

Direct and indirect interactions between ants (*Pheidole megacephala*), scales (*Coccus viridis*) and plants (*Pluchea indica*)

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Summary. This study investigated direct and indirect interactions between the ant, *Pheidole megacephala* (Fabr.), the green scale, *Coccus viridis* (Green), and the scale's host plant, *Pluchea indica* (L.). To examine the influence of ants on scales and host plants, scale population densities, scale mortality rates, and plant performance were studied on control host plants with ants and host plants from which ants had been removed. Plants with ants present had significantly greater scale population densities and scale reproductive rates than did plants without ants. Scale mortality from both parasitism and other causes was increased on plants without ants relative to plants with ants. Predator introduction experiments showed that *P. megacephala* removes predatory coccinellid larvae, even when they are covered with a protective coating. Host plants from which ants had been removed had significantly higher degrees of honeydew accumulation, which resulted in greater colonization by sooty mold and greater rates of leaf death and abscission. Ants also removed herbivorous lepidopteran larvae from plants. Results are discussed in terms of the potential of *P. megacephala* to exert direct and indirect positive effects on scale populations and an indirect positive effect on *Pluchea indica*.

Key words: Ant-Homopteran interactions – Honeydew accumulation – Leaf abscission – Mutualism – Scale insects

functioning as “nannies” and thus increasing reproduction (Bristow 1983), and transportation to more favorable feeding sites (Nixon 1951; Way 1963). Ants benefit from the sugar-rich food source produced by the homopterans (Way 1963; Carroll and Janzen 1973), and ant colonies that feed on honeydew in addition to other foods have higher population sizes (Way 1954).

Decreased homopteran densities in the absence of ants are well-documented (Bess 1958; Jutsum et al. 1981; Bristow 1984; Grant and Moran 1986), but very few studies have tested more than one possible mechanism (but see Bristow 1984). Moreover, the indirect effect of ants tending homopterans on plant fitness has received little attention. Those studies that have examined how ants influence plant fitness have focused on the role of ants in removing herbivores and predators (Messina 1981; Buckley 1983; Fritz 1983). No studies have specifically examined the effects of ants removing honeydew on the plant. This is surprising, since honeydew build-up encourages colonization by sooty mold, which decreases photosynthetic rates (Williams and Kosztarab 1972; Carter 1973).

The goals of this study were to examine the mechanisms underlying the effects of ants on homopteran densities and mortality rates, and the subsequent effects of ants on the host plant. The system studied consisted of the green scale, *Coccus viridis* (Green), tended by *Pheidole megacephala* (Fabr.), on the host plant *Pluchea indica* (L.), all of which were recently introduced to Hawaii. I was particularly interested in studying a non-coevolved system. The following specific questions were investigated: (1) Does the presence of tending ants result in an increase in the densities of scales?, (2) If so, are the increased densities in the presence of ants caused by differences in scale reproductive rates, parasitism rates, or rates of mortality from other sources?, (3) Do ants remove predators from the plant?, and (4) What is the effect of ants on the host plant, in terms of honeydew build-up, colonization by sooty mold, plant performance, and herbivore removal?

Interactions between homopterous insects and ants that tend them have been studied by ecologists for nearly a century. Positive benefits of ants on homopterans include protection from predation (Way 1963; Jutsum et al. 1981; Bristow 1984), parasitism (Bartlett 1961; Buckley 1987), provision of shelter (Nixon 1951), sanitation in terms of honeydew removal (Way 1963; Buckley 1987),

The study system

The herbivore studied was the green scale, *Coccus viridis* (Homoptera: Coccoidea: Coccidae). This scale insect is polyphagous and is a serious pest of coffee, guava, citrus, and other crops. It was first recorded in Hawaii in 1905 and is thought to be either of Brazilian (Zimmerman 1948) or Ethiopian origin (Gill et al. 1977). The host plant was Indian fleabane, *Pluchea indica* (Compositae). This plant species is native to Southeast Asia and typically occurs in salt marshes and coral fills in coastal areas. Scales were tended by the ant, *Pheidole megacephala* (Hymenoptera: Formicidae: Myrmecinae), originally native to Africa with a current tropicopolitan distribution. It is the dominant ground-nesting species in most of the lowland agricultural areas of Hawaii and is a major pest of pineapple because it tends the pineapple mealybug which spreads mealybug wilt (Beardsley et al. 1982; Rohrbach et al. 1988).

