicordata* is in contrast to that recorded for *F. montana* Blume, another dioecious fig tree from Asia, where receptivity is longer in female, rather than male syconia (Suleman et al. 2011). A short period of receptivity in male syconia of *F. montana* may be necessary because fruiting in this species is asynchronous, with syconia of different developmental stages present together on larger plants. Persistently receptive male syconia could inhibit the departure of recently-emerged pollinators away from male trees, behavior that is necessary if the plants are to achieve reproductive success (Suleman et al. 2011). With its synchronous fruiting, there are no such constraints on male *F. semicordata*. Also in contrast to *F. semicordata*, the figs of *F. montana* are small, and a single foundress can fully utilize the female flowers of both male and female figs. The diameter of *Ficus semicordata* syconia gradually increases with syconium age throughout the period of receptivity, which means that larger receptive figs are also older and of lower quality to foundresses. This contrasts with the situation in *Ficus hispida* and *Ficus pertusa*, where attractiveness first increases with diameter and then decreases, and larger syconia attracted more pollinators than smaller syconia (Patel et al. 1995; Anstett et al. 1996). Taken together, the differences recorded between different *Ficus* species suggest that reproductive traits associated with floral longevity in the genus are adaptive and have been subject to natural selection. More generally, previous studies of the relative attraction of male and female syconia have paid little attention to the age of the syconia that were included in the experiments, except by size matching (Anstett et al. 1998; Moore et al. 2003). Our results suggest that spurious results could be obtained if syconium age is not explicitly taken into account in such experiments.

We used two different methods to assess whether syconia were receptive. Recording of whether or not wasps that were placed at the ostiole attempted to enter the syconia (the relatively convenient method used in most previous studies) was found to broadly reflect differences in the likelihood of pollinators entering male or female syconia presented under more natural conditions. However, ostiolar placement of pollinators considerably overestimated the ability of older syconia to attract pollinators under natural circumstances. The contrasting results of the ostiolar placement and free choice methods reflect the need for syconia in natural conditions to attract flying wasps from a distance under circumstances where the pollinators have a choice of which syconia to enter and there is competition with other syconia to attract them. Syconia that had been waiting for a few days were probably releasing less volatile attractant than younger syconia, but sufficient to stimulate entry of the wasps once they landed on their surface. Consequently, placing fig wasps onto older syconia over-estimates their likelihood of being pollinated. Field experiments to assess

differences in aging of male and female syconia are difficult to carry out, but there may be a more convenient way of assessing whether syconia of one or other sex ages more quickly than the other because in both *F. semicordata* and *F. Montana*, the sex with un-pollinated syconia that aborted more quickly was also the one where receptivity to pollinators declined more rapidly (Suleman et al. 2011).

In male figs of *F. semicordata* the decline in pollinator offspring numbers in older syconia is linked to increasing numbers of empty galls, implying either more deaths of pollinator larvae or a higher proportion of flowers that are galled but no eggs are laid. The lower value of older figs should exert a strong selection pressure on fig wasps to avoid them, in the same way that selection should favour avoidance of female syconia, where their reproductive success is always zero. Both older syconia and female syconia are entered, nonetheless. A favoured explanation for the latter has been ‘selection to rush’ (Patel et al. 1995; Moore et al. 2003), because the wasps’ brief adult life span means they cannot afford the time to choose high quality hosts. Despite this, the wasps do not have a total lack of control over events. Ovipositing females also gall the ovules where eggs are laid and thereby exert an influence on syconium development. This may explain why male syconia entered by wasps were less prone to abortion than their female syconium equivalents.

We have quantified the costs of inflorescence longevity for *F. semicordata* and its pollinator. The results have implications for our understanding of the fig–fig wasp mutualism, in particular the selection pressures generated by the plants that influence pollinator choice. Comparison of our results with those from other *Ficus* species with different inflorescence sizes and phenologies points to floral longevity as a labile character integrated into their broader reproductive strategies. Floral longevity is likely to play an equally integral part in the reproductive strategies of other insect pollinated plants.

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