

Complex interactions on fig trees: ants capturing parasitic wasps as possible indirect mutualists of the fig–fig wasp interaction

Bertrand Schatz, Magali Proffit, B. V. Rakhi, Renee M. Borges and Martine Hossaert-McKey

Schatz, B., Proffit, M., Rakhi, B. V., Borges, R. M. and Hossaert-McKey, M. 2006. Complex interactions on fig trees: ants capturing parasitic wasps as possible indirect mutualists of the fig–fig wasp interaction. – *Oikos* 113: 344–352.

Like other mutualisms, pollination mutualisms attract parasites, as well as opportunistic and specialist predators of the pollinators and parasites. These associated species influence the evolutionary dynamics of pairwise mutualisms. Predatory ants are frequent associates of pollination mutualisms, but their effects on the complex interactions between plants, pollinators and parasites have not yet been clearly established, even in the case of the well-described obligate interaction between figs and fig wasps. We attempted to quantify such effects for ants associated with three fig species, two dioecious (*Ficus condensa* [Brunei], *F. carica* [France]) and one monoecious (*F. racemosa* [India]). In all these cases, ant presence on a fig tree strongly reduced the number of parasitic wasps on the figs. Experimental exclusion of ants resulted in an increase in the number of non-pollinating fig wasps on *F. condensa* and *F. racemosa*. Experimental ant supplementation led to a decrease in the number of non-pollinating fig wasps on *F. carica*. Moreover, on *F. condensa*, the level of reduction of the number of parasitic wasps depended on the number and identity of the ants. On *F. carica*, non-pollinating fig wasps even avoided trees occupied by the dominant predatory ant. The consistency of the effect of ants in these three cases, representing a geographically, ecologically, and taxonomically broad sample of figs, argues for the generality of the effect we observed. Because reduction of parasitism benefits the pollinator, ants may be considered as indirect mutualists of plants and pollinators in the network of complex interactions supported by fig trees.

B. Schatz, M. Proffit and M. Hossaert-McKey, Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), UMR 5175, 1919 route de Mende, FR-34293 Montpellier cedex 5, France (schatz@cefe.cnrs.fr). – B. V. Rakhi and R. M. Borges, Centre for Ecological Sciences, Indian Inst. of Science, Bangalore 560 012, India.

Mutualisms offer resources that may also attract species not directly involved in the mutualism (Bronstein 2001, 2003, Yu 2001). Obligate interactions between pairs of species thus do not evolve in isolation but are integrated into a complex network of associates (Bronstein 1988, 1991, 2001, 2003, Compton and Hawkins 1992, Kerdelhué et al. 2000, Schatz and Hossaert-McKey 2003). These associates include parasites or predators of one or the other of the mutualists and they may influence the net benefits of the mutualism for one or both partners (Heithaus et al. 1980, Thompson 1982, Bronstein 1991,

2001, West and Herre 1994, West et al. 1996, Bronstein and Ziv 1997, Bao and Addicott 1998, Gaume et al. 1998, Gaume and McKey 1999, 2002). These associates may evolve adaptations to exploit the interaction, as some non-protecting plant-ants (Heil and McKey 2003) or galling fig wasps (Kerdelhué et al. 2000, Cook and Rasplus 2003) have done. Such interlopers contribute to the variability of outcomes observed in many mutualisms (Thompson 1988, Cushman and Whitham 1989, Bronstein 1994, 2001, Del-Claro and Oliveira 2000, Morales 2000, Yu 2001, Gaume and McKey 2002).

Accepted 4 July 2005

Copyright © OIKOS 2006
ISSN 0030-1299

Among these mutualistic interactions, the associations between fig trees (*Ficus* spp.) and fig wasps have long been studied as classical models of specialised pollination mutualisms, each involving one species of pollinating wasp and one species of fig tree (Anstett et al. 1997, Herre et al. 1999, Weiblen 2002, Jusselin et al. 2003, Kjellberg et al. 2005). Understanding the biotic constraints exerted on a two-partner mutualism involved in a complex network of antagonistic interactions requires identifying the factors which stabilise or destabilise the mutualism, which in turn requires clear assessment of the impact of these factors on the mutualistic partners (Schatz and Hossaert-McKey 2003). However, in the case of fig trees, while numerous studies have examined the impact of seed predators or frugivores on female reproductive function (Jordano 1983, Thomas 1988, Shanahan 2000), much less is known about species that interact with the mutualism via their direct or indirect impact on the pollinating wasps (Bronstein 1988, West and Herre 1994). Several studies have shown that the fig–fig wasp mutualism is the target of a large variety of arthropod species, including specialised non-pollinating chalcidoid wasps (Compton and Hawkins 1992, West et al. 1996, Kerdelhué et al. 2000, Weiblen 2002, Cook and Rasplus 2003) and other non-pollinating hymenoptera, including several ant species (Bronstein 1988, Compton and Robertson 1988, 1991, Zachariades 1994, Dejean et al. 1997, Schatz and Hossaert-McKey 2003). Each *Ficus* species is specifically associated with a cohort of non-pollinating wasps, which in general are believed to have a negative impact on the mutualism. Most of the non-pollinating wasps are externally ovipositing species which are equipped with a long ovipositor to lay eggs from the outside, through the wall of the fig, but some are also internally ovipositing wasps which enter into the fig through the ostiole (reviewed by Weiblen 2002, Cook and Rasplus 2003). In contrast, ants associated with different *Ficus* species have mainly been described as predators of pollinating fig wasps (Bronstein 1988, Compton and Robertson 1988, 1991, Thomas 1988, Zachariades 1994, Dejean et al. 1997, Cushman et al. 1998, Schatz and Hossaert-McKey 2003) but their impact on both figs and pollinating fig wasps has not often been quantified. Moreover, ants could also affect the outcome of the mutualistic interaction by modifying the impact of non-pollinating fig wasps. Ants can directly affect parasites by preying on them or disturbing their activity when they are ovipositing on the external surface of the fig (Bronstein 1988, Compton and Robertson 1988, 1991, Zachariades 1994). By reducing the negative effect of parasitic wasps, as indirectly shown by a long term study on *F. sur* Forsskål (Compton and Robertson 1988, 1991), ants can strengthen the fig–wasp mutualism. However, as pointed out by Zachariades (1994), detailed behavioural and functional studies of such interactions, as well as

quantification of their direct effect on the mutualism, are still lacking. More generally, theoretical models that demonstrate variation in the outcome of mutualisms caused by the impact of other associated species have been developed (Law et al. 2001, Morris et al. 2003), but empirical data are still rare.

