This is a repository copy of *Female figs as traps: Their impact on the dynamics of an experimental fig tree-pollinator-parasitoid community*.

White Rose Research Online URL for this paper:
http://eprints.whiterose.ac.uk/85568/

Version: Accepted Version

Article:

Suleman, N, Sait, S and Compton, SG (2015) Female figs as traps: Their impact on the dynamics of an experimental fig tree-pollinator-parasitoid community. Acta Oecologica, 62. 1 - 9. ISSN 1146-609X

https://doi.org/10.1016/j.actao.2014.11.001

© 2015. This manuscript version is made available under the CC-BY-NC-ND 4.0 license http://creativecommons.org/licenses/by-nc-nd/4.0/

Reuse

Unless indicated otherwise, fulltext items are protected by copyright with all rights reserved. The copyright exception in section 29 of the Copyright, Designs and Patents Act 1988 allows the making of a single copy solely for the purpose of non-commercial research or private study within the limits of fair dealing. The publisher or other rights-holder may allow further reproduction and re-use of this version - refer to the White Rose Research Online record for this item. Where records identify the publisher as the copyright holder, users can verify any specific terms of use on the publisher's website.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

eprints@whiterose.ac.uk
https://eprints.whiterose.ac.uk/

Female figs as traps: their impact on the dynamics of an experimental fig tree-pollinator-parasitoid community

Nazia Suleman[a,b*], Steve Sait [a] and Stephen G. Compton[a,]

[a]School of Biology, University of Leeds, LS2 9JT, UK.

[b] Present Address: Plant Protection Division. Nuclear Institute for Agriculture and Biology (NIAB), Faislabad 38000, Pakistan.

[*] Corresponding author: Tel.: +92 41 9201751; Fax: +92 41 9201776,
E-mail address: nazianasir2002@yahoo.co.in (N. Suleman).

Abstract

Interactions between fig trees (Ficus) and their pollinating fig wasps (Agaonidae) result in both a highly species-specific nursery mutualism and mutual exploitation. Around half of the 800 or so fig tree species are functionally dioecious. Figs on male plants produce pollen and wasp offspring, whereas figs on female plants produce only seeds. Figs on female plants are traps for pollinators. The fig wasps enter the female figs to oviposit, but lose their wings on entry and are then prevented from oviposition by the long styles that characterise the flowers in female figs. Continuation of the mutualism depends on the pollinators’ failure to distinguish between male and female figs before entry. Female plants may also have a negative impact on the parasitoid fig wasps that feed on pollinators, if they are also attracted to female figs. We used glasshouse populations of figs (with and without female plants), pollinators and parasitoids to infer the impact of female figs on fig wasp dynamics. Female plants may dampen the amplitudes of pollinator population cycles, and parasitoid populations may be less tightly coupled with host populations, but the presence of female figs did not reduce parasitism rates, nor parasitoid and pollinator densities, only parasitoid sex ratios were affected. Our glasshouse experimental design was likely to favour the impact of female figs on the wasp populations, which suggests that female plants in the field are unlikely to have a major negative impact on their pollinators, despite being a major mortality factor.

Keywords: dioecy; Ficus; intersexual mimicry; fig wasp; population dynamics; parasitism; sex ratio.

Introduction

Mutualistic interactions involving figs (Ficus spp., Moraceae) and their pollinating wasps (Hymenoptera, Agaonidae) represent a classic case of species-specific obligate mutualism and co-evolution (Compton 1993; Compton et al. 1996; Dunn et al. 2008; Herre et al. 2008). Mated adult female wasps are attracted to the volatile blends produced by young receptive figs (Proffit et al. 2009)In monoecious figs, when seeds and the next generation of wasps mature, adult females exit through a hole constructed by males and transport the pollen of their natal plant. In dioecious figs, where male and female functions are performed by separate plants, female wasps are only able to reproduce within male figs, while wasps entering female figs only pollinate and die without reproducing. On female plants, longer styles of female flowers prevent oviposition and as a result only seeds are produced by pollinated figs (Raja et al. 2008b). The pollination system of dioecious fig species is therefore an example of pollination by deceit (sensu Dafni 1984). Female figs in dioecious figs are therefore a dead end for wasp reproduction. There has been much debate on the conflicts involved between the two mutualists, especially in dioecious figs, where the pollinator wasps entering female figs ensure pollination of the plant, but fail to reproduce (Patel et al. 1995).

In some dioecious fig species, wasps that live only few hours, enter the female figs because they have no other choice available, as most male trees are receptive well before or after the receptivity of female figs (for example Ficus carica, Kjellberg et al. 1987 and Soler et al. 2012). In Ficus montana, like some other dioecious figs (F. hispida, Patel et al. 1995; and F. fistulosa, Corlett 1987) male and female figs are receptive simultaneously (Suleman et al. 2011a) and thus selection should favour wasps that avoid female figs (Anstett et al. 1998), although this could lead eventually to the potential extinction of both the plant and the pollinator wasps. However, this selection pressure also favours female plants that mimic males so as to deceive wasps into pollinating them (Suleman et al. 2011b). Males similarly need to mimic females to ensure that the next generation of wasps bearing their pollen enter female figs ('vicarious selection', Grafen and Godfray 1991; Soler et al. 2012). Such female mimicry has been described in many other plant species (Agren et al. 1986; Aronne et al. 1993; Dufaÿ and Anstett 2004). The inability of fig wasps to differentiate between male and female figs means that female fig plants act as an additional mortality factor that will reduce the pollinator numbers.

Kradibia (=Liporrhopalum) tentacularis foundresses, the pollinators of F. montana, under natural and experimental conditions, typically contribute unequally to shared broods, producing smaller and less female-biased clutches in multi-foundress figs than they would have produced when ovipositing alone (Zavodna, 2004). This increase in K. tentacularis brood sex ratios (proportion males) with increasing foundress density is similar to that seen in many other studies conducted on fig wasps, and has generally been attributed to sex ratio adjustments in response to local mate competition (LMC) and inbreeding (Hamilton 1967; Frank 1985; Herre 1985; Pereira and Prado 2006; Greeff and Newman 2011). However, it should be noted that realized sex ratios (based on numbers of adult male and female offspring) in K. tentacularis do not necessarily reflect primary sex ratios in this species, because larval mortalities are sometimes high and may not necessarily be similar among male and female offspring (Ghana et al. 2012). Sex ratio adjustment by foundresses entering their second figs (wingless foundresses) was found to be different to that shown by winged foundresses entering their first figs, probably because of clutch size differences (Raja et al. 2008a; Suleman et al. 2013c).