Various species of fungi that grow on honeydew, sooty molds, are also important in this system. Sooty molds colonize leaves with large amounts of honeydew and eventually cause mortality of scales (Nixon 1951), simultaneously decreasing plant photosynthetic rates (Carter 1973).

The study was carried out on Coconut Island, property of University of Hawaii Marine Laboratory, 100 m off the coast of Kaneohe, on the east side of the island of Oahu, Hawaii. At this site, *Pluchea indica* was growing along coral rubble dredged up for a breakwater for the University of Hawaii Marine Laboratory. All plants were growing within 5 m of the ocean, in an open area with scattered ironwood trees (*Casuarina equisetifolia* L.).

Effects of ants on scales

Methods. To examine the effects of ants on scale population densities, rates of scale parasitism, and plant performance, an ant removal experiment was conducted during April and May 1988. Six pairs of plants were located which were similar in size, and one plant of each pair received the ant-removal treatment and the other plant served as a control (ants present). Plants varied in height from 33 to 75 cm. Plants receiving the ant-removal treatment had all ants physically removed, followed by an application of tanglefoot to the base of the plant to ensure that no ants re-colonized the plant. Ants were allowed to remain on control plants.

All plants were sampled on the day of the ant-removal manipulation, and on 8, 15, 29, and 41 days after removal. Manipulations were carried out on two pairs of plants on each of three dates: April 6, 12, and 15, 1988. Sampling involved counting the number of scales on the second, fourth, sixth, eighth, and tenth leaf of each branch of each plant. Scale numbers were recorded for 2 size classes of scales (small = < 1 mm; large = > 1 mm). In addition two other categories of scales were recorded: parasitized (identified by characteristic color/shape and/or parasite emergence hole) and dead from other mortality sources (identified by brown coloration; Frederick 1943). The actual cause of death of the scales was not determined, except for those that contained parasites.

Data were analyzed by repeated-measures one-way ANOVA, because densities on different sampling dates for the same plants were not independent. Since densities on individual leaves within plants were not independent, ANOVAs were carried out on the average density per leaf for each plant. ANOVAs tested for effects of treat-

ment (control vs. ant-removal), sampling date, and an interaction between treatment and sampling date. Numbers of parasitized scales and parasitism rates were analyzed in a similar manner.

Repeated-measures ANOVAs were also used to compare relative population growth rates for each pair of sequential sampling dates, calculated as the difference in average density between sampling dates divided by the average density on the first date of that sampling period. Because of some leaf abscission (and thus inaccurate leaf identification), these relative changes in scale densities were calculated per plant rather than per leaf.

Results. Before the ant-removal manipulations were done, scale densities did not differ between control and ant-removal plants (Fig. 1). After removal, scale densities on plants with ants more than doubled, whereas densities on plants without ants remained constant throughout the period of the study. Thus, the removal of ants prevented scale populations from increasing, as they did when tended by ants. Although the number of scales per leaf did not significantly differ between plants with and without ants during this post-removal phase of the study ($F = 3.02$, $df = (1,10)$, $P = 0.11$), there was a significant interaction between sampling date and treatment ($F = 3.38$, $df = (3,30)$, $P = 0.031$), indicating an increasing difference in scale densities between plants with ants present and plants with ants removed as the experiment progressed.

Relative population growth rates were significantly greater on plants with ants than on plants without ants (Fig. 2; $F = 6.23$, $df = (1,10)$, $P = 0.032$). In fact, by the last time period (29–41 days after removal), scale densities decreased by 30% on plants without ants, whereas numbers increased by 10% on plants with ants (see Fig. 2). Differences between relative population growth rates on plants with and without ants were consistent for all four sampling periods (interaction effect; $F = 0.50$, $df = (3,30)$, $P = 0.50$).

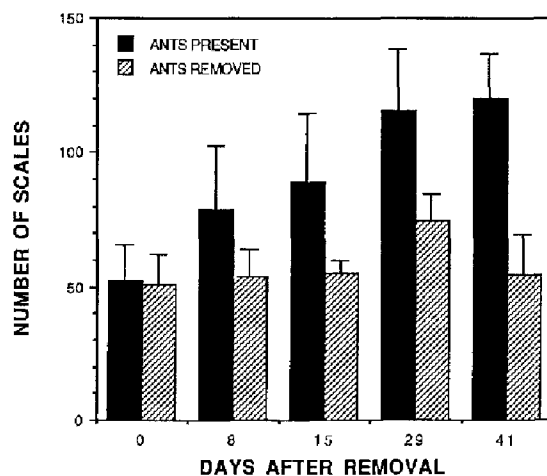


Fig. 1. Number of scales per leaf on plants with ants present and plants from which ants had been removed. Means and standard errors for per-plant values ($N = 6$ for each treatment) are presented for the day of removal and 4 post-removal dates