In this study, we examine the effect of ants on the presence of parasites specifically associated with the mutualism between figs and their pollinators. In order to quantify the impact of ants, we compared their effects on three different species of figs: *Ficus condensa* King in Brunei (northern Borneo), *F. racemosa* L. in India and *F. carica* L. in France. These species present particular advantages for such a study. In the first two species, figs grouped in clusters on the trunk (cauliflory) facilitate the observation of a large sample of figs for each tree, while in the third species, a small tree, figs are on branches generally situated at eye-level. In addition to their respective pollinators, these fig species have two other kinds of associates: parasitic wasps (one common species per fig species) and ants, usually one or two dominant tree-nesting species. The similarity of parameters for these three species allowed us to quantify the effect of ant presence on the occurrence of parasitic wasps under natural conditions and during experimental manipulation of ant numbers by exclusion or supplementation, and to compare these effects across species. Data from these observations and experiments yield insight into the short-term dynamics of the interaction between ants and parasitic wasps.

Material and methods

Species and study sites

Observations and experiments on *F. condensa* (subgenus *Sycomorus*; a dioecious species pollinated by *Ceratosolen constrictus* Mayr) were performed from mid-April to mid-May 2002 in Brunei Darussalam (northern Borneo) on the grounds of the Museum of Natural History and in neighbouring degraded secondary forests of Bandar Seri Begawan (4°30'N, 114°40'E). Observations and experiments on *F. racemosa* (subgenus *Sycomorus*; monoecious species pollinated by *Ceratosolen fusciceps* Mayr), were performed in May 2003 on the campus of the Indian Institute of Science in Bangalore (Karnataka, India) (12°58'N, 77°35'E). For *F. carica* (subgenus *Ficus*; dioecious species pollinated by *Blastophaga psenes* L.), experiments were conducted in the experimental garden of the CEFÉ (Montpellier, France) (43°40'N, 3°53'E). Both tropical species of figs produce clusters of cauliflorous figs on the trunk, while figs are present at the extremities of branches in *F. carica*.

Species of pollinators, parasites and ants respectively associated with the three species of figs are listed in Table 1. Species of parasites mentioned in this paper for

Table 1. Species of pollinating wasp, parasitic wasps, and ant(s) respectively associated with the three studied fig species. Pollinator and parasitic wasps were specifically associated with the fig species, while ant species indicated here only correspond to the occurrence locally observed. At the time of these observations, *Apocrypta* sp. was the dominant parasite present on *F. racemosa*.

Site of study	Species of fig	Associated species of pollinating wasp	Associated species of parasitic wasp	Main associated ant species
Brunei	<i>Ficus condensa</i> K.	<i>Ceratosolen constrictus</i> Mayr	<i>Apocrypta</i> sp.	<i>Oecophylla smaragdina</i> Fab. and <i>Crematogaster</i> sp.
India	<i>F. racemosa</i> L.	<i>Ceratosolen fusciceps</i> Mayr	<i>Apocrypta</i> sp.	<i>Oecophylla smaragdina</i> Fab.
France	<i>F. carica</i> L.	<i>Blastophaga psenes</i> L.	<i>Philotrypesis caricae</i> L.	<i>Crematogaster scutellaris</i> Ol.

the two tropical figs were the major species observed at the time of the experiment, while the parasite *Philotrypesis caricae* L. is the sole parasite on *F. carica*. This last species has been described as a kleptoparasite (it oviposits through the fig wall into fig ovules containing pollinator eggs) (Joseph 1957) and both *Apocrypta* species are parasitoids (J.-Y. Rasplus, pers. comm.). All parasites studied here oviposit into the florets by inserting their long ovipositors through the fig wall. Parasites were observed ovipositing on fig trees shortly after pollinator visitation to the tree. In this paper we use the more general term 'parasite' for the three species of non-pollinating wasps we studied.

Concerning ants, this study deals only with the ecologically (and behaviourally) dominant species observed during our experiments. All three ant species nested within the fig trees and were polydomous. *Oecophylla smaragdina* Fab. (Formicinae) builds nests by weaving together leaves, while *Crematogaster* sp. (Myrmicinae) in Brunei inhabited cavities in dead parts of the trunk or in fig clusters of *F. condensa*. In Mediterranean habitats of France, *Crematogaster scutellaris* Ol. lives under thick cork and in dead parts of the trunk or branches of trees (Schatz and Hossaert-McKey 2003). Present on the two tropical species of figs, *O. smaragdina* is a large (~10 mm long) and aggressive ant species, efficient in capturing large prey, while *Crematogaster* sp. (co-dominant on *F. condensa*) is a smaller ant (~2 mm long) that sprays a defensive secretion and displays rapid local recruitment (Hölldobler 1983, Dejean 1990, Hölldobler and Wilson 1990). Although *F. carica* is visited by ten species of ants, *C. scutellaris* is behaviourally and ecologically dominant, excluding the others, and is the only species to show a significant impact on the presence of parasites within fig trees (Schatz and Hossaert-McKey 2003).