Each species of fig tree has figs that are attacked by a number of non-pollinating fig wasps (up to 29 species were recorded from one tree species by Compton and Hawkins 1992). Non-pollinators include some species that oviposit externally and some that enter the figs like pollinators. Regardless of their oviposition time, all fig wasp species usually emerge from figs at the same time as the pollinators, which means there must be varying larval growth rates between species (Bronstein 1991; Kerdelhue and Rasplus 1996). Sycoscapter, a non-pollinator genus, belongs to the subfamily Sycoryctinae. Sycoscapter species have long ovipositors and lay their eggs from the outside of the fig, through the wall. They often are believed to be parasitoids or inquilines, mostly of the pollinators (Galil and Eisikowitch 1968, Compton and van Noort 1992). They oviposit a few hours to several days after pollinators enter the figs, depending on the species (Kerdelhue and Rasplus 1996). They oviposit in figs of a large range of diameters (Kerdelhue and Rasplus 1996; Kerdelhue et al. 2000). Four Sycoscapter species were studied by Kerdelhue et al. (2000); one associated with F. sagittifolia and three others on F. ovata. The four species appeared to have varying relationships with the pollinators; having negative, positive or no correlation with the numbers of pollinator larvae inside the figs.

Female fig plants of dioecious species are not only a dead end for pollinators, they also potentially act as ecological sinks for non-pollinating wasps that do not avoid female figs when searching for oviposition sites, which may explain why dioecious figs to generally have a lower incidence of parasitism (and fewer non-pollinator species) than monoecious species and why pollinator production is often higher (Weiblen et al. 2001). Also, in F. montana, female figs if unpollinated, tend to stay longer on female plants and prolong their attractiveness (Suleman et al. 2011a) but there are no other phenological differences between sexes as far as fig initiation and fig composition are concerned (Suleman et al. 2011b). Here for the first time we test the impact of female plants of a dioecious fig on its pollinator and an associated parasitoid. We look at population trends of the pollinator and parasitoid in the presence or absence of female plants. As the female plants act as a drain on pollinators there should be fewer foundresses available to enter male figs when this sex is present. This in turn may result in more female-biased sex ratios, as reduced competition for oviposition sites should allow larger clutches to be laid by individual females. Also, if the parasitoids are distracted by the female figs, then higher rates of parasitism might be expected in the absence of female plants, especially as pollinator larval densities are expected to be higher (Weiblen et al. 2001).

Study site and species

The study was conducted using glasshouse populations of a dioecious fig tree Ficus montana Blume, its pollinator Kradibia (= Liporhoppalum) tentacularis Grandi and the parasitoid Sycoscapter sp., originating from the Centre for International Forestry Research (CIFOR) plantation, West Java, Indonesia and from Rakata (Krakatau), Indonesia. These populations had been maintained continuously at the Experimental Gardens, University of Leeds, UK since 1995 (Moore 2001). In F. montana, significant variation in flower number among figs has been observed by different individual trees growing under uniform conditions (Suleman et al. 2013a). Pollinating females of K.

tentacularis seek out the figs at the receptive stage, enter, oviposit, pollinate and then either die or sometimes leave the fig in an attempt to oviposit in another fig (Suleman 2007). Wingless foundresses (passing through the ostiole physically removes the wings of female fig wasps) are able to locate and enter figs up to 60 cm from the first fig they enter (Suleman et al. 2013c). The non-pollinating wasps (Sycoscapter sp.) need figs that have already been pollinated (Raja 2007). It oviposits from the outside of the figs. The larvae develop into adults inside the ovules of the fig. Male are apterous and mating occur inside the female galls. Both species complete their development at the same time, hatch and mate. Sycoscapter sp. can significantly reduce the numbers of pollinators emerging from the figs, although the host sex ratios remain undistorted (Suleman et al. 2013b). Also the males of this species are able to construct exit holes for females as male pollinators (Suleman et al. 2012).

Methods

We monitored changes in the numbers of figs and their developmental stages and estimated the population sizes of the pollinator and its parasitoid based on counts made at 14 days intervals for a period of 15 months from November 2002 to February 2004. This period covered two winter and one summer seasons. Fig plants of similar size (small shrubs) were divided into two largely independent, but adjacent, populations separated by a physical barrier (a door) and a buffer zone of other Ficus species. Only premature figs (A phase) were left on plants. All others were removed at the beginning of the experiment. The door was kept closed except during brief transits by staff. One glasshouse contained exclusively male plants and the other had male and female plants arranged together in lines with one male plant followed by one female plant and then one male followed by two female plants throughout. In this way a ratio of 2:3 was maintained, with 80 male and 120 female plants. The male only population consisted of 80 plants. All plants had individual pots placed close together. Daylight, watering, and soil nutrition were similar in the two glasshouses, as was the spacing between plants.

Minimum day lengths were maintained as 16L: 8D by providing artificial lights during periods when natural daylight hours were lower. The minimum temperature was maintained at 15 ^{o}C. Overall temperatures during the 15 month monitoring period were similar in the adjacent glasshouses with mean monthly minimum temperatures varying between 17.9 ^{o}C to 21.8 ^{o}C (mixed glasshouse) and 17.6 ^{o}C to 21.7 ^{o}C (male plants-only glasshouse), and mean monthly maximum temperatures ranging from 22.1 ^{o}C to 32.4 ^{o}C (mixed glasshouse) and 20.4 ^{o}C to 30.3 ^{o}C (male plants-only glasshouse).

Fig numbers and population trends

The numbers of figs on 20 randomly selected female plants and 20 randomly-selected male plants in each glasshouse were counted after 14 days interval. Developmental stages of the figs were recorded as described by Galil and Eisikowitch (1968) and Valdeyron and Lloyd (1979). Phase B figs are receptive and attract adult female wasps (loaded with pollen) to enter them. K. tentacularis routinely re-emerges from figs and so can pollinate and lay eggs in several figs. Phase C female figs contain developing seeds, whereas Phase C male figs contain wasp larvae developing in galled ovules. Sycoscapter sp. females lay their eggs from the outside of male figs, a few weeks after pollination. Male figs at D phase release the next generation of fig wasps, with female pollinators then flying away in search of B phase figs to enter. Female figs have an extended post receptive phase, which ends when the figs are soft and fleshy and attractive to seed dispersers (E phase).

The contents of the male figs were assessed on the basis of samples of ten D phase figs taken at random 10 different trees from both populations each fortnight. The figs were left within fine mesh-covered plastic containers for 24 hours to allow the wasps to emerge. The figs were then split open and all the wasps were identified, sexed and counted. Male flowers, female flowers and their contents were also recorded (as un-utilised, wasp-producing or failed empty galls (‘bladders’).

Variables were log transformed for time series analysis. Parasitism rates and sex ratios were arcsine transformed for all analyses. One and two way analysis of variance (ANOVA) for normal and Kruskal-Walis tests for non-normal data were used.

Results

Fig numbers

During the 15 month sampling period the number of figs on male plants in the males-only population was 63.9 ± 3.5 (mean ± SE), compared with 54.5 ± 2.7 on male plants in the mixed population was and 50.7 ± 3.0 figs on the female plants. There was strong seasonal variation in the numbers of figs present on the plants (Fig. 1), with both sexes having far more figs during the summer months (May-July) (Kruskal-Wallis test, $X^2_{[29]} = 268.17$, $P < 0.001$ for male and $X^2_{[29]} = 285.78$, $P < 0.001$ for female plants in the mixed population and $X^2_{[29]} = 269.54$, $P < 0.001$ for male plants in the males-only population).

Approximately equal numbers of figs were present on the male and female plants in the mixed population (overall ratio = 1: 0.93, during spring and summer (April-September) = 1: 0.91 and autumn and winter (October-March) 1: 0.98). The abundance of male and female figs in the mixed population and of male figs in the two populations did not differ significantly (Kruskal-Wallis test, $X^2_{[2]} = 3.14$, $P = 0.21$, Fig 1 and 2).

