Ant-coccid mutualism in citrus canopies and its effect on natural enemies of red scale, *Aonidiella aurantii* (Maskell) (Hemiptera: Diaspididae)

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Abstract

Mutualistic relationships between honeydew-producing insects and ants have been widely recognized for several decades. *Iridomyrmex rufoniger* (Lowne) is the commonest ant species associated with black scale, *Saissetia oleae* (Olivier), in the citrus orchards of the mid latitudes of coastal New South Wales. Citrus trees with high densities of both red and black scale and high ant activity were identified and the results of excluding ants from half of those trees (using a polybutene band on each trunk) were compared with the results of not excluding ants from the other half. Trees with a low incidence of black scale and ants were also studied. Exclusion of ants from trees was soon followed by collapse of black scale populations because most individuals were asphyxiated by their own honeydew. Also, parasitism of the red scale *by Encarsia perniciosi* (Tower) and *Encarsia citrina* Craw was significantly higher than in the control trees over the following year, as was the predation rate on red scale due to three coccinellid predators, *Halmus chalybeus* (Boisduval), *Rhyzobius hirtellus* Crotch and *Rhyzobius lophanthae* (Blaisdell). In contrast, another coccinellid, *Orcus australasiae* (Boisduval), and a noctuid moth larva, *Mataeomera dubia* Butler, were seen in low numbers on banded (ant exclusion) trees, probably because of the low availability of their black scale prey, but were significantly higher on control trees apparently because of their invulnerability to ants.

Keywords: honeydew, red scale, black scale

Introduction

Honeydew produced by black scale, *Saissetia oleae* (Olivier) (Hemiptera: Coccidae) attracts ants, the commonest of which in the citrus orchards of the mid latitudes of coastal New South Wales is *Iridomyrmex rufoniger* (Lowne) (Hymenoptera: Formicidae). Mutualistic relationships between honeydew-producing scale insects and ants have been widely recognized for several decades. The benefits of such mutualism to soft scales (Coccidae) can include disposal of honeydew and deterrence of natural enemies.

Some ant-attended coccid species appear to lack an effective method of voiding honeydew away from the body and in the absence of ants are likely to asphyxiate themselves as a result (reviews by Way, 1963; Gullan & Kosztarab, 1997). Asphyxiation of *Saissetia zanzibariensis* Williams has been recorded after exclusion of the African weaver ant, *Oecophylla longinoda* (Latreille) under field conditions in Zanzibar (Way, 1954). However, there are no records of asphyxiation of *S. oleae* by its honeydew in the absence of ants.

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The role of ant attendance in protection of scale from natural enemies has been recognized within the context of biological control of scale (DeBach *et al.*, 1951; Bartlett, 1961; Samways *et al.*, 1982; James *et al.*, 1999). Moreover, the presence of ants can also deter the natural enemies of insects that apparently have no mutualistic relationship with them. Diaspidids such as red scale do not produce honeydew (Gullan & Kosztarab, 1997). Yet apparently, red scale can be protected by ants (including those species associated with soft scales) because they have been observed to rise to high densities in the presence of ants (Flanders, 1945; James *et al.*, 1997; Pekas *et al.*, 2010).

Reported here is an experimental field study in coastal New South Wales that quantifies the relation of ant numbers to black scale levels and the parasitism and predation rates of red scale.

Black scale can be found on the twigs and leaves but not on the fruit of all citrus varieties. It is seldom of economic significance in Australia (Smith *et al.*, 1997). It is usually found with red scale, *Aonidiella aurantii* (Maskell) (Hemiptera: Diaspididae) which is seen on twigs, leaves and fruit of citrus and is a major pest in Australia, California, Spain and South Africa (Samways *et al.*, 1982; Smith *et al.*, 1997; Martinez-Ferrer *et al.*, 2002; Pekas *et al.*, 2010). Red scale parasitoids in and around the study area include two ectoparasitoids (*Aphytis chrysomphali* (Mercet) and *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae)) and three endoparasitoids, *Encarsia citrina* Craw, *Encarsia perniciosi* (Tower) (Hymenoptera: Aphelinidae) and *Comperiella bifasciata* Howard (Hymenoptera: Encyrtidae). Four coccinellid general predators (Coleoptera: Coccinellidae) prey on red scale; *Halmus chalybeus* (Boisduval), *Rhyzobius lophanthae* (Blaisdell), *Rhyzobius hirtellus* Crotch (Coleoptera: Coccinellidae) and *Orcus australasiae* (Boisduval) (Coleoptera: Coccinellidae). The last two also prey upon black scale but the larvae of the moth *Mataeomera dubia* Butler (Lepidoptera: Noctuidae) prey only on black scale (Smith *et al.*, 1997).