Relationship between the numbers of ants and parasites under natural conditions

Observations on *F. condensa* were made on male trees (n = 16) during eight non-consecutive days between 0900 and 1400 h, the time of maximal activity of ants and parasitic wasps. Using scan sampling (visual observa-

tions during the five minutes after we arrived near the fig tree), we recorded the number and species of ant workers present per cluster (each cluster consisting of 10–20 figs). We divided the observations into six categories according to the number and species of ants on the figs: (1) no ants present (not even those of other species), (2) between one and four *O. smaragdina* and no *Crematogaster* sp. or other ants, (3) between one and four *Crematogaster* sp. but no *Oecophylla* or other ants, (4) more than four *O. smaragdina*, and no other ants (5) more than four *Crematogaster* sp. and no other ants and (6) total of the two ant species greater than four individuals, with fewer than five workers of each species and no other ant species. When we observed capture of parasitic wasps by ants, we also noted whether the wasps were ovipositing (ovipositor inserted into the fig). We then analyzed the effects of these different categories of ant presence on the number of parasites observed on figs using an ANOVA (type 3 error) (Proc Genmod [SAS 1999], Poisson distribution, dscale correction for overdispersion). This analysis was followed by a post-hoc pairwise comparison of the mean numbers of parasites observed for each ant category using a Tukey-Kramer test. We did not conduct observations on the natural occurrence of ants and parasites on *F. racemosa*.

In *F. carica* we recorded the presence or absence of the parasite *P. caricae* as well as of the dominant ant *C. scutellaris* in the experimental plantation of the CNRS using instantaneous one-zero sampling. These observations were performed on 144 trees (63 males and 81 females) in June 2002 and between 1000 and 1600 h, the time of maximal ant activity. Using a Fisher exact test (SAS 1999), we compared the number of times parasites were recorded in the presence and in the absence of ants.

Experimental determination of the effect of ant number on abundance of parasitic wasps

Ant-exclusion experiments

We used two clusters of cauliflorous figs per tree of the two tropical species of figs, patrolled by their respective species of ants and bearing parasitic wasps (which were present almost exclusively on male trees in *F. condensa*).

Exclusion experiments were performed on eleven male *F. condensa* trees and on 13 male *F. racemosa* trees. We chose trees between 3 and 10 m in height growing at least 50 m apart, to minimise any effect of spatial proximity between the trees. For each tree, both clusters of figs were located at similar height, and had the same number of figs (artificially adjusted). The number of figs per cluster varied between 5 and 38 among the 11 trees of *F. condensa* and between 4 and 31 among the 13 trees of *F. racemosa*. One of the two fig clusters was used as the control while the other was surrounded by glue placed directly on the trunk to exclude ants. A visual check during the first few minutes of the experiment, as well as counts of ants throughout the exclusion, allowed us to verify that ants were effectively excluded. All ants and parasites were removed at the start of the exclusion experiment (T_0) for the two species. For the first set of five trees in *F. condensa*, we counted the numbers of the two ant species and the parasites after 10, 20, 30, 40, 50, 60, 90, 120, 150 and 180 min. Because these preliminary results obtained on five trees of *F. condensa* showed that the number of parasites became stable after 30 min, observations on subsequent trees were made only at 30 and 90 min (T_{30} and T_{90}). This allowed us to minimize effects of differences in time of arrival of parasitic wasps and timing of ant activity. However, such a protocol was not applied in the case of *F. racemosa*, because the number of parasites was more variable. To facilitate comparison, for each of the two tropical fig species and for each value of the number of parasites recorded, we calculated the percentage of the maximal value of parasites recorded for each tree. The number of parasites was compared between control and test situations using paired t-tests (SAS 1999).

Ant-supplementation experiments

In the case of *F. carica*, previous experiments showed that the parasitic fig wasp *P. caricae* was rarely found on individual figs on which the ant *C. scutellaris* occurred. We experimentally added *C. scutellaris* workers onto a branch where parasites were observed in large numbers, surrounding the base of this branch with glue to prevent

the escape of ants. The *C. scutellaris* workers were taken from a nest that exploited pollinating wasps as prey. These observations were performed between 1000 and 1600 h in April-May 2002 and 2003. We randomly chose sixteen pairs of branches with three branches, all bearing similar numbers of figs and of parasites. One of the two branches was used as the control while on the other at T_0 we placed ten individuals of *C. scutellaris*. The resulting ant density was roughly equivalent to the natural density of this species in the presence of pollinators (B. Schatz, pers. obs.). Workers were placed at the base of the branch to prevent the departure of parasites (control counts confirmed the effectiveness of this measure), which were mainly present on figs and leaves. We counted the number of parasites every five minutes for 40 minutes on both branches. To compare parasite occurrence, we calculated for each value the percentage of the maximal number of parasites recorded for the same branch. We tested for an effect of ants on the number of parasites using paired t-tests for each census (SAS 1999).

Results

Relationship between the numbers of ants and parasites under natural conditions

On *F. condensa*, parasite number was clearly negatively associated with ant presence on the branch (effect of ant category on total number of parasites (ANOVA): $\chi^2 = 374.0$; $df = 1$; $P < 0.001$; Fig. 1). This effect was highly significant for both ant species. The number of parasites was lower for figs with larger numbers of ants (comparisons [between one and four individuals] vs [more than four individuals] for both *O. smaragdina* [$\chi^2 = 11.2$; $df = 1$; $P < 0.0001$] and for *Crematogaster* sp. [$\chi^2 = 8.9$; $df = 1$; $P < 0.003$]). There was also a marginally significant effect of ant species on parasite abundance, with fewer parasites on figs with *O. smaragdina* than on figs with comparable numbers of *Crematogaster* sp. (for the category [1–4 individuals]: $\chi^2 = 6.1$; $df = 1$; $P < 0.02$; $P < 0.059$ after Sidak's correction) and for the category