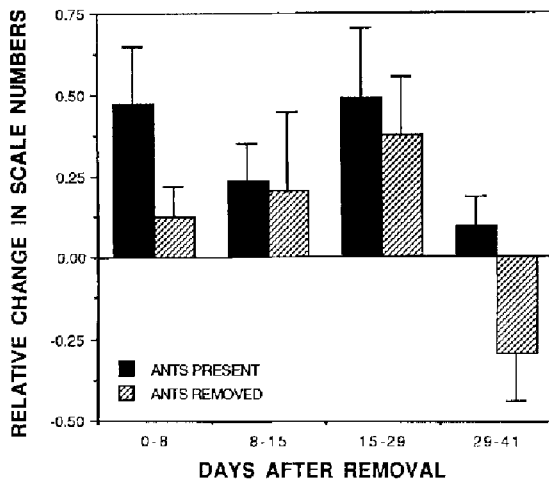


Fig. 2. Relative population growth rates of scales, calculated as the relative change in the number of scales per leaf between sequential sampling dates (see text). Means and standard errors are presented for per-plant values for plants with and without ants

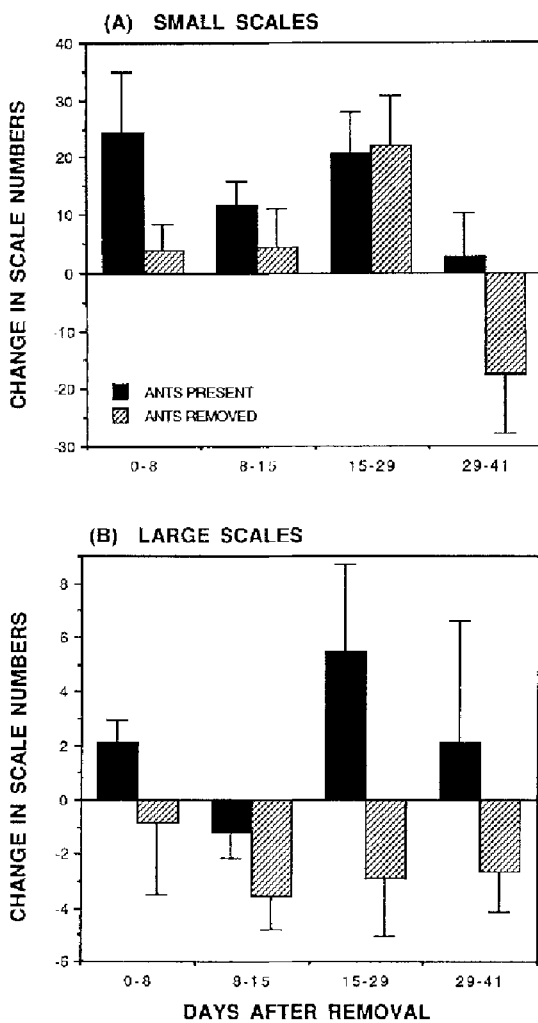


Fig. 3. Change in the number of scales per leaf between sequential sampling dates for two size categories of scales: (A) small scales, and (B) large scales. Means and standard errors are presented for per-plant values for plants with and without ants