Fig wasp population changes

The summer peak in the abundance of figs was not reflected in clear seasonal changes in the mean abundance of pollinators or parasitoids per fig, though wasp numbers varied significantly between sample dates (Table 1 and 2, Fig. 3). No differences in abundance were detected between the populations with and without female figs (Table 3) though the numbers of pollinators and of all wasps combined approached being significantly higher in the glasshouse where no female figs were present (Table 3). Interactions between glasshouses and sampling dates were generally significant, showing that wasp population densities in the two populations were not well synchronised.

The numbers of pollinators and parasitoids in the figs showed a pattern of alternating peaks and troughs in densities over time in both glasshouses (Fig. 4). The peaks appear to have greater amplitude in the males-only population, but the difference was not significant (Table 3). Despite clear cyclical dynamics in both species for both treatments, autocorrelation function analysis (ACF), which detects significant periods or frequencies of cycles in census data (Chatfield 1996), did not reveal strong evidence for consistent cycle periods for pollinator and parasitoids (Fig. 4). This may reflect the relatively short time series, which make detection of significant periods more difficult.

A tight coupling between pollinator and parasitoid numbers in the male-only glasshouse is revealed by cross correlation function analysis (CCF, Fig. 5a), which detects significant lags between the two populations (whether or not their respective peaks or troughs are in phase with each other, Chatfield 1996). However, there was no significant correlation between pollinators and parasitoids in the mixed population (Fig. 5b), which suggests that the tight coupling between pollinators and parasitoids is weakened by the presence of the female figs.

Parasitism rates differed among sampling dates (ANOVA, $F_{(29, 599)} = 3.40$, $P < 0.001$) but were not significantly different in the two glasshouses (29.63% $\pm$ 1.38 in the mixed population and 30.01% $\pm$ 1.51 in the males-only populations; ANOVA, $F_{(1, 599)} = 0.02$, $P = 0.88$). There was a significant interaction between glasshouses populations and sampling dates, showing that on dates when parasitism rates were high in one population they were not necessarily high in the other (ANOVA, $F_{(29, 599)} = 1.63$, $P = 0.02$).

The pollinators had highly female biased sex ratios that did not differ between the two glasshouse populations (Table 4), nor between sampling dates (ANOVA, $F_{(29, 596)} = 1.01$, $P = 0.46$), with a non-significant interaction between populations and sampling dates (ANOVA, $F_{(29, 596)} = 0.69$, $P = 0.88$). In contrast, the parasitoid had less female-biased sex ratios overall, that also varied between glasshouses, with a higher proportion of males present in the population where no female figs were present (Table 4). Parasitoid sex ratios also showed significant variation between sampling periods (ANOVA, $F_{(29, 494)} = 1.88$, $P = 0.004$), with a non significant interaction between populations and sampling dates (ANOVA, $F_{(29, 494)} = 1.37$, $P = 0.09$).

Discussion

The fifteen-month duration of the experiment covered two winter periods and one summer period. Despite artificial heating and lighting, the fig trees responded to the seasonal changes, producing many more figs during the summer period (probably due to increased day length and temperature). This increase in fig production during the summer was seen in both sexes of fig trees, so the proportion of male and female figs available to the pollinators did not vary between them dramatically. Despite the higher numbers of figs in the summer, the densities of wasps inside the figs did not display any seasonal effect. This suggests that there may have been a super-abundance of pollinators throughout the study period. Another study also reported that in F. montana, fig composition stays unaffected from seasonal effects (Suleman et al. 2011b).

Our results showed that pollinator and parasitoid populations exhibited remarkably similar discrete cyclic fluctuations in the male-plants-only glasshouse, but in the presence of female plants the amplitude of the cycles seemed to be reduced and peaks and troughs were less evident but with almost no effect on the parasitoids in both populations. It is difficult to detect strong signals of cyclicity or density-dependence in short time series, so we could not get significant patterns for the 15 months of data.

Predators are known to be able to reduce the amplitude of cyclic oscillations (Turchin et al. 1999). Female fig plants in effect act in a similar way to predators in the sense that they drain out foundresses from the system by trapping them without allowing them to reproduce. The parasitoids in both glasshouses did not seem to have any dramatic negative impact on the plant-pollinator mutualism as their numbers most of the time were lower than those of pollinators. Pollinator progeny numbers were almost always higher than those of parasitoids. Though it has been suggested earlier that distraction by the presence of female plants might lower parasitism rates in male figs as compared to monoecious species (Weiblen et al. 2001), our results did not show any significant variation in parasitism rates in the presence or absence of female plants.

The densities of female figs were very similar to those of male figs in the two populations. If equal numbers of foundresses are being attracted by female figs and, thus, being lost from the mixed population, then the population densities of pollinators might be expected to be reduced. However, our results indicated that although the female plants were clearly removing foundresses from the system, they had no effect on progeny densities, perhaps due to a super abundance of pollinator females as mentioned above. If the female plants were reducing the numbers of foundresses entering figs and ovipositing in the mixed population, then the progeny sex ratio was expected to be more female biased, but again this was not observed, suggesting that the number of foundresses laying in each fig was not altered. Larger pollinator clutches contain a higher proportion of females (Moore et al. 2005). In K. tentacularis, brood sex ratios (percentage of males) increase with increasing foundress densities (Moore et al. 2002). This is in agreement with many other studies conducted on fig wasps (Hamilton 1967; Frank 1985; Herre 1985; Pereira and Prado 2006). However, it is worth mentioning that realized sex ratios (based on numbers of adult male and female offspring) in K. tentacularis do not necessarily reflect primary sex ratios in this species, because larval mortalities are sometimes high and may not necessarily be similar among male and female offspring (Ghana et al. 2012). K. tentacularis foundresses have also been shown often to contribute unequally to two foundress broods and also to adjust their sex ratios according to the size of clutch they lay (Moore et al. 2005). Foundresses of this species adjust the proportion of males in their clutches by laying mostly males eggs first (Raja et al. 2008a). The same study revealed that K. tentacularis foundresses lay different brood sizes when they are allowed to oviposit for different lengths of time. In addition, the foundresses of this species often re-emerge and are capable of ovipositing in as many as four figs on the same tress (Suleman et al. 2013c). In the second and subsequent figs, the foundresses show similar sex ratio adjustment behaviour to that in the first, but lay fewer eggs (Moore 2001; Zavonda 2004; Raja et al. 2008a) so are less likely to be limited by oviposition sites, and therefore to respond to competition with other foundresses. Pollinator sex ratios in this species are therefore controlled by many factors. The sex ratios of the pollinators were similar in the two populations. More female biased sex ratios might have been expected if female figs had killed substantial numbers of foundresses, because fewer foundresses would have entered each fig, allowing each foundress to lay more male eggs.