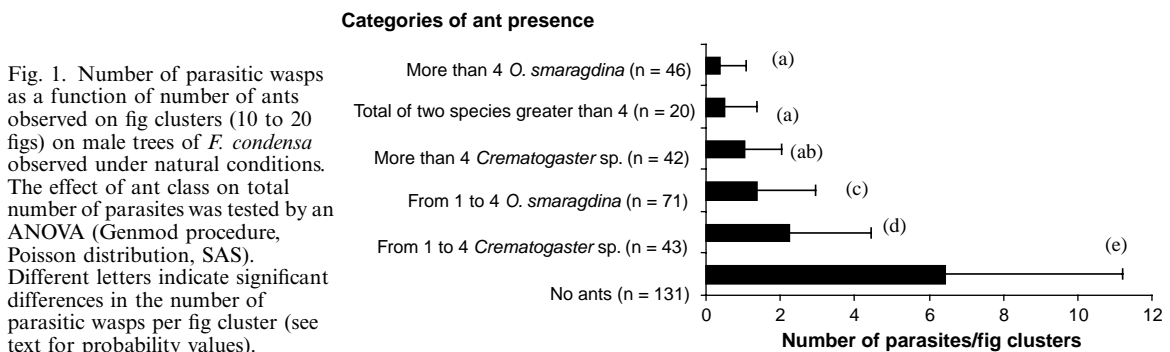


Fig. 1. Number of parasitic wasps as a function of number of ants observed on fig clusters (10 to 20 figs) on male trees of *F. condensa* observed under natural conditions. The effect of ant class on total number of parasites was tested by an ANOVA (Genmod procedure, Poisson distribution, SAS). Different letters indicate significant differences in the number of parasitic wasps per fig cluster (see text for probability values).

[>4 individuals]: $\chi^2=5.6$; $df=1$; $P<0.02$; $P<0.059$ after Sidak's correction). Despite this ant species effect, once the total number of ant workers on a fig reached four individuals, the effect on parasite abundance was always significant. Parasite abundance on fig clusters in the category [total number of workers of the two species >4] was not significantly different from that on figs in the two categories [>4 *Crematogaster* sp.] ($\chi^2=2.0$; $df=1$; $P>0.15$) and [>4 *O. smaragdina*] ($\chi^2=0.2$; $df=1$; $P>0.50$). The presence of more than four *Crematogaster* sp. or more than four *O. smaragdina* ants was associated respectively with a reduction of 84.1% and 93.9% of the number of parasites per fig cluster, being reduced to 1.02 ± 1.02 and 0.39 ± 0.68 parasite wasps, respectively, compared to the mean number of parasitic wasps per fig cluster in the absence of ants (6.43 ± 4.77 parasite wasps). We also observed both *O. smaragdina* and *Crematogaster* sp. capturing parasitic wasps, which were in most cases in the process of ovipositing (for *O. smaragdina* workers, 38 of the 49 observed cases; $\chi^2=8.05$; $df=1$; $P<0.005$; for *Crematogaster* sp. workers, 28 of the 34 observed cases; $\chi^2=7.95$; $df=1$; $P<0.005$). We also frequently observed ants trying to capture both parasitic wasps and pollinators that were flying above figs before landing.

On *F. carica*, the parasites were concentrated on 25 trees of the 144 observed. They were more frequent on male trees (22 cases; 88%) than on females (3 cases; 12%). On male trees, the presence of parasites was significantly higher in the absence of ants (19 trees with parasites vs 15 trees without) than with ants patrolling the tree (3 trees with parasites vs 26 trees without) (Fisher exact test: $\chi^2=14.28$; $df=1$; $P<0.0002$). In the cases where ants and parasites co-occurred on trees, we observed *C. scutellaris* workers capturing pollinating fig wasps and attempting unsuccessfully to capture parasites, which flew away, mainly towards other trees. In fact, if we consider these cases of co-occurrence as temporary, we can distinguish three kinds of male trees: those occupied by the ant *C. scutellaris* (and not by the parasites and non-dominant ants), those occupied by the parasite alone (with non-dominant ants) and those with neither *C. scutellaris* nor parasites (but with non-dominant ants). The last group comprised trees in the buffer zone between territories of two *C. scutellaris* colonies, or smaller trees, or trees with a small number of figs, and these attributes could explain the absence of parasites in this group.

Experimental determination of the effect of ant number on abundance of parasitic wasps

Exclusion experiments on *F. condensa*

The dynamics of parasite visits were similar among the first five fig trees studied (Fig. 2). After the beginning of

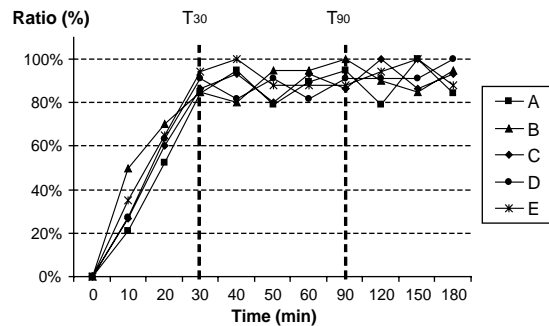


Fig. 2. Dynamics of the arrival of parasitic wasps from the start of the exclusion experiment on *F. condensa*. The number of parasites is expressed as the ratio between the values observed at each time and the maximal value observed for that tree. Five trees were studied (A to E).