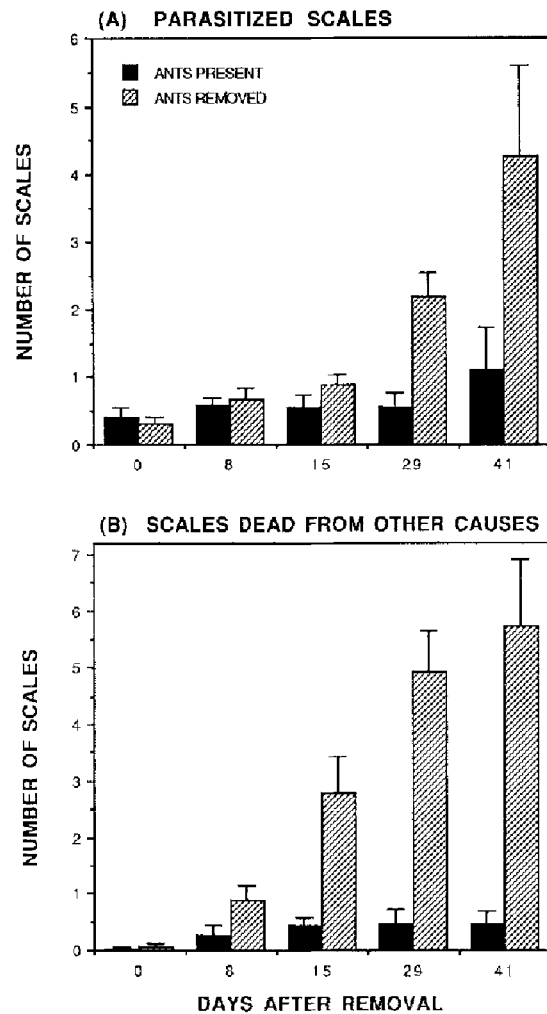


Fig. 4. Number of scales per leaf on plants with and without ants that were: (A) parasitized and (B) dead from other causes. Means and standard errors are presented for per-plant values

Because scales are usually stationary except during the first instar "crawler" stage, these differences in population growth rates do not result from scale movement. Instead, changes in scale numbers most likely result from differences in local reproduction and/or differences in mortality rates. To examine the importance of reproduction in influencing scale abundance patterns, absolute changes in the density of small scales between sampling periods were compared. Small scales showed greater increases in numbers on plants with ants than on plants without ants (Fig. 3A, $F = 8.93$, $df = (1,10)$, $P = 0.014$), indicating greater reproductive rates on plants with ants present. Large-sized scales also exhibited larger increases in numbers between sampling periods on plants with ants than on plants without ants (Fig. 3B, $F = 5.04$, $df = (1,10)$, $P = 0.049$), indicating greater survival and/or growth on plants with ants present.

Densities of parasitized scales were similar on control and ant-removal plants before removal (Fig. 4A), but densities of parasitized scales were significantly greater on plants without ants than on plants with ants during the post-removal phase of the study ($F = 6.69$, $df = (1,10)$, $P = 0.027$). Sampling period and treatment interacted to

influence parasitized scale density ($F=8.12$, $df=(3,30)$, $P<0.001$), indicating an increasing difference between plants with and without ants as the study proceeded. Densities of scales dead from other causes also were significantly greater on plants with ants removed than on plants with ants present (Fig. 4B; $F=43.11$, $df=1,10$, $P<0.001$), and this difference also increased throughout the study ($F=7.78$, $df=3,30$, $P=0.001$).

Effects of ants on scale predators

Methods. To determine how ants respond to predators of scales, I released predators onto plants and observed subsequent ant behavior. Experiments were performed on a variety of plants (some of which were used in the ant removal experiments). A total of 19 ladybird beetle larvae (Coccinellidae) were introduced. The majority ($N=16$) were covered with white waxy material and were either *Cryptolaemus montrouzieri* Mulsant or *Azya orbiger* Mulsant; these larvae are often mistaken for mealybugs. The two species of larvae were combined for purposes of analysis because larvae were not identified to species. Three individuals were of a different species and were covered with black spines. In order to determine whether predator size affects the behavior of ants, three size classes of ladybird larvae were introduced: small (<8 mm; $N=5$), medium (8–12 mm; $N=8$), and large (>12 mm; $N=6$). Introductions were carried out on three days: 27 May ($N=6$), 31 May ($N=10$), and 1 June ($N=3$).

The procedure involved introducing a larva onto a plant and directly observing ant behavior. The ants and larvae were watched continually for the first 10 min, then behaviors were recorded approximately every 3 min until either the larva was removed from the plant or 3 h had passed. Other studies have shown that some ant species attack predators and remove them from the plant (Kirkpatrick 1927; Bartlett 1961; Jutsum et al. 1981; Bristow 1984). Preliminary observations indicated that the minor workers of *P. megacephala* kill the larval coccinellids and remove the waxy covering before removing them from the plant. Thus, data recorded included: (1) the time at which the ants discovered the larva, (2) the time it took for the ants to remove the waxy coating or spines from the larva, (3) the number of ants involved in removing the covering/spines from the larva, (4) the time at which the ants began to carry the larva off the plant, (5) the number of ants involved in carrying the larva, and (6) the time the larva was removed from the plant. Comparisons between these parameters were made with one-way ANOVAs testing for effects of predator size.

Results. Of the 19 predators that were introduced onto plants, 17 were removed within the 3-h observation period; the other 2 predators were not present the following day. Ants spent an average of 40 min removing the predators. There were no differences between the two types of predators (waxy coating vs. spines) in any of the measures of ant discovery or removal ($P>0.05$ for all). Thus, both groups of predators were combined for purposes of further analysis.

