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COMPLEX INTERACTIONS BETWEEN MUTUALISMS: ANTS TENDING HOMOPTERANS PROTECT FIG SEEDS AND POLLINATORS[1]

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Ants are commonly attracted onto plants bearing honeydew-producing insects, particularly homopterans. The presence of ants often increases the survival of the homopterans and consequently can increase their deleterious effects on the host plant (Way 1963, Banks and Macauley 1967). However, ants tending homopterans can also exclude other herbivores. If this protection outweighs the damage caused by the honeydewproducer, then an indirect mutualism is established, with all three parties benefitting (Carroll and Janzen 1973).

Evidence that ants tending homopterans can provide benefits for host plants is limited. Room (1972) demonstrated increased shoot growth by the mistletoe *Tapinanthus* when homopteran-tended ants were present. Nickerson et al. (1977) found that on soybean, ant predation of lepidopteran eggs was sometimes significantly greater on plants inhabited by a membracid. Ants tending aphids on trees can also reduce defoliation (Laine and Niemela 1980, Skinner and Whittaker 1981). In a study of ants tending a membracid on *Solidago,* Messina (1981) produced evidence that the plants increased their seed output in the presence of ants and concluded that the benefits of membracid presence did, on occasion, outweigh the disadvantages.

Here we describe exclusion experiments that demonstrate how a mutualism between ants and homopterans can benefit another mutualism, that between fig trees (*Ficus* species, Moraceae) and their insect pollinators. Fig trees are entirely dependent on fig wasps of the family Agaonidae for pollination, while the larvae of agaonids develop only in the seeds of the *Ficus* they pollinate (Wiebes 1979). Figs also support a specialized fauna of parasitoids and seed predators, many of which oviposit into the fig from the outside. We tested the hypothesis that ants visiting branches with figs to tend homopterans would hinder oviposition by wasps on the outside of the figs and reduce both seed predation and parasitism of the pollinator.

The Species Studied

The Cape fig tree, *Ficus sur* Forsk., is pollinated by *Ceratosolen capensis* Grandi (Hymenoptera, Agaonidae). Female wasps enter the ostiole of the fig, pollinate the female flowers, and oviposit in some of the ovules. While figs are being pollinated, females of *Sycophaga cyclostigma* Waterst. (Torymidae) may also enter the figs. These wasps are strictly seed predators, with adults that do not pollinate and larvae that develop inside galled ovules. Larvae of the closely related sycophagine wasp *Idarnes* sp. also gall the ovules of *F. sur,* but they develop from eggs inserted into ovules from the outside of the fig. A fourth fig wasp, *Apocrypta guineensis* Grandi, is parasitic on larvae of the other species. Like *Idarnes* it is equipped with a long ovipositor and oviposits through the wall of the fig. Exceptionally (on three occasions) two adult *A. guineensis* emerged from a single seed.

Hilda patruelis Stal. (Homoptera, Tettigometridae) produces honeydew and is often abundant on the fig-producing branches of *F. sur,* where ants are almost invariably found tending both nymphs and adults. *Pheidole megacephala* Forel. and *Polyrachis schistacea* (Gerstaecker) were the major ant species at our sites. Ant presence may reduce the incidence of egg parasitism by the encyrtid *Psyllechthrus oophagus* Ghesquiere (Weaving 1980).

Methods

Exclusion experiments were carried out on two *F. sur* trees growing at Howison's Poort near Grahamstown (33°22′ S, 26°29′ E). The trees were growing ≈50 m apart and had initiated large fruit crops at about the same time in June 1985. Tree 1 was ≈3 m high and Tree 2 ≈7 m high. Fig-producing branches were treated in pairs, the branches of each pair being within 50 cm of one another. One of the branches was banded at the base with Formex to exclude ants, while the other was the control. Bands needed to be renewed at about fortnightly intervals. Seven pairs of branches were chosen on Tree 1, which had many ants present, and three pairs on Tree 2, which had very few ants.

Ants, *H. patruelis,* and fig wasps were counted on each of the marked branches eight times between June and August, after which the figs had matured and were ready to harvest. Insect numbers were subsequently divided by the initial number of figs, to adjust for differences in numbers of figs between branches. We harvested figs over a period of 4 wk and excluded any from which wasps had already emerged. Each fig was placed in a sealed bottle. After the emergence of the wasps was completed, figs were placed in a freezer for later counting. As the males of sycophagine species cannot be distinguished at present (Wiebes 1968), we assigned these males to the same species as the females present in each fig. On the rare occasions (10 figs) when females of both sycophagine species were present, we assigned the males in the same proportions.