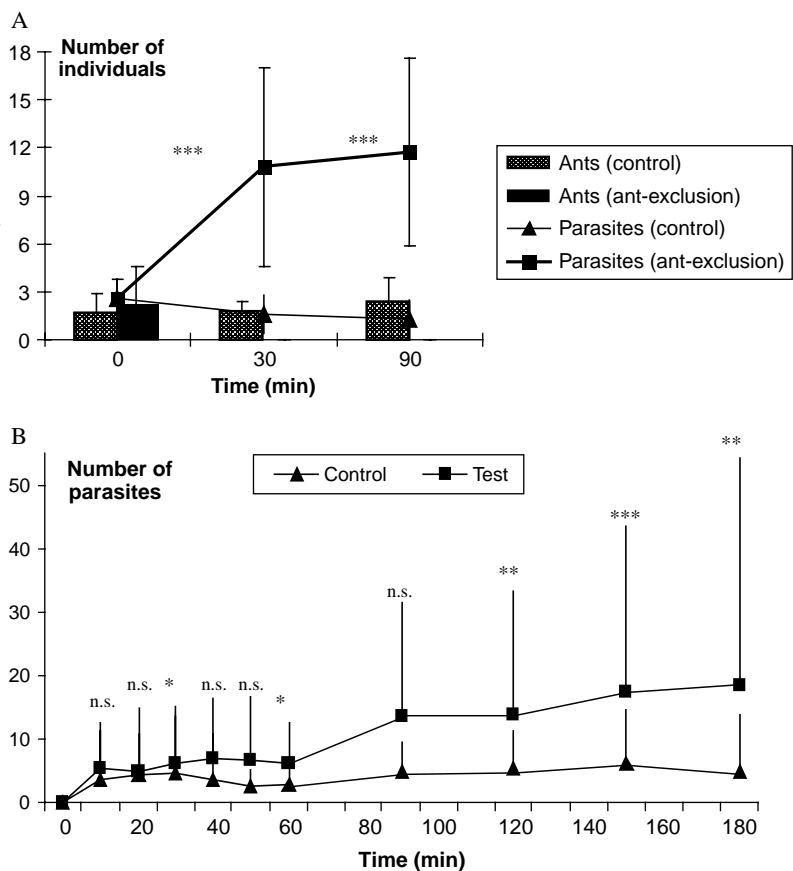
the exclusion experiment at T_0 , parasite numbers steadily built up to T_{30} . From T_{30} and until T_{180} , the number of parasites reached a plateau, with values varying between 79 and 100% of the maximum observed values for each tree. The census of parasite visits at T_{30} and T_{90} thus gave a good estimate of parasite abundance, since they respectively represented 84–94% and 87–100% of the maximum observed values.

Parasite numbers per fig cluster were significantly higher under ant exclusion conditions than under natural conditions at T_{30} (paired t-test: $P<0.00013$) and at T_{90} (paired t-test: $P<0.000025$; Fig. 3A). Moreover, when ants were excluded, the number of parasites at T_{90} was significantly correlated with the number of figs in the cluster (Spearman rank correlation: $r_s=0.762$; $P<0.01$; $df=9$), while no correlation existed under natural conditions ($r_s=0.596$; $P>0.1$; $df=9$). Under ant-less conditions then, parasites saturated their resources. The number of parasites was 21–50% of the maximum at T_{10} and 53–70% of the maximum at T_{20} . Numbers of parasites observed under ant exclusion were 10.0–22.2% of those observed under natural conditions, suggesting that ants should patrol figs on average once per 10 minutes to maintain such low numbers of parasites (graphic determination).

Exclusion experiments on *F. racemosa*

Parasite numbers per fig cluster were significantly higher under ant exclusion conditions than under natural conditions. This difference was small at the beginning, i.e. at T_{30} and at T_{60} ($P<0.05$), and larger later, i.e. at T_{120} and at T_{180} ($P<0.025$), and at T_{150} ($P<0.001$; paired t-test in all cases; Fig. 3B). The difference in the number of parasites between control and experimental conditions steadily increased over the duration of the experiment, even though the considerable variance in the experimental situation contributed to an underestimation of this difference. At T_{180} , the number of parasites in the control situation (4.9 ± 9.1 individuals) repre-

Fig. 3. Effect of ant exclusion on the number of parasitic wasps in *F. condensata* (A) and in *F. racemosa* (B). In the case of *F. condensata*, comparison of the numbers of parasites (lines connected by symbols) and of ants (histograms) in control and ant-exclusion treatments. Mean numbers (\pm SD) of parasites on the control and test fig clusters were each compared at T₃₀ and T₉₀ in the case of *F. condensata* and at each time in the case of *F. racemosa* using paired t-tests (ns: non-significant result; *: P < 0.05; **: P < 0.025; ***: P < 0.001).



sented about a quarter (26.4%) of the number of parasites in the ant-exclusion situation (18.4 ± 35.8 individuals). No correlation was found between numbers of figs per cluster and numbers of parasites [using the observed maximal value of parasites (Spearman rank correlation): $r_s > 0.176$; $df = 14$; $P > 0.50$], suggesting that parasites did not saturate their resource.

Supplementation experiments on *F. carica*

Parasite numbers per branch were significantly lower under ant supplementation conditions than under natural conditions after five minutes ($P < 0.05$) and for all subsequent times ($P < 0.01$; paired t-test in all cases; Fig. 4). While numbers of parasites remained stable on control branches, they rapidly decreased on test branches over the period of observations to reach a quarter (25.6%) of the initial value after 40 min of observation. We also observed that the addition of ants rapidly led parasites to cease oviposition behaviour (most ovipositions had stopped before the termination of the observation period at five minutes), resulting in movement of the parasites toward neighbouring fig leaves before flying toward other branches of the same tree or towards other trees.

Discussion

This study clearly demonstrated that presence of ants on three species of figs in three different geographical areas (Brunei, India and France), representing very different ecological situations, reduced the number of parasitic

Presence of parasites

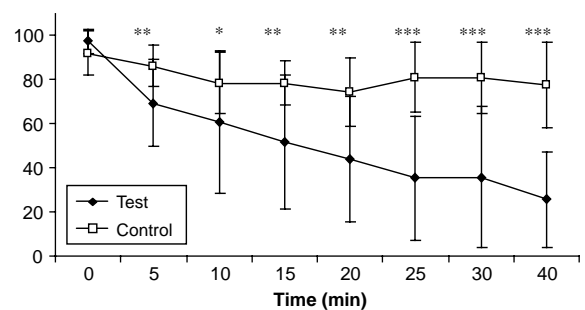


Fig. 4. Effect of ant supplementation on the number of parasitic wasps in *F. carica*. Presence of parasites corresponds to the percentage of the number of parasites at each observation time compared to the number of parasites at the initial time (T₀). Numbers of parasites on the control and test branch were compared at each observation time using paired t-tests (*: P < 0.05; **: P < 0.005; ***: P < 0.001).