Materials and methods

Orchard and trees

The study was undertaken in a citrus orchard at Kulnura (33°13′S, 151°13′E, altitude 386 m). The orchard consisted mainly of sweet orange trees, *Citrus × aurantium* L., syn. *Citrus sinensis* (L.) Osbeck, (Sapindales: Rutaceae). There were three blocks of mature Valencia trees and three Hamlin blocks that were four years old. The ant exclusion experiment was confined to the Hamlin blocks because the others had only trees with low numbers of black scale and ants. However, the presence of mature trees is worth noting as they were a potential source of natural enemies, especially highly motile general predators such as Coccinellidae. The Hamlin trees were 1–1.5 m high and planted on 4 × 2.5 m grid, with rows running east to west. Canopies were separated by at least 1.5 m within rows and 3 m between rows. Each block was regarded as an experiment site. Sites 1 and 2 had 126 and 133 trees, respectively, in 7 rows. Site 3 comprised 90 trees in 5 rows. No insecticides were sprayed on experimental trees during the study.

Ant exclusion method

Ants were excluded from selected tree canopies by banding the trunk of each selected tree with a 50 mm-wide strip of black gaffer cloth tape smeared thickly with polybutene (Tangletrap®, Australian Entomological Supplies, Sydney, Australia). Each band was 150–200 mm above ground level. To prevent the polybutene bands from damaging trees, another strip of tape was wrapped around the trunk beneath each coated band. Bands were replaced every month and positions on trunks varied in order to minimize any potential for damaging the trees. Coarse (10 × 10 mm) 150 mm-wide black plastic mesh ('gutter guard') was wrapped around trunks at a point just above each band to reduce the risk of general predators being trapped on the sticky surface.

Experimental design

Within each block, 12 trees with black scale, red scale and *I. rufoniger* present were selected on the basis of high and similar levels of black scale, red scale and the ant. Six of these trees were randomly selected and banded on 10 April 2010. The remaining six trees served as the 'high ant control' treatment. Another six trees on which red scale was present, and black scale and *I. rufoniger* either absent or at low levels, were selected in each site as 'low ant control' trees. Black scale mortality on the banded trees from self-induced asphyxiation (due to accumulation of honeydew in the absence of *I. rufoniger*) led to inclusion of an additional banded treatment (late ant exclusion) from 16 February 2011.

Activity of ants and predators

Ant activity was assessed monthly from July 2010 to June 2011 by counting the number of ants moving downwards past a point on the trunk of each tree during 4 min of observation (2 min on the northern side and 2 min on the southern side). Observations were conducted on fine sunny days when ambient temperatures ranged from 20 to 35°C from August 2010 to April 2011 and from 13 to 16°C in July 2010 and in May and June 2011. Predator activity was assessed during visual inspections of each canopy for 1 min per tree on the same day that ant activity was recorded. Ambient temperatures were recorded by a shaded data logger in a nearby orchard, approximately 1.25 km to the southwest.

Parasitism of red scale

Parasitism was assessed on 7 April and early June 2011. Fruits were collected from each tree in sufficient numbers (2–10) to ensure that at least 100 live adult female scales were present in each case. All susceptible stages were examined under a stereomicroscope and signs of past predation of red scale were also noted. Parasitized and unparasitized individuals were recorded separately for second instar male (2I♂) and second instar female (2I♀), second moult female (2M♀), prepupal male (PP♂) and pupal male (P♂), third instar virgin female (3V♀) and third instar mated female (3M♀) stages. Data were recorded separately for each fruit. Percentage parasitism was based on the occurrence of that parasitoid in or on living scale, or in the case of dead scale, the types of meconia and exit holes left by the parasitoids (Rosen & DeBach, 1978; Forster *et al.*, 1995; Smith *et al.*, 1997; Schmidt & Polaszek, 2007).

Percentage parasitism was based only on the susceptible stages of scale. Those susceptible to *Aphytis* spp. were 2I♀, 3M♀, 3V♀, 2I♂ and PP♂; those susceptible to *Encarsia* spp. were 2I♀, 2M♀, 2I♂, 3V♀ and PP♂ and the stage susceptible to *C. bifasciata* was considered to be 3M♀ because although the