Table 1. Results from predator introduction experiments. Means and standard errors of times (minutes) and numbers of ants are presented separately for small ($N=5$), medium ($N=7$), and large ($N=5$) larvae

Behavior of ants in response to predators	Size class of predator larvae		
	Small	Medium	Large
Time to discovery	3.5 ± 1.9	1.2 ± 0.4	9.2 ± 5.7
Time to remove outer covering	12.2 ± 5.5	22.7 ± 5.0	57.0 ± 7.6
Time to carry off plant	3.0 ± 0.8	8.0 ± 0.6	6.0 ± 1.6
Total time to remove larva from plant	16.6 ± 5.0	34.7 ± 9.8	72.0 ± 9.2
No. ants removing covering	7.0 ± 2.2	14.7 ± 2.0	21.0 ± 5.1
No. ants carrying off plant	3.2 ± 0.7	4.5 ± 1.5	10.2 ± 1.8

Predator size had a significant influence on the total time it took ants to remove predators (Table 1; $F=9.11$, $df=(2,14)$, $P=0.003$), with greater time for removal required for larger larvae. On average, it took ants over 4 times as long to remove large larvae compared with small larvae. This greater time to removal was a result of significantly greater time required to remove the outer covering of larger larvae (Table 1; $F=13.78$, $df=(2,12)$, $P=0.001$), not from a difference in the time to discovery ($F=1.84$, $df=(2,14)$, $P=0.20$) nor the time to carry the larva off the plant ($F=3.63$, $df=(2,10)$, $P=0.065$). In addition to the greater length of time spent removing the outer covering of larger larvae and removing them from the plant, there also were more ants involved in both of these processes (Table 1). For larger larvae, a greater number of ants participated in the process of removing the outer covering ($F=4.38$, $df=(2,14)$, $P=0.033$) as well as the carrying of the larva off the plant ($F=8.28$, $df=(2,8)$, $P=0.011$).

Effects of ants on plants

Methods. To assess effects of ants on degree of honeydew accumulation and fungal attack, all leaves were evaluated for amount of honeydew and degree of colonization by sooty mold on 15 and 41 days after removal. Both of these parameters were visually rated on a scale of 0–5, where 0 = none, 1 = 1–5% of leaf surface covered, 2 = 6–25% covered, 3 = 26–50% covered, 4 = 51–75% covered, and 5 = 76–100% covered. The median scores per plant for honeydew build-up and incidence of fungal attack were compared with Mann-Whitney U tests. The effect of ants on plant performance was assessed by comparing leaf death and abscission rates of plants with and without ants. Because it was not possible to measure fitness directly, leaf loss was measured because it is an important ecological variable. The percentages of leaves per plant that abscised were arcsin transformed and then compared with a Mann-Whitney U test.

Results. Plants without ants had significantly greater quantities of honeydew on leaves than did plants with ants for both sampling dates (Table 2; $T^*=21$, $df=6,6$, $P=0.001$; $T^*=15$, $df=5,5$, $P=0.004$, respectively).

Table 2. Percentage of leaves with various degrees of honeydew cover on plants with ants present and plants with ants removed on 15 and 41 days after removal. Sample sizes were: plants with ants (83, 47, respectively); plants without ants (95, 48, respectively)

% leaf area covered by honeydew	15 d after removal		41 d after removal	
	ants present	ants removed	ants present	ants removed
0%	94.0	10.5	97.9	14.6
1-5%	6.0	44.2	2.1	2.1
6-25%	0	41.0	0	20.8
26-50%	0	4.2	0	33.3
51-75%	0	0	0	2.1
76-100%	0	0	0	27.1

Table 3. Percentage of leaves with various degrees of sooty mold on plants with ants present and plants with ants removed on 15 and 41 days after removal. Sample sizes were: plants with ants (83, 51, respectively); plants without ants (95, 50, respectively)

% leaf area covered by sooty mold	15 d after removal		41 d after removal	
	ants present	ants removed	ants present	ants removed
0%	74.7	54.7	45.1	9.8
1-5%	22.9	28.4	39.2	27.4
6-25%	2.4	9.5	11.8	13.7
26-50%	0	7.4	3.9	25.5
51-75%	0	0	0	11.8
76-100%	0	0	0	11.8

Associated with this accumulation of honeydew was significantly greater colonization by sooty mold on plants from which ants had been removed (Table 3; $T^2 = 28$, $df = 6,6$, $P = 0.047$; $T^2 = 26$, $df = 6,6$, $P = 0.021$, on the two sampling dates respectively). The higher degrees of honeydew and sooty mold accumulation on plants without ants were a direct function of the removal of ants, since no plants had honeydew or sooty mold on their leaves prior to ant removal. Furthermore, a significantly higher percentage of leaves died and fell off of plants without ants ($47.5 \pm 7.2\%$) than for plants with ants ($31.3 \pm 4.2\%$; $T^2 = 28$, $P = 0.047$). Thus, plants without ants had higher amounts of honeydew and sooty mold on their leaf surfaces, as well as higher leaf abscission rates.