The proportion of males of the parasitoid Sycoscapter sp. was higher in the population where no female plants were present. Little is known about the sex ratios of non-pollinating fig wasps (Patel 1998), though they are often closer to 50:50 than those seen in pollinator species, reflecting the more out-bred population structure exhibited by species which oviposit from the outside of the figs. As Sycoscapter oviposits externally, through the fig wall, they can spread their offspring across several figs; hence sex ratio adjustments in these wasps do not fulfil the requirements for LMC. If, like the pollinators, Sycoscapter females adjust their sex ratios in response to the number of progeny laid by other female parasitoids, then higher sex ratios in the males-only population may reflect various possibilities. Either there were higher densities of adult female parasitoids, or there are fewer adult females present, but they are revisiting the same figs to oviposit and are not able to distinguish between the figs that had been visited by them previously. This might end up in a less female biased sex ratio. In the mixed population, more female biased sex ratios might be attributable to the distraction and wastage of time due to the presence of female figs, but there was no other evidence to suggest this.

This study for the first time throws some light on the impact of female plants on plant-pollinator-parasitoid relationships in dioecious fig species, but perhaps because the wasp species were always present in abundance, we could not get remarkably different scenarios with the presence or absence of female figs. Also, for the time series analysis 15-month period turned out to be too short to assess the population dynamics of the wasps. Further work will be needed to fully depict the extent of the variation we observed and its implications for both figs and wasps.

Acknowledgements

Funding to N. Suleman for this research was provided by Ministry of Education, Pakistan. Martin Lappage provided the helpful service of maintaining the population of fig trees at the University Experimental Gardens.

References

Anstett, M.C., Gibernau, M., Hossaert-McKey, M. 1998. Partial avoidance of female inflorescences of a dioecious fig by their mutualistic pollinating wasps. Proc. R. Soc. B. 265, 45-50.

Agren, J., Elmqvist, T., Tunlid, A. 1986. Pollination by deceit, floral sex ratios and seed set in dioecious Rubus chamaemorus L. Oecologia 70, 332-338.

Aronne, G., Wilcock, C.C., Pizzolongo, P. 1993. Pollination biology and sexual differentiation of Osyris alba (Santalaceae) in the Mediterranean region. Plant Syst. Evol. (Historical Archive) 188, 1-16.

Bronstein, J.L. 1991. The nonpollinating wasp fauna of Ficus pertusa: exploitation of a mutualism? Oikos 61, 175–186.

Compton, S.G. 1993. One way to be a fig. Afr. Entomol. 1, 151-158.

Compton, S.G., Weibes, J.T., Berg, C.C. 1996. The biology of fig trees and their associated animals. J. Biogeogr. 23: 405-407.

Compton, S.G., Hawkins, B.A. 1992. Determinants of species richness in southern African fig wasp assemblages. Oecologia 91, 68-74.

Compton, S.G., Van Noort, S. 1992. Southern African fig wasps (Hymenoptera: Chalcidoidea): resource utilization and host relationships. Proc. Kon. Ned. Akad. v Wetensh. 95, 423-435.

Corlett, R.T. 1987. The Phenology of Ficus Fistulosa in Singapore. Biotropica 19, 122-124.

Dafni, A. 1984. Mimicry and deception in pollination. Ann. R. Ecol. Sys. 15, 259-278.

Dufaÿ, M., Anstett, M.C. 2004. Cheating is not always punished: killer female plants and pollination by deceit in the dwarf palm Chamaerops humilis. J. Evol. Biol. 17, 862-868.

Dunn, D.W., Yu, D.W., Ridley, J., Cook, J.M. 2008. Longevity, early emergence and body size in a pollinating fig wasp – implications for stability in a fig-pollinator mutualism. J. Animal Ecol. 77, 927-935.

Frank, S.A. 1985. Hierarchical selection theory and sex ratios. II. On applying the theory, and test with fig wasps. Evolution 39, 949-964.

Galil, J., Eisikowitch, D. 1968. Flowering cycles and fruit types in Ficus sycamorus in Israel. New Phytol. 67, 745-758.

Grafen, A., Godfray, H.C.J. 1991. Vicarious selection explains some paradoxes in dioecious fig pollinator systems. Proc. R. Soc. B 245, 73-76.

Ghana, S., Suleman, N., Compton, S.G. 2012. Factors influencing realized sex ratios in fig wasps: Double oviposition and larval mortalities. J. Insect Behav. 25, 254-263.

Greeff, J.M., Newman, V.K. 2011. Testing models of facultative sex ratio adjustment in the pollinating fig wasp Platyscapa awekei. Evolution 65, 203-219.

Hamilton, W.D. 1967. Extraordinary sex ratios. Science 156, 477-488.

Herre ,E.A. 1985. Sex ratio adjustment in fig wasps. Science 228, 896-898.

Herre, E.A., Jand´er, K.C., Machado, C.A. 2008. Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. Ann. R. Ecol. Sys. 39: 439-458.

Kerdelhue, C., Rasplus, J.Y. 1996. Non-pollinating Afrotropical fig wasps affect the fig pollinator mutualism in Ficus within the subgenus Sycomorus. Oikos 75, 3-14.

Kerdelhue, C., Rossi, J.P., Rasplus, J.Y. 2000. Comparative community ecology studies on old world figs and fig wasps. Ecology 81, 2832- 2849.

Kjellberg, F., Gouyon, P.H., Ibrahim, M., Raymond, M., Valdeyron, G. 1987. The stability of the symbiosis between dioecious figs and their pollinators: a study of Ficus carica L and Blastophaga psenes L. Evolution 41, 693-704.

Moore, J.C. 2001. The ecology and evolution of gynodioecious figs (Ficus: Moraceae) and their pollinators (Agaoninae: Agaonidae). PhD thesis, University of Leeds, U.K.

Moore, J.C., Compton, S.G., Hatcher, M.J., Dunn, A.M. 2002. Quantitative tests of sex ratio models in a pollinating fig wasp. Anim. Behav. 64, 23-32.

Moore, J.C., Zavodna, M., Compton, S.G., Gilmartin, P.M. 2005. Sex ratio strategies and the evolution of cue use. Proc. R. Soc. B 272, 1287-1294.

Patel, A. 1998. Wasp composition in inflorescences of two dioecious fig species- Implications for the Fig-wasp mutualism. Biotropica 30, 474-480.

Patel, A., Anstett, M.C., Hossaert-McKey, M., Kjellberg, F. 1995. Pollinators entering female dioecious figs: why commit suicide? J. Evol. Biol. 8, 301-313.

Periera, R.A.S., Prado, A.P. 2006. Effect of local mate competition on fig wasp sex ratios. Braz. J. Biol. 66, 29-41.

Proffit, M., Chen, C., Soler, C., Bessière, J.-M., Schatz, B., & Hossaert-McKey, M. 2009. Can chemical signals, responsible for mutualistic partner encounter, promote the specific exploitation of nursery pollination mutualisms? The case of figs and fig wasps. Entomol Exp Appl, 131, 46-57.

Raja, S., Suleman, N., Compton, S.G., Moore, J.C. 2008a. The mechanism of sex ratio adjustment in a pollination fig wasp. Proc. R. Soc. B 275, 1603-1610.

Raja, S., Suleman, N., Compton, S.G. 2008b. Why do fig wasps pollinate female figs? Symbiosis 45, 25-28.