wasps visiting the figs, thus pointing to a generality of the results. In comparison with the control situation, the change in the number of parasites was estimated to be an increase of 85% and 74% after the exclusion experiments on *F. condensa* and *F. racemosa* respectively, and a reduction of about 75% after the ant-supplementation experiment on *F. carica*. A similar change in the number of parasites has been suggested during exclusion experiments on ants of *Philidris* sp. patrolling *F. schwarzii* Koord figs (Harrison 1996). Moreover, observations on *F. condensa* under natural conditions also showed that parasitic fig wasps avoided figs with larger numbers of ants. Similarly, on *F. carica*, parasitic wasps strongly preferred trees without workers of the dominant ant, regardless of which non-dominant ants were present. As a result of this behaviour, the presence of ants was negatively correlated with the presence of the parasite wasps. Such responses of parasitic wasps to ant presence can be rapidly induced, as shown by the rapid change in the number of parasites in response to the experimental manipulation of ant numbers, and by the low frequency of co-occurrence of ants and parasitic wasps on *F. carica*. This dynamical pattern of variation in density of parasitic wasps on figs can be a consequence of their resource exploitation. If the parasites saturate their resource, as in the case of *F. condensa*, the number of parasitic wasps increased quite rapidly. If the resource was not saturated, the number of parasites visiting the figs should increase slowly as observed in *F. racemosa*.

Based on our study of the interactions between predatory ants and parasitic fig wasps on three different *Ficus* species, we attempt to identify biological features common to each of the three partners of the interaction.

(1) Concerning the parasitic fig wasps, our results showed that their co-occurrence with dominant ants was associated with a predation risk, despite the differences in size and variation in density among ant species. In response to this predation risk, the parasitic wasps displayed appropriate evasive action as previously described in other wasps (Curio 1976, Hölldobler and Wilson 1990). Such a situation has been documented only rarely among insects or other invertebrates (reviewed by Wcislo and Schatz 2003). Other experiments are still needed to determine what cues are used by parasitic fig wasps to detect presence of ants. Vision may be quite important since parasitic wasps commonly appear to be able to discriminate predators from a distance (Wcislo and Schatz 2003). This was the case on *F. condensa*, where parasitic wasps more frequently avoided figs occupied by the larger *O. smaragdina* workers than they avoided figs occupied by the smaller *Crematogaster* sp. workers. Our results on *F. condensa* also suggest that ants could exert a sufficiently important selective pressure to explain the unusual fig

approach behaviour observed in the parasitic fig wasps. These wasps hovered several centimetres above fig clusters before landing on an ant-free fig. This peculiar behaviour was also observed for pollinating wasps on *F. hispida* (A. Patel, pers. comm.) and *F. racemosa*. In *F. condensa*, parasitic wasps, which oviposit from outside the figs, were certainly more vulnerable to ant attacks, because retracting their ovipositor from the fig delays their escaping flight (Bronstein 1988). In addition, ant presence on a fig tree can also explain some of the observed behaviours of parasitic wasps (e.g. inter-individual avoidance, syconium choice and local aggregation on an ant-free fig, correlation between the number of parasites and the number of figs per cluster, rapid retraction of the ovipositor, etc.). These behaviours are yet to be studied.

(2) Concerning the ants, the two dominant ant genera observed in our study, *Oecophylla* and *Crematogaster*, possess several traits in common leading to efficient predation on wasps. Their large and polydomous colonies (Hölldobler 1983, Hölldobler and Wilson 1990) include nests within the fig trees, allowing them to rapidly exploit fig-associated wasps as prey. They are known to be ecologically dominant and efficient predators, able to catch very mobile insects by rapid movement of the whole body during the seizure behaviour (Schatz et al. 1997, Richard et al. 2001, Schatz and Hossaert-McKey 2003). Moreover, the greater temporal availability of parasitic wasps (generally present several days before and after the onset of fig receptivity; Kerdelhué and Rasplus 1996) may facilitate learning by ants. This learned behaviour may have led them to greater success in capturing parasites and thereby to behavioural specialisation on this type of prey. This was the case for *F. condensa*, where the predatory ants ensured an active and efficient patrolling behaviour on each fig cluster at short time intervals (about 10 min).

(3) Concerning the fig tree itself, the position of figs on the trunk and their occurrence in clusters, in the case of the tropical fig species studied, is likely to favour the efficiency of ant visits. Aggregation of figs could reduce the probability that a given fig will be found by parasitic fig wasps. Aggregation of figs is also likely to favour ant activity, as it would be more difficult for them to patrol the same number of figs dispersed on the twigs. Such an effect of fig dispersion remained limited in the case of *F. carica*, since the trees were small in size.

Interactions among pollinators, parasites and ants could also have at least two other important impacts on the insect fauna present on fig trees. In *F. carica*, the trees occupied by *C. scutellaris* were avoided by the other ant species (Schatz and Hossaert-McKey 2003) as well as by the parasitic fig wasps, as shown in this study. As a result, the presence of *C. scutellaris* is an important factor structuring the hymenopteran fauna