Results

Ant densities were much greater on Tree 1 than on Tree 2 (Table 1; unbanded branches only). *Pheidole megacephala* was the only ant species recorded on Tree 1, while on Tree 2 *Polyrhachis schistacea* was the most common species, with *Tetraponera* sp. and *Technomyrmex* sp. also present. Exclusion of ants from banded branches was found to be incomplete because "bridges" were sometimes formed as the growth of the figs brought them into contact with other branches.

H. patruelis densities followed a similar trend to those of ants (Table 1). Ant numbers on unbanded branches of Tree 1 were significantly correlated with numbers of *H. patruelis* ($r = 0.447$, $P < .001$, $n = 87$, observations where neither ants nor homopterans recorded were excluded), confirming that ants were attracted by the bugs. Significantly more females of the parasitoid *A. guineensis* were observed on the outside of figs on banded than on unbanded branches of Tree 1 (Table 1: paired t test, $t = 3.298$, $P < .002$, $n = 24$, paired zero values excluded). On Tree 2 (with low ant densities), there was no significant difference in *A. guineensis* numbers between the two treatments ($t = 1.262$, $P > .1$, $n = 10$).

As would be expected from the larger number of *A. guineensis* females observed on banded branches of Tree 1, the mean number of their progeny was ≈4.2 times as great as on unbanded branches, the difference being highly significant (Table 2). Seed predation by *Idarnes* sp. was also significantly greater on banded than on unbanded branches. Because of the lower parasitism of pollinators by *A. guineensis* on unbanded branches of Tree 1, over three times as many *C. capensis* emerged from these figs as from those of banded branches. Once again the difference was highly significant (Table 2). *S. cyclostigma* females enter the figs to oviposit and so escape most of the ant interference. Their numbers did not differ significantly between two treatments (Table 2).

On Tree 2, with its much lower ant densities, there were no significant differences at all between treatments (Table 2). Parasitism by *A. guineensis* was uniformly high and pollinator emergence correspondingly very low in figs of both unbanded and banded branches. Parasitism by *A. guineensis* and seed predation by *Idarnes* sp. and *S. cyclostigma* were higher on both branch types on Tree 2 than on banded branches of Tree 1. As a result over four times more *C. capensis* emerged from figs on banded branches of Tree 1 than from either unbanded or banded figs on Tree 2. It is

TABLE 1. Comparison of ant, *Hilda patruelis*, and female *Apocrypta guineensis* densities on unbanded (ant-accessible) and banded (ant-excluded) fig-producing branches of two *Ficus sur* trees.

	Tree 1		
	Unbanded	Banded	Total
No. branches	7	7	14
Initial no. figs per branch (mean ± SE)	12.286 ± 0.622	15.143 ± 0.671	13.714 ± 0.454
Density per branch (mean ± SE)*			
Ants	7.920 ± 0.792	0.369 ± 0.162	4.145 ± 0.539
H. patruelis	0.145 ± 0.031	0.030 ± 0.010	0.088 ± 0.017
A. guineensis females	0.056 ± 0.025	0.136 ± 0.037	0.096 ± 0.023

* Mean densities per branch were calculated by dividing each number counted by the initial number of figs on the branch. Insect counts were made on eight occasions between June and August 1985. Counts of *Ceratosolen capensis*, *Idarnes* sp., and *Sycophaga cylcostigma* are not presented in this table because they were rarely seen.

possible that the high density of ants on Tree 1 deterred *A. guineensis* and the seed predators from frequenting that tree even though there were some ant-free branches.

The overall number of wasps emerging per fig on unbanded branches of Tree 1 was 1.5 times as great as from figs on banded branches and from all the branches on Tree 2 (Table 2). This suggests that the detrimental effects of *A. guineensis* are not fully reflected by counts of the numbers of the parasite's progeny. Host feeding was not observed, but probing by this parasitoid may have caused the additional mortalities.

The results in Tables 1 and 2 are combined in Table 3 to show the degree of correlation between counts of *A. guineensis*, ants, and *H. patruelis* outside the figs and numbers of *C. capensis* and *A. guineensis* progeny recorded subsequently inside the figs. These results confirm the link between the presence of *H. patruelis*, the presence of ants, and the reduction in numbers of the parasitoid *A. guineensis*. For instance, ants and *H. patruelis* counted outside the figs are directly correlated with numbers of pollinators produced inside the figs.

Likewise, both ant and *H. patruelis* numbers are negatively correlated with the number of *A. guineensis* produced inside the figs.