Soler, C. C. L., proffit, M., Bessière, J.-M., Hossaert-McKey, M., & Schatz, B. 2012. Evidence for intersexual chemical mimicry in a dioecious plant. Ecol Lett, 15, 978-985.

Suleman, N. 2007. Population biology of a fig plant-pollinator and parasitoid system under laboratory conditions. Ph.D. Thesis. The University of Leeds, UK.

Suleman, N., Raja, S., Zhang, Y., Compton, S.G. 2011a. Sexual differences in the attractiveness of figs to pollinators: females stay attractive for longer. Ecol. Entomol. 36, 417-424.

Suleman, N., Raja, S., Compton, S.G. 2011b. A comparison of growth and reproduction, under laboratory conditions, of males and females of a dioecious fig tree. Plant Syst. Evol. 296, 245-253.

Suleman, N., Raja, S., Compton, S.G. 2012. Only pollinator fig wasps have males that collaborate to release their females from figs of an Asian fig tree. Biol. Lett. 8, 344-346.

Suleman, N., Quinell, R.J., Compton, S.G. 2013a. Variation in inflorescence size in a dioecious fig tree and its consequences for the plant and its pollinator fig wasp. Plant Syst. Evol. 299, 927-934.

Suleman, N., Raja, S., Compton, S.G. 2013b. Parasitism of a pollinator fig wasp: mortalities are higher in figs with more pollinators, but are not related to local densities of figs. Ecol. Entomol. 38, 478-484.

Suleman, N., Raja, S., Compton, S.G. 2013c. Putting your eggs in several baskets: oviposition in a wasp that walks between several figs. Entomol. Exp. Appl. 149, 85-93.

Turchin, P., Taylor, A.D., Reeve, J.D. 1999. Dynamical role of predators in population cycles of a forest insect: an experimental test. Science 285, 1068-1071.

Valdeyron, G., Lloyd, D.G. 1979. Sex differences and flowering phenology in the common fig, Ficus carica L. Evolution 33, 673-685.

Verrill, S. 2006. A confidence interval on the ratio of the coeficients of variation of two normally distributed populations. Forest Product Laboratory, United States Department of Agriculture. Software link http://www.fpl.fs.fed.us/covratio.html

Weiblen, G.D., Yu, W., West, S.A. 2001. Pollination and parasitism in functionally dioecious figs. Proc. R. Soc. B 268, 651-659.

Table 1 (Variation in numbers of male and female pollinators; male and female parasitoids and the total wasps in male figs only and the male and female mixed populations (N= 300 figs from each population)

Factors tested	**Male figs only Population**			**Male and female figs Population**		
	Mean	**SE**	**Range**	**Mean**	**SE**	**Range**
Female pollinators	22.17	1.13	0-139	20.52	0.98	0-122
Male pollinators	5.49	0.53	0-78	4.41	0.39	0-55
Total pollinators	27.65	1.29	0-165	24.93	1.07	0-136
Female parasitoids	5.54	0.48	0-71	7.80	0.54	0-49
Male parasitoids	5.71	0.44	0-45	3.04	0.21	0-30
Total parasitoids	11.25	0.76	0-94	10.84	0.70	0-79
Total wasps	38.88	1.45	3-166	35.77	1.24	3-148

Table 2. Two-way ANOVA comparing numbers of pollinators and their parasitoid per fig over a period of fifteen months. One glasshouse contained only male figs, the other a mixed population of male and female plants.

Factors tested	**Glasshouse populations**			**Sampling dates**			**Glasshouses * sampling dates**		
	F	df	P	F	df	P	F	df	P
Female pollinators	1.92	1	0.16	4.17	29	< 0.001	1.66	29	0.120
Male pollinators	2.31	1	0.13	1.92	29	0.003	1.12	29	0.300
Total pollinators	3.06	1	0.08	3.69	29	< 0.001	1.78	29	0.008
Female parasitoids	0.53	1	0.46	3.23	29	< 0.001	2.07	29	0.001
Male parasitoids	0.95	1	0.33	2.51	29	< 0.001	2.01	29	0.002
Total parasitoids	0.002	1	0.96	3.01	29	< 0.001	2.06	29	0.001
Total wasps	2.74	1	0.09	3.77	29	< 0.001	2.15	29	0.001

Table 3. Variations in densities per fig of fig wasps in fig tree populations with and without female plants. Coefficients of variation (CV) are from Verrill, 2006).

Factors tested	**CV2**	**CV1**
	Male figs only Popn.	**Male and female figs Popn.**
Female pollinators	88.46%	82.53%
Male Pollinators	167.35%	153.79%
Pollinators	81.09%	74.42%
Female Parasitoids	130.14%	120.32%
Male Parasitoids	122.04%	111.02%
Parasitoids	117.75%	112.39%
Total wasps	64.64%	60.14%

Table 4. Sex ratios (proportion males) of pollinators and parasitoids in fig tree populations with and without female plants.

Factors tested	**Male figs only Popn.**		**Male and female figs Popn.**		**F (df)**	**P**
	Mean	SE	Mean	SE		
Pollinators	0.19	0.01	0.18	0.01	0.88 $_{(1,\ 596)}$	0.35
Parasitoids	0.39	0.02	0.33	0.02	9.89 ($_{1,\ 494)}$	0.002

Figure Legends:

Fig. 1 Total figs produced by female plants (a) and male plants (b) in the mixed population and male plants (c) in the males only population over a period of fifteen months.

Fig. 2 Mean numbers of different phases of figs on female (a) and male plants (b) in the mixed population and on male plants (c) in the males only population over a period of fifteen months.

Fig. 3 Population trends of pollinators and parasitoids in (a) the mixed population of male and female figs and (b) the male figs-only glasshouse over a period of fifteen months.

Fig. 4 Autocorrelation function analyses (ACF) of mean pollinator and parasitoid numbers per fig in (a) the males-only population and (b) the mixed population. The solid lines represent the correlation coefficients, and the sloping lines represent the confidence intervals of two standard errors that identify significant lags and their periods in fortnights ($p < 0.05$).

Fig. 5 Cross correlation function analysis (CCF) of mean pollinator and parasitoid numbers per fig in (a) the males-only population and (b) the mixed population.