Effects of ants on lepidopteran herbivores

Methods. To determine whether ants indirectly benefited plants by removing other herbivores, nine herbivores were introduced onto plants on 3 June using methods similar to those described above for the predator introductions. All herbivores were last instar larvae of the diamondback moth, *Plutella xylostella* (L.) and were 6-8 mm in length. This species is not an herbivore of *Pluchea*, but was chosen as a representative herbivore because larvae were readily available from a lab culture at the University of Hawaii. Again, ant behavior was recorded for several hours. Student t-tests were used to compare ant responses to herbivores vs. predators.

Results. All nine lepidopteran larvae were removed from the plants onto which they were introduced. The time it took ants to discover the introduced larva ranged from 0.1-23 min, with total removal times varying from 6-30 min (Table 4). In comparisons of ant response to her-

Table 4. Results from lepidopteran larvae introduction experiments. Sample sizes were 9 for all categories except time to carry off plant and number of ants carrying ($N = 7$)

Behavior of ants in response to lepidopteran larvae	Mean \pm standard error
Time to discovery of larva (min.)	3.8 \pm 2.5
Time to carry larva off plant (min.)	4.9 \pm 0.8
Total time to remove larva from plant (min.)	12.0 \pm 2.5
No. ants attracted to larva	10.1 \pm 3.0
No. ants carrying larva off plant	7.1 \pm 0.8

bivores vs. predators, there was no difference in the time to discovery ($t = 0.14$, $df = 24$, $P = 0.89$), time spent carrying the larva off the plant ($t = 0.34$, $df = 18$, $P = 0.74$), the number of ants participating in the carrying process ($t = -0.67$, $df = 16$, $P = 0.51$), nor in the number of ants attracted to the introduced larva ($t = 1.1$, $df = 24$, $P = 0.27$). The total time required for removal, however, was significantly longer for predators than for herbivores ($t = 2.8$, $df = 24$, $P = 0.01$). This difference was a direct function of the large amount of time required to remove the waxy covering from predators.

Discussion

Effects of ants on scales

It appears from this study that the relationship between *Pheidole megacephala* and *Coccus viridis* is mutualistic. Ants positively affected scale population densities. The greater increase in numbers of small scales on plants with ants than on plants without ants strongly suggests that scales have higher reproductive rates in the presence of ants. Mortality rates of scales from both parasitism and

other sources were also significantly lower in the presence of ants.

The strong mutualistic effects found in this study are particularly interesting in this noncoevolved system. The ants, scales, and plants are each native to a different continent and have been together in Hawaii for less than a hundred years. Although this mutualism is not obligate for either *P. megacephala* or *C. viridis*, several pieces of additional evidence suggest that scales are rare unless tended by ants: (1) scale density was positively correlated with ant density in broad-scale surveys of *Pluchea indica*, and (2) coccinellid predators were present only on *P. indica* plants with untended scales (Bach, personal observation).

The results of this study documenting lower population sizes of homopterans on plants from which ants have been excluded agree with virtually all studies of ant-homopteran interactions (Bess 1958; Jutsum et al. 1981; Bristow 1984; Grant and Moran 1986). The differences in leaf abscission rates in this study suggest that the lower scale densities when ants were removed are actually underestimates of the magnitude of the effects of ants on scale populations. If analyses had been conducted on averages for all leaves (including abscised leaves), the measured decreases on plants without ants would have been even greater.

The mechanisms underlying the lack of increase in scale densities on plants without ants include decreased scale reproduction and increased mortality rates, but not scale movement. Very little, if any, scale movement occurred; scales did not even move off dead leaves before abscission (Bach, personal observation). The actual increase in mortality when ants were removed was most likely even greater than the 23-fold increase found in this study, since many species of ants remove dead scales from plants (Way 1963). Increased mortality rates in the absence of ants could be caused by: (1) increased honeydew build-up and resultant colonization by sooty mold, (2) higher parasitism rates, and/or (3) higher predation rates. This study is consistent with all three of these indirect effects of ants on scale mortality.