on fig trees. It would be interesting to investigate whether this structuring effect by the local dominant ant species exists within tropical cauliflorous fig trees, in which the groups of figs on the trunk should be otherwise highly attractive to parasites. The second effect of the interaction among these partners on fig trees corresponds to the reduction of the number of parasites due to the presence of ants, which could lead to substantial protection of pollinator larvae from larvae of parasitoid wasps. Our results are thus the first quantitative data available to evaluate the ratio of displacement performed by ants on parasitic wasps, which constitutes a key factor in determining the impact of ants on the mutualism (Schatz and Hossaert-McKey 2003). However, the estimation of this ratio is made difficult by the considerable variability in the populations of the two kinds of wasps, and in the ant effect itself (Bronstein 1988, 1991, 1994, Compton and Robertson 1988, 1991, Zachariades 1994, Cushman et al. 1998, Schatz and Hossaert-McKey 2003). For example, ants very rarely capture *P. caricae* on *F. carica* (Schatz and Hossaert-McKey 2003), whereas predation intensity on parasites was greater on *F. pertusa* L. (Bronstein 1988), and on *F. sur* Forsskål (Zachariades 1994). We thus suggest that in the case of the three fig species studied here, the positive effect of displacement of parasitic wasps by ants could compensate for their possible negative effect on pollinating wasps. Initially considered as exploiters of the fig–fig wasp mutualism, ants may in some cases confer some advantage to pollinating fig wasps. If these advantages outweigh any negative effect on pollinators, ants could be considered as indirect mutualists of figs and fig wasps (Dawkins and Krebs 1979, Bronstein 1991) as in the case of the myrmecophytic species *F. obscura* Bl. var. *borneensis* Miq. (Maschwitz et al. 1994). The hypothesis of indirect mutualism would be supported by demonstration of a fitness increase for the fig tree, such as increased seed production in figs patrolled by ants. Whatever the net impact of ants on fig–wasp mutualisms, our results reinforce the argument that this two-partner mutualism is enmeshed in a network of complex interactions (Bronstein 1988, 2003, Compton and Robertson 1988, 1991, Zachariades 1994, Dejean et al. 1997). Figs and their associated insects provide suitable biological models to test recent hypotheses on the impact of third parties such as ants on the evolutionary dynamics of mutualisms.

Acknowledgements – This research was supported by CNRS (PICS No. 935) to M. Hossaert-McKey and by a CEFIPRA grant (No. 2609) to R. M. Borges and M. Hossaert-McKey. We wish to thank the staff in the Biology Dept at the Univ. of Brunei Darussalam and at the Centre for Ecological Sciences, Indian Inst. of Science, Bangalore. We also thank the Director of the Brunei Museum and the Forestry Dept for allowing us to export specimens. We also thank Samhan Nyawa (Brunei) and Pierre Pagés (France) for help in the field, Jean-Yves Rasplus for identifying agaonid wasps, and Doyle McKey, John Addicott,

Finn Kjellberg and Marcel Lambrechts for their helpful comments on the manuscript.

References

- Anstett, M.-C., Hossaert-McKey, M. and Kjellberg, F. 1997. Figs and fig pollinators: evolutionary conflicts in a coevolved mutualism. – *Trends Ecol. Evol.* 12: 94–99.
- Bao, T. and Addicott, J. F. 1998. Cheating in mutualism: defection of *Yucca baccata* against its yucca moths. – *Ecol. Lett.* 1: 155–159.
- Bronstein, J. L. 1988. Predators of fig wasps. – *Biotropica* 20: 215–219.
- Bronstein, J. L. 1991. The non-pollinating wasp fauna of *Ficus pertusa*: exploitation of a mutualism? – *Oikos* 61: 175–186.
- Bronstein, J. L. 1994. Our current understanding of mutualism. – *Q. Rev. Biol.* 69: 31–51.
- Bronstein, J. L. 2001. The exploitation of mutualisms. – *Ecol. Lett.* 4: 277–287.
- Bronstein, J. L. 2003. The scope for exploitation within mutualistic interactions. – In: Hammerstein, P. (ed.), Genetic and cultural evolution of cooperation. MIT Press, pp. 185–202.
- Bronstein, J. L. and Ziv, Y. 1997. Costs of two non mutualistic species in a yucca/yucca moth mutualism. – *Oecologia* 112: 379–395.
- Compton, S. G. and Robertson, H. G. 1988. Complex interactions between mutualisms: ants tending homopterans protect fig seeds and pollinators. – *Ecology* 69: 1302–1305.
- Compton, S. G. and Robertson, H. G. 1991. Effects of ant-homopteran systems on fig–fig wasp interactions. – In: Huxley, C. R. and Cutler, D. F. (eds), Ant–plant interactions. Oxford Univ. Press, pp. 120–130.
- Compton, S. G. and Hawkins, B. A. 1992. Determinants of species richness in southern African fig wasp assemblages. – *Oecologia* 91: 68–74.
- Cook, J. and Rasplus, J.-Y. 2003. Mutualists with attitude: coevolving fig wasps and figs. – *Trends Ecol. Evol.* 18: 241–248.
- Curio, E. 1976. The ethology of predation. – Springer.
- Cushman, J. H. and Whitham, T. G. 1989. Conditional mutualism in a membracid-ant association: temporal, age-specific, and density-dependent effects. – *Ecology* 70: 1040–1047.
- Cushman, J. H., Compton, S. G., Zachariades, C. et al. 1998. Geographic and taxonomic distribution of a positive interaction: ant-tended homopterans indirectly benefit figs across southern Africa. – *Oecologia* 116: 373–380.
- Dawkins, R. and Krebs, J. R. 1979. Arms races between and within species. – *Proc. R. Soc. B* 205: 489–511.
- Dejean, A. 1990. Prey capture strategy of the African weaver ant. – In: Vander Meer, R. K., Jaffe, K. and Cedeno, A. (eds), Applied myrmecology, a world perspective. Westview Press, Boulder, pp. 472–481.
- Dejean, A., Bourgoïn, T. and Gibernau, M. 1997. Ant species that protect figs against other ants: result of territoriality induced by a mutualistic homopteran. – *Ecoscience* 4: 446–453.
- Del-Claro, K. and Oliveira, P. 2000. Conditional outcomes in a neotropical treehopper–ant association: temporal and species-specific variation in ant protection and homopteran fecundity. – *Oecologia* 124: 156–165.
- Gaume, L. and McKey, D. 1999. An ant–plant mutualism and its host-specific parasite: activity rhythm, young leaf patrolling, and effects on herbivores of two specialist plant–ants inhabiting the same myrmecophyte. – *Oikos* 84: 130–144.
- Gaume, L. and McKey, D. 2002. How identity of the homopteran trophobiont affects sex allocation in a symbiotic plant–ant: the proximate role of food. – *Behav. Ecol. Sociobiol.* 51: 197–205.