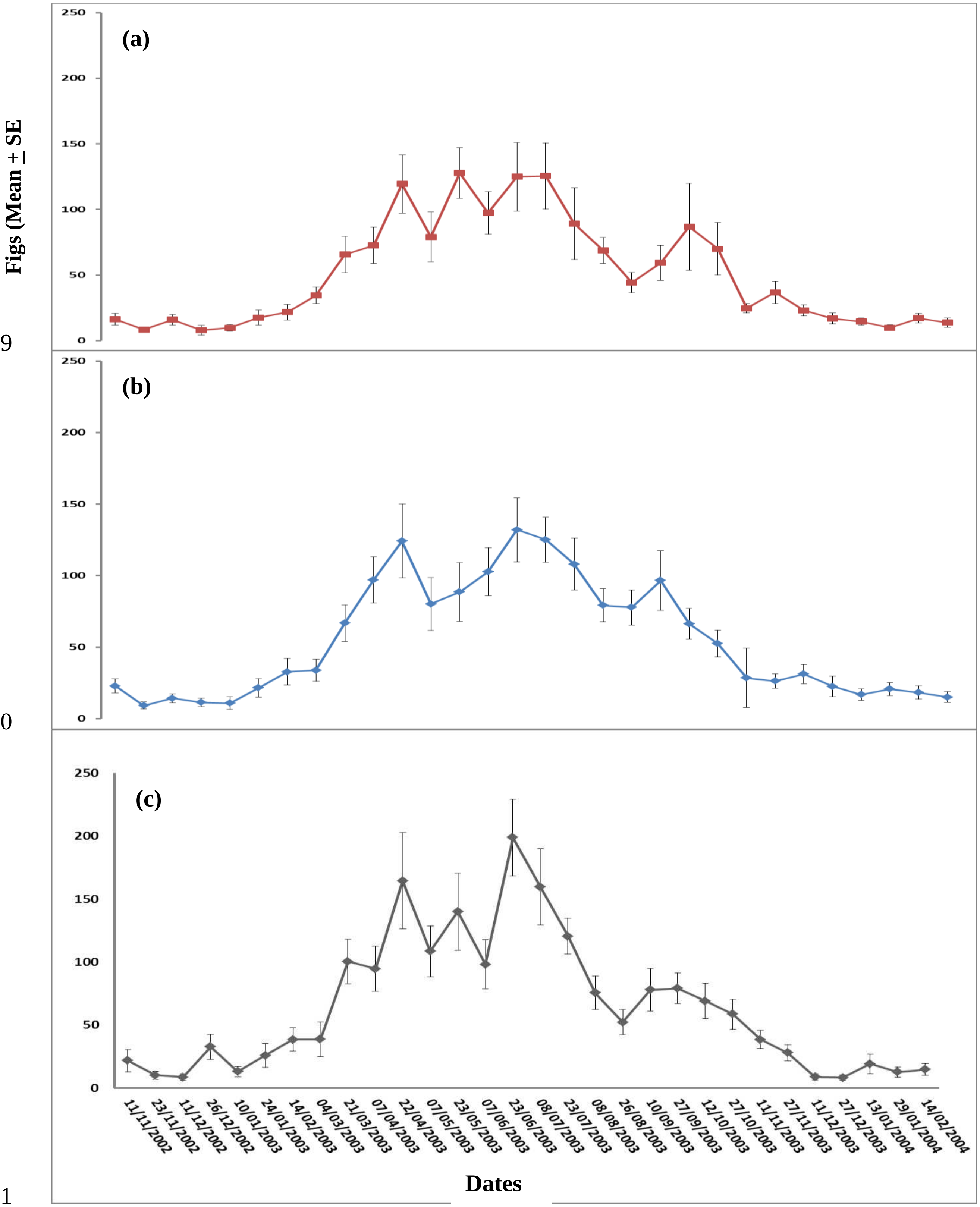

Figs (Mean +̲ SE
(a)
(b)
(c)
250
200
150
100
50
0
11/11/2002
23/11/2002
11/12/2002
26/12/2002
10/01/2003
24/01/2003
14/02/2003
04/03/2003
21/03/2003
07/04/2003
22/04/2003
07/05/2003
23/05/2003
07/06/2003
23/06/2003
08/07/2003
23/07/2003
08/08/2003
26/08/2003
10/09/2003
27/09/2003
12/10/2003
27/10/2003
11/11/2003
27/11/2003
11/12/2003
27/12/2003
13/01/2004
29/01/2004
14/02/2004
Dates