Although there is no strong evidence that honeydew removal alone affects scale mortality, sooty mold has been shown to interfere with crawler settling (Bess 1958) and affect scale mortality in many systems (Nixon 1951; Way 1954; Das 1959). Because sooty mold was so prevalent in this study (24% of leaves on ant-removal plants with greater than 50% of the leaf surface covered with sooty mold), it could have increased the rate of scale death.

The increase in parasitism rate in the absence of ants agrees with other studies showing that ants interfere with parasites (Nixon 1951; Way 1963; Bartlett 1961; Buckley 1987). Although predation was not directly measured, the rapid loss of potential predators to ants and the increased loss to "other causes" (see Fig. 4) suggest a relatively high predation rate on plants without ants. Other studies also report that ants attack *Azya* sp. (Jutsum et al. 1981) and *Cryptolaemus montrouzieri* (Kirkpatrick 1927; Bartlett 1961). However, this study is the first to document that *P. megacephala* removes the protective

covering from predatory larvae. Several studies have shown that ants do not attack predatory larvae that are camouflaged (Nixon 1951; Das 1959; Fisner et al. 1978). In the case of this system, the coccinellids were not camouflaged, since the green scale does not produce a white waxy coating. Reimer (personal communication) reports observing *P. megacephala* ignoring *Cryptolaemus* larvae when associated with mealybugs (in which case the larval coccinellids were camouflaged). Thus, results from this study showing that ants remove larval coccinellids with protective coatings appear to be unique. Because densities of coccinellids can be as high as 23 larvae per plant on host plants without ants (Bach, personal observation), it is likely that this predator removal by ants could have a significant impact on scale population densities.

Effects of ants on plants

This study documented a strong increase in the incidence of honeydew build-up and colonization by sooty mold on plants from which ants had been removed. The incidence of sooty mold on leaf surfaces has been shown to decrease photosynthetic rates in other systems (Williams and Kosztarab 1972; Carter 1973). In this system, leaves browned and died before abscising. It seems likely that the increased leaf abscission rates of plants without ants were caused by the increased incidence of sooty mold, rather than scale feeding alone (as in Cockfield and Potter 1986), since that would have caused greater leaf abscission on plants with ants and greater scale densities.

The higher abscission rates of plants without ants could potentially affect plant fitness. Assuming that sooty mold is the main cause of leaf abscission, then it seems likely that all leaves would have eventually fallen off the plants without ants. Although it is possible that losing leaves might actually stimulate growth, other studies suggest that defoliation negatively affects the fitness of perennials (Bentley et al. 1980; Marquis 1984). However, these results on honeydew and sooty mold accumulation may be slightly exaggerated because of the artificiality of the ant-removal manipulation; in natural situations, scales occurring without ants occur at lower population densities (Bach, personal observation), for which there would be less honeydew build-up.

P. megacephala also indirectly benefited the host plant by removing lepidopteran larvae from the plant. These results support those of Messina (1981) and Whittaker and Warrington (1985), who found that plants with ants had reduced herbivory and resultant higher plant performance, but are in contrast to those of Buckley (1983), who found that ants and treehoppers negatively affected fitness of a host plant with extrafloral nectaries. Although no other herbivores were observed during the period of this study, the presence of other herbivores on this host plant at other times of the year seems likely. In addition, on other host plants of *Coccus viridis* where herbivores other than homopterans have a significant impact on plant fitness, *P. megacephala* has the potential to indirectly benefit the host plant via herbivore removal.

In conclusion, this study documented that *P. megacephala* positively affected green scale populations in two ways: (1) directly by increasing scale reproductive rates, and (2) indirectly by decreasing scale mortality (by removing predators and decreasing parasitism rates). This study also suggests that ants increased scale survivorship by decreasing the incidence of honeydew and sooty mold. Ants also indirectly positively affected *P. indica* host plants by decreasing the degrees of both honeydew and sooty mold on their leaves, as well as lowering leaf abscission rates and eliminating other herbivores. Results from this study support those from other studies emphasizing the complicated dynamics involved in ant-scale-plant interactions and the need to study indirect as well as direct interactions.