Discussion

Ant presence can have a dramatic effect on the degree of parasitism of fig wasp pollinators by *A. guineensis* and on the extent of seed predation by *Idarnes* sp. Ants were observed to reduce parasitism and seed predation by disturbing or even capturing female wasps on the surface of the fig. Even though the pollinator *C. capensis* enters the fig to oviposit, it is not immune to predation by ants because it is vulnerable when locating the ostiole of the fig. However, the large number of *C. capensis* emerging from ant-protected figs (Table 2) suggests that this was not an important factor for the pollinator population.

We believe that the net effect of *H. patruelis* and its associated ants is generally beneficial for fig trees colonized by the bug (Fig. 1). Observations of *F. sur* in Zululand and the Transvaal suggest that *H. patruelis* and its attendant ants are found on this tree throughout

TABLE 2. Numbers of wasps that emerged from figs on unbanded (ant accessible) and banded (ant excluded) branches of two *F. sur* trees. Data are means ± SE.

	Tree 1			Tree 2		
	Unbanded ($n = 50$)	Banded ($n = 49$)	Z†	Unbanded ($n = 16$)	Banded ($n = 15$)	Z†
No. *C. capensis* (pollinator)	319.7 ± 23.04	104.2 ± 11.62	6.66***	19.3 ± 4.90	22.6 ± 3.85	0.85NS
No. *A. guineensis* (parasitoid)	31.8 ± 5.78	134.4 ± 12.68	6.67***	187.8 ± 23.21	211.7 ± 22.39	0.71NS
No. *Idarnes* sp. (seed predator)	0.02 ± 0.02	7.2 ± 2.23	3.90***	12.7 ± 6.24	11.3 ± 4.87	1.02NS
No. *S. cyclostigma* (seed predator)	29.9 ± 7.96	11.9 ± 3.94	0.55NS	41.1 ± 7.52	61.9 ± 8.30	1.53NS
Total no. wasps	381.4 ± 20.52	257.7 ± 17.28	4.23***	260.9 ± 30.43	307.4 ± 28.90	1.42NS

*** $P < .001$, NS = nonsignificant.
† Mann-Whiteny U test, Z = normal deviate of U.

TABLE 1. Continued.

	Tree 2	
Unbanded	Banded	Total
3	3	6
10.334 ± 0.452	9.667 ± 0.284	10.000 ± 0.248
0.016 ± 0.009	0.000 ± 0.000	0.008 ± 0.005
0.000 ± 0.000	0.004 ± 0.004	0.002 ± 0.002
0.267 ± 0.119	0.441 ± 0.195	0.354 ± 0.114

southern Africa, and that parasitism of the pollinator is markedly reduced whenever ant densities are high.

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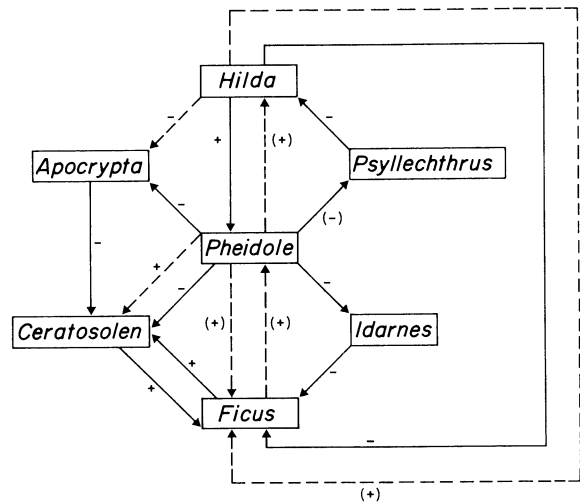

FIG. 1. Positive and negative interactions between some of the species described in this study. These species are *Ficus sur* (fig tree), *Hilda patruelis* (homopteran), *Psyllechthrus oophagus* (hymenopteran egg parasitoid), *Pheidole megacephala* (ant), *Ceratosolen capensis* (fig tree pollinator), *Apocrypta guineensis* (parasitoid) and *Idarnes* sp. (seed predator). —— direct effects; – – – indirect, net effects. Note that indirect effects via other species may have an opposite sign to the direct interaction. Signs in parentheses indicate relationships that have not yet been confirmed.

TABLE 3. Correlations (Pearson's r) between mean numbers of ants, *H. patruelis,* and *A. guineensis* per fig counted on fig-producing branches, and the mean number and percentage of *Ceratosolen capensis* (pollinator wasp) and *A. guineensis* progeny that emerged from the figs on those branches ($n = 20$).

	No. counted outside figs		
Emerging from inside figs	Ants	*H. patruelis* (homopteran)	*A. guineensis* females (parasitoid)
No. *Ceratosolen*	.713***	.554*	−.522*
No. *A. guineensis*	−.728***	−.672**	.630**

* $P < .05$, ** $P < .01$, *** $P < .001$.

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