- Gaume, L., McKey, D. and Terrin, S. 1998. Ant-plant-homopteran mutualism: how the third partner affects the interaction between a plant-specialist ant and its myrmecopyte host. – *Proc. R. Soc. B* 265: 569–575.
- Harrison, R. 1996. The ecology of the fig-fig wasp mutualism in a lowland tropical forest in Sarawak, Malaysia. PhD thesis, Kyoto Univ., Kyoto, Japan.
- Heil, M. and McKey, D. 2003. Protective ant-plant interactions as model systems in ecological and evolutionary research. – *Annu. Rev. Ecol. Evol. Syst.* 34: 425–453.
- Heithaus, E. R., Culver, D. C. and Beattie, A. J. 1980. Models of some ant-plant mutualisms. – *Am. Nat.* 116: 347–361.
- Herre, E. A., Knowlton, N., Mueller, U. G. et al. 1999. The evolution of mutualisms: exploring the paths between conflict and cooperation. – *Trends Ecol. Evol.* 14: 49–53.
- Hölldobler, B. 1983. Territorial behaviour of the green tree ant (*Oecophylla smaragdina*). – *Biotropica* 15: 241–250.
- Hölldobler, B. and Wilson, E. O. 1990. The ants. – Harvard Univ. Press.
- Jordano, P. 1983. Fig-seed predation and dispersal by birds. – *Biotropica* 15: 38–41.
- Joseph, K. J. 1957. Le parasitisme de *Philotrypesis caricae* (L.) et l'influence de la vie parasitaire sur le parasite. – *C. R. Acad. Sc. Paris* 244: 1269–1272.
- Jousselin, E., Rasplus, J. Y. and Kjellberg, F. 2003. Convergence and coevolution in a mutualism: evidence from a molecular phylogeny of *Ficus*. – *Evolution* 57: 1255–1269.
- Kerdelhué, C. and Rasplus, J. Y. 1996. Non-pollinating Afro-tropical fig wasps affect the fig-pollinator mutualism in *Ficus* within the subgenus *Sycomorus*. – *Oikos* 75: 3–14.
- Kerdelhué, C., Rossi, J. P. and Rasplus, J. Y. 2000. Comparative community ecology studies on old world figs and fig wasps. – *Ecology* 81: 2832–2849.
- Kjellberg, F., Jousselin, E., Hossaert-McKey, M. et al. 2005. Biology, ecology and evolution of fig-pollinating wasps (Chalcidoidea, Agaonidae). – In: Raman, A., Schaefer, W. and Whithers, T. M. (eds), *Biology, ecology and evolution of gall-inducing arthropods*. Science Publishers, Inc., Plymouth (UK), pp. 539–572.
- Law, R., Bronstein, J. L. and Ferriere, R. G. 2001. On mutualists and exploiters: plant-insect coevolution in pollinating seed-parasite systems. – *J. Theor. Biol.* 212: 373–389.
- Maschwitz, U., Fiala, B., Saw, L. G. et al. 1994. *Ficus obscura* var. *borneensis* (Moraceae), a new non-specific ant-plant from Malesia. – *Malay. Nat. J.* 47: 409–416.
- Morales, M. A. 2000. Mechanisms and density dependence of benefit in an ant-membracid mutualism. – *Ecology* 81: 482–489.
- Morris, W. F., Bronstein, J. L. and Wilson, W. G. 2003. Three-way coexistence in obligate mutualist-exploiter interactions: the potential role of competition. – *Am. Nat.* 161: 860–875.
- Richard, F. J., Fabre, A. and Dejean, A. 2001. Predatory behavior in dominant arboreal ant species: the case of *Crematogaster* sp. (Hymenoptera: Formicidae). – *J. Insect Behav.* 14: 271–282.
- SAS 1999. SAS Institute Inc.
- Schatz, B. and Hossaert-McKey, M. 2003. Interactions of the ant *Crematogaster scutellaris* (Formicidae; Myrmicinae) with the fig-fig wasp mutualism. – *Ecol. Entomol.* 28: 359–368.
- Schatz, B., Lachaud, J. P. and Beugnon, G. 1997. Graded recruitment and hunting strategies linked to prey in the neotropical ponerine ant, *Ectatomma ruidum* Roger. – *Behav. Ecol. Sociobiol.* 40: 337–349.
- Shanahan, M. J. 2000. *Ficus* seed dispersal guilds: ecology, evolution and conservation implications. Thesis, Univ. of Leeds, UK.
- Thomas, D. W. 1988. The influence of aggressive ants on fruit removal in the tropical tree, *Ficus capensis* (Moraceae). – *Biotropica* 20: 49–53.
- Thompson, J. N. 1982. Interaction and coevolution. – John Wiley and Sons.
- Thompson, J. N. 1988. Variation in interspecific interactions. – *Annu. Rev. Ecol. Syst.* 19: 65–87.
- Wcislo, W.T. and Schatz, B. 2003. Predator recognition and evasive behavior by sweat bees, *Lasioglossum unbripenne* (Hymenoptera: Halictidae), in response to predation by ants, *Ectatomma ruidum* (Hymenoptera: Formicidae). – *Behav. Ecol. Sociobiol.* 53: 182–189.
- West, S. A. and Herre, E. H. 1994. The ecology of the New World fig-parasitizing wasps *Idarnes* and implications for the evolution of the fig-pollinator mutualism. – *Proc. R. Soc. B* 258: 67–72.
- West, S. A., Herre, E. H., Windsor, D. M. et al. 1996. The ecology and evolution of the New World non-pollinating wasp communities. – *J. Biogeogr.* 23: 447–458.
- Weiblen, G. D. 2002. How to be a fig wasp. – *Annu. Rev. Entomol.* 47: 299–330.
- Yu, D. W. 2001. Parasites of mutualisms. – *Biol. J. Linn. Soc.* 72: 529–546.
- Zachariades, C. 1994. Complex interactions involving the Cape fig, *Ficus sur* Forsskål, and its associated insects. Thesis, Rhodes Univ., South Africa.

Subject Editor: Jane Memmott