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References

- Bartlett BR (1961) The influence of ants upon parasites, predators, and scale insects. *Ann Entomol Soc Am* 54:543-551
- Beardsley JW, Su TH, McEwen FL, Gerling D (1982) Field investigations on the interrelationships of the big-headed ant, the gray pineapple mealybug, and pineapple mealybug wilt disease in Hawaii. *Proc Hawaii Entomol Soc* 24:51-67
- Bentley S, Whittaker JB, Malloch AJC (1980) Field experiments on the effects of grazing by a chrysomelid beetle (*Gastrophysa viridula*) on seed production and quality in *Rumex obtusifolius* and *Rumex crispus*. *J Ecol* 68:671-674
- Bess HA (1958) The green scale, *Coccus viridis* (Green) (Homoptera: Coccidae), and ants. *Proc Hawaii Entomol Soc* 16:349-355
- Bristow CM (1983) Treehoppers transfer parental care to ants: a new benefit of mutualism. *Science* 220:532-533
- Bristow CM (1984) Differential benefits from ant attendance to two species of Homoptera on New York Ironweed. *J Anim Ecol* 53:715-726
- Buckley R (1983) Interaction between ants and membracid bugs decreases growth and seed set of host plant bearing extrafloral nectaries. *Oecologia* 58:132-136
- Buckley RC (1987) Interactions involving plants, Homoptera, and ants. *Ann Rev Ecol Syst* 18:111-135
- Carroll CR, Janzen DH (1973) Ecology of foraging by ants. *Ann Rev Ecol Syst* 4:231-257
- Carter W (1973) *Insects in Relation to Plant Disease*, 2nd edition. John Wiley and Sons, New York
- Cockfield SD, Potter DA (1986) Interaction of *Euonymus* scale (Homoptera: Diaspididae) feeding damage and severe water stress on leaf abscission and growth of *Euonymus fortunei*. *Oecologia* 71:41-46
- Das GM (1959) Observations on the association of ants with coccids of tea. *Bull Entomol Res* 50:437-448
- Eisner T, Hicks K, Eisner M, Robson DS (1978) "Wolf-in-sheep's clothing" strategy of a predaceous insect larva. *Science* 199:790-794
- Frederick JM (1943) Some preliminary investigations of the green scale, *Coccus viridis* (Green), in South Florida. *Fla Entomol* 26:12-15
- Fritz RS (1983) Ant protection of a host plant's defoliator: consequence of an ant-membracid mutualism. *Ecology* 64:789-797
- Gill RJ, Nakahara S, Williams ML (1977) A review of the genus *Coccus* Linnaeus in America north of Panama (Homoptera: Coccoidea: Coccidae). *Occas Pap Entomol* 24:1-44
- Grant S, Moran VC (1986) The effects of foraging ants on arboreal insect herbivores in an undisturbed woodland savanna. *Ecol Entomol* 11:83-93
- Jutsum AR, Cherrett JM, Fisher M (1981) Interactions between the fauna of citrus trees in Trinidad and the ants *Atta cephalotes* and *Azteca* sp. *J Appl Ecol* 18:187-195
- Kirkpatrick TW (1927) The common coffee mealybug (*Pseudococcus lilacinus*, Ckll.) in Kenya Colony. *Bull Dept Agric Kenya* No 18
- Marquis RJ (1984) Leaf herbivores decrease fitness of a tropical plant. *Science* 226:537-539
- Messina FJ (1981) Plant protection as a consequence of an ant-membracid mutualism: interactions on goldenrod (*Solidago* sp.). *Ecology* 62:1433-1440
- Nixon GEJ (1951) The association of ants with aphids and coccids. Commonwealth Institute of Entomology, London
- Rohrbach KG, Beardsley JW, German TL, Reimer NJ, Sanford WG (1988) Mealybug wilt, mealybugs, and ants on pineapple. *Plant Dis* 72:558-565
- Way MJ (1954) Studies on the association of the ant *Oecophylla longinoda* (Latr.) (Formicidae) with the scale insect *Saissetia zanzibarensis* Williams (Coccidae). *Bull Entomol Res* 45:113-134
- Way MJ (1963) Mutualism between ants and honeydew producing Homoptera. *Ann Rev Entomol* 8:307-344
- Whittaker JB, Warrington S (1985) An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*). III. Effects on tree growth. *J Appl Ecol* 22:797-811
- Williams ML, Kosztarab M (1972) *Insects of Virginia no. 5. Morphology and systematics of the Coccidae of Virginia, with notes on their biology* (Homoptera: Coccoidea). Virginia Polytech Inst Research Div Bull 52
- Zimmerman EC (1948) *Insects of Hawaii, Vol 5, Homoptera: Sternorhyncha*. University of Hawaii Press, Honolulu