Fig. 1

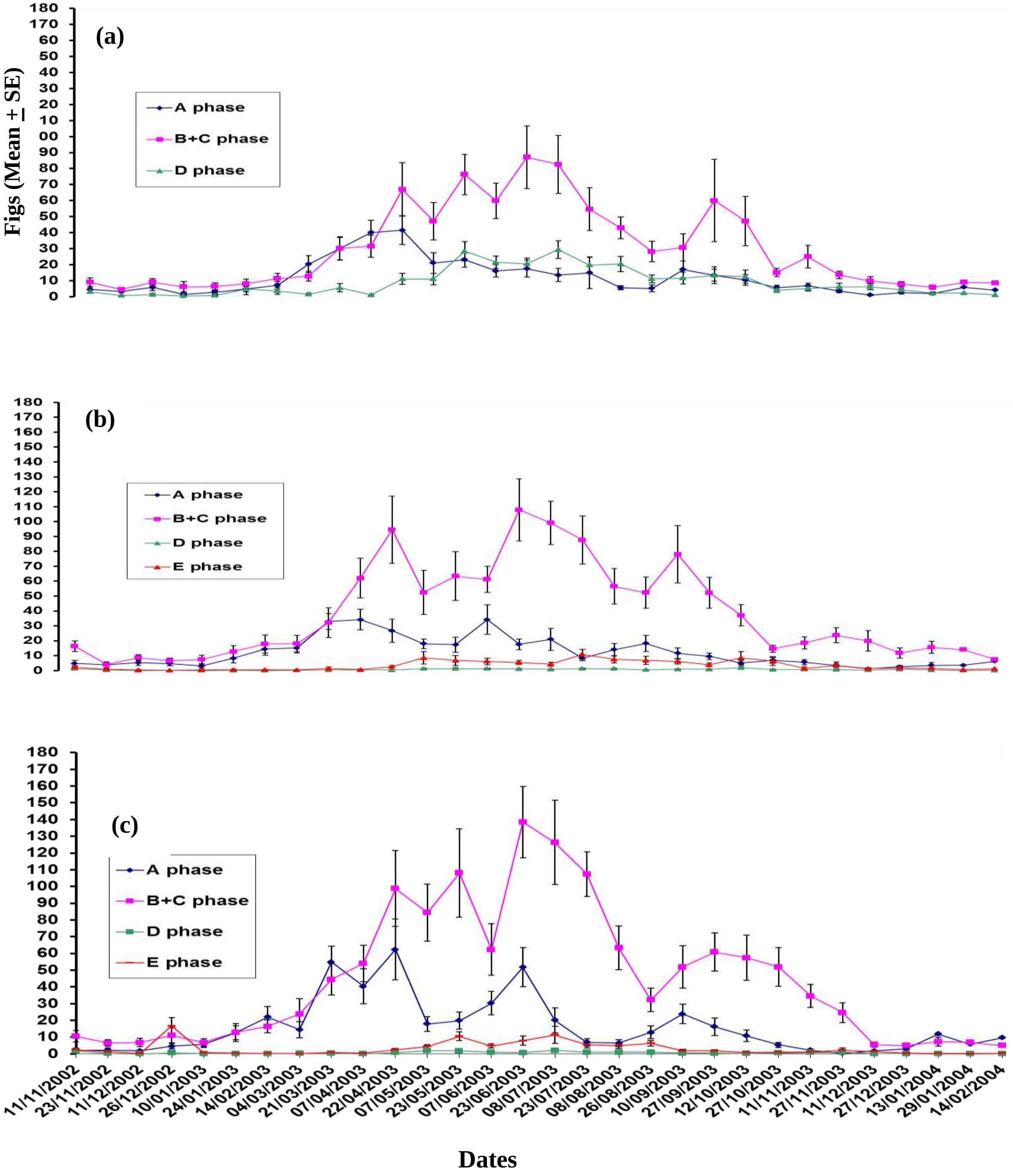
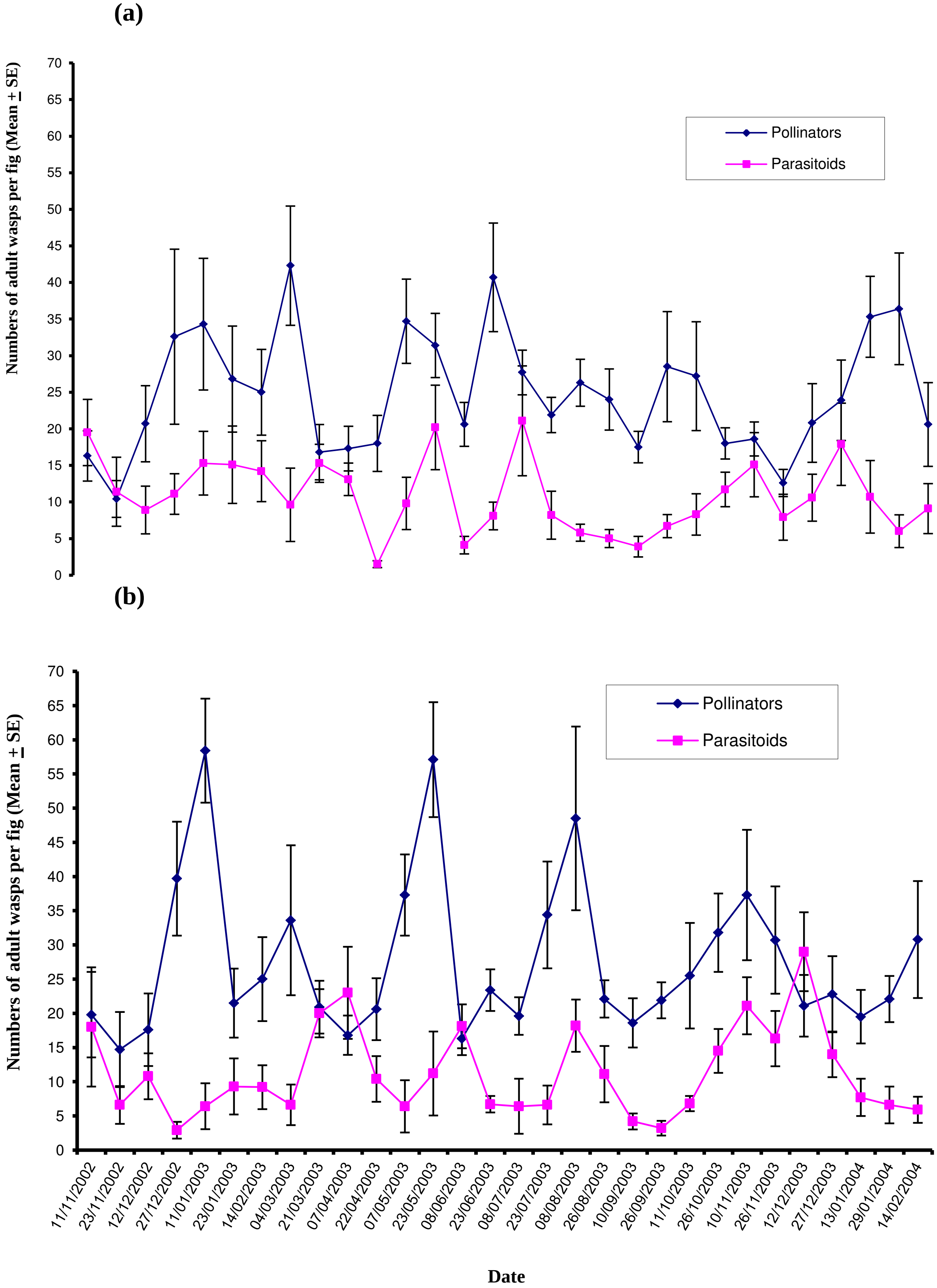

(a)
Figs (Mean + SE)
A phase
B+C phase
D phase
(b)
A phase
B+C phase
D phase
E phase
(c)
A phase
B+C phase
D phase
E phase
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
11/11/2002
23/11/2002
11/12/2002
26/12/2002
10/01/2003
24/01/2003
14/02/2003
04/03/2003
21/03/2003
07/04/2003
22/04/2003
07/05/2003
23/05/2003
07/06/2003
23/06/2003
08/07/2003
23/07/2003
08/08/2003
26/08/2003
10/09/2003
27/09/2003
12/10/2003
27/10/2003
11/11/2003
27/11/2003
11/12/2003
27/12/2003
13/01/2004
29/01/2004
14/02/2004
Dates

Fig. 2


(a)
Numbers of adult wasps per fig (Mean ± SE)
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
Pollinators
Parasitoids
(b)
Numbers of adult wasps per fig (Mean ± SE)
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
Pollinators
Parasitoids
11/11/2002
23/11/2002
12/12/2002
27/12/2002
11/01/2003
23/01/2003
14/02/2003
04/03/2003
21/03/2003
07/04/2003
22/04/2003
07/05/2003
23/05/2003
08/06/2003
23/06/2003
08/07/2003
23/07/2003
08/08/2003
26/08/2003
10/09/2003
26/09/2003
11/10/2003
26/10/2003
10/11/2003
26/11/2003
12/12/2003
27/12/2003
13/01/2004
29/01/2004
14/02/2004
Date

Fig, 3

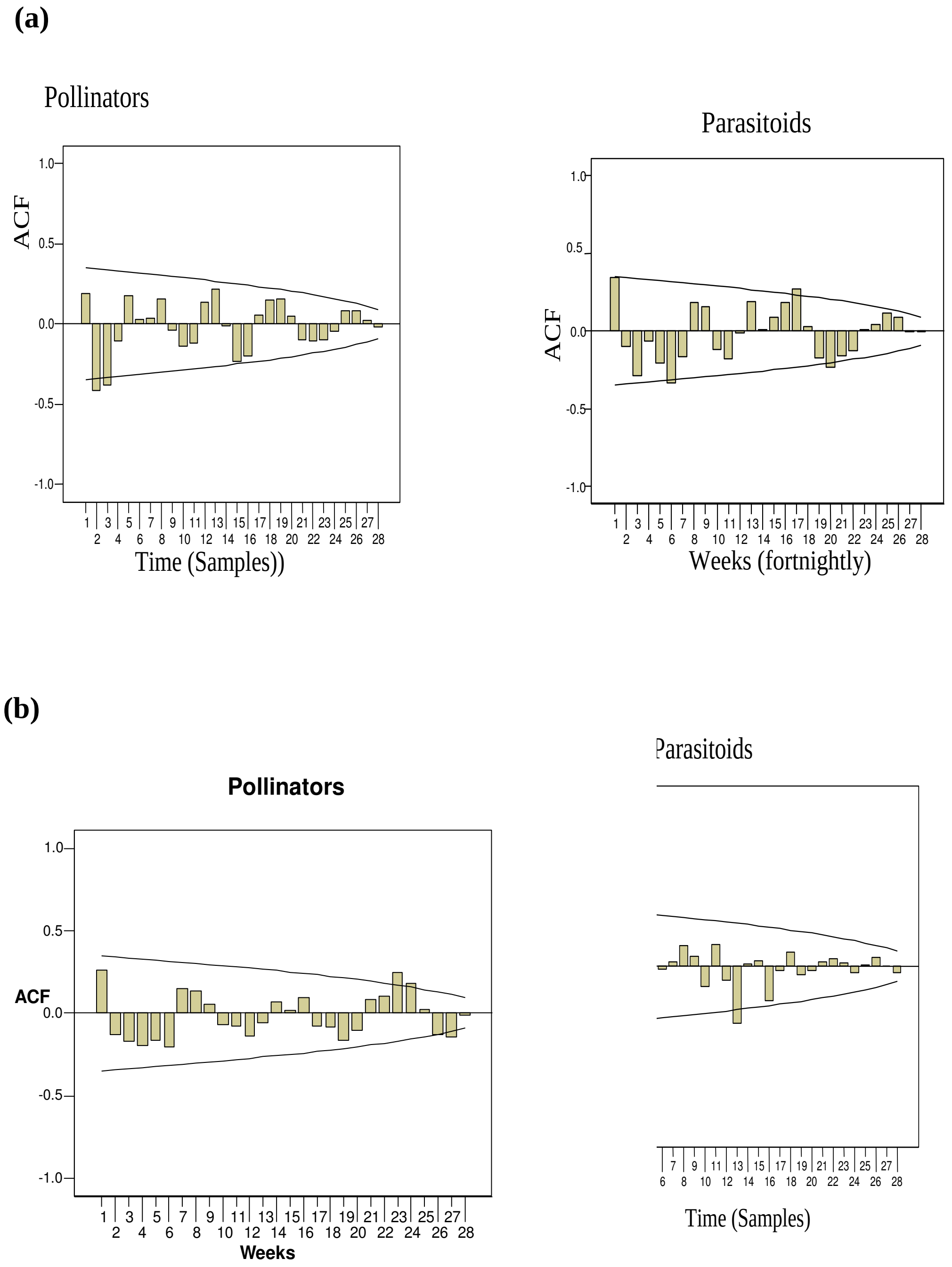

(a)
Pollinators
ACF
1.0
0.5
0.0
-0.5
-1.0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
Time (Samples))
Parasitoids
ACF
1.0
0.5
0.0
-0.5
-1.0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
Weeks (fortnightly)
(b)
Pollinators
ACF
1.0
0.5
0.0
-0.5
-1.0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
Weeks
Parasitoids
6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
Time (Samples)

Fig.4

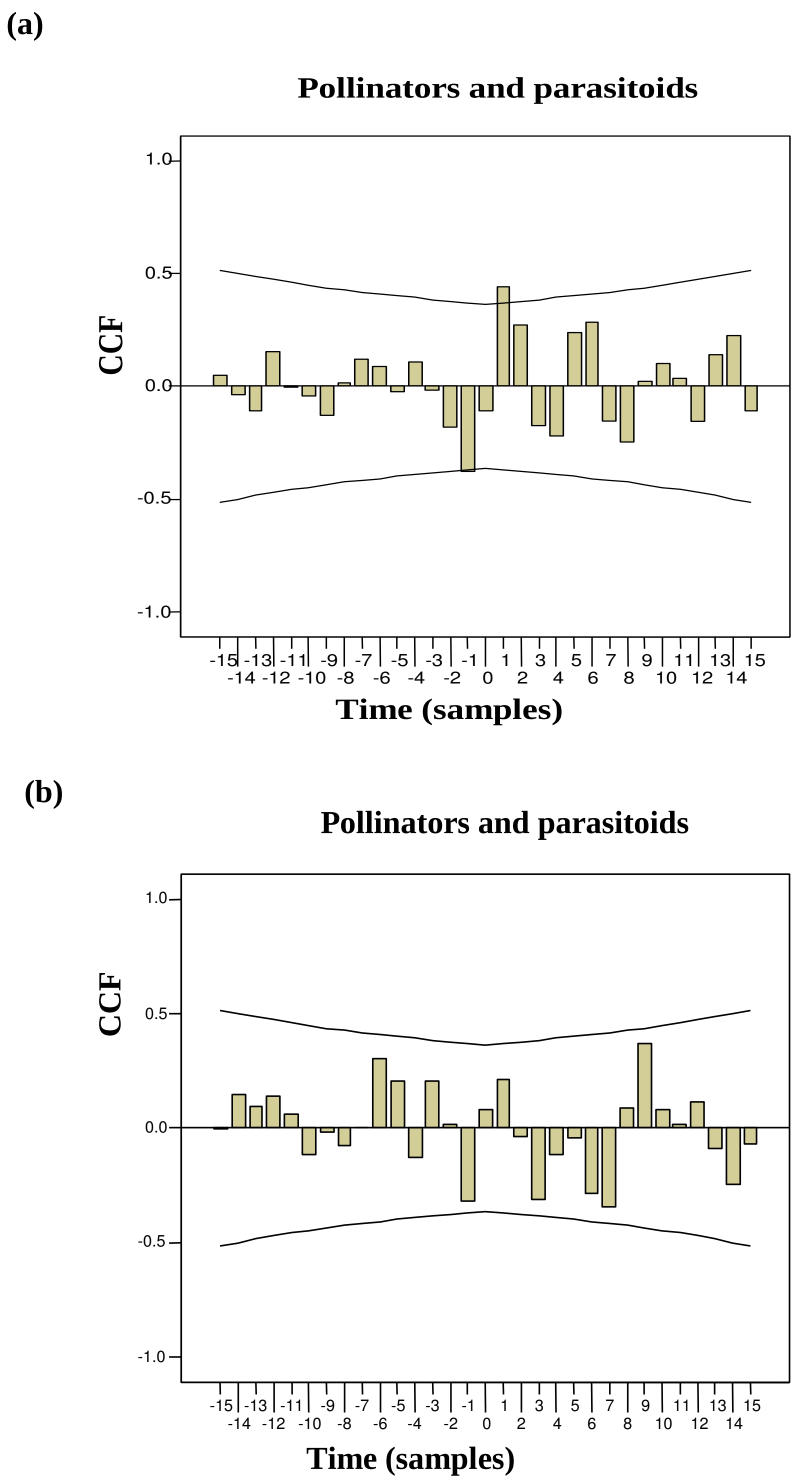

(a)
Pollinators and parasitoids
CCF
1.0
0.5
0.0
-0.5
-1.0
-15 -13 -11 -9 -7 -5 -3 -1 1 3 5 7 9 11 13 15
-14 -12 -10 -8 -6 -4 -2 0 2 4 6 8 10 12 14
Time (samples)
(b)
Pollinators and parasitoids
CCF
1.0
0.5
0.0
-0.5
-1.0
-15 -13 -11 -9 -7 -5 -3 -1 1 3 5 7 9 11 13 15
-14 -12 -10 -8 -6 -4 -2 0 2 4 6 8 10 12 14
Time (samples)

Fig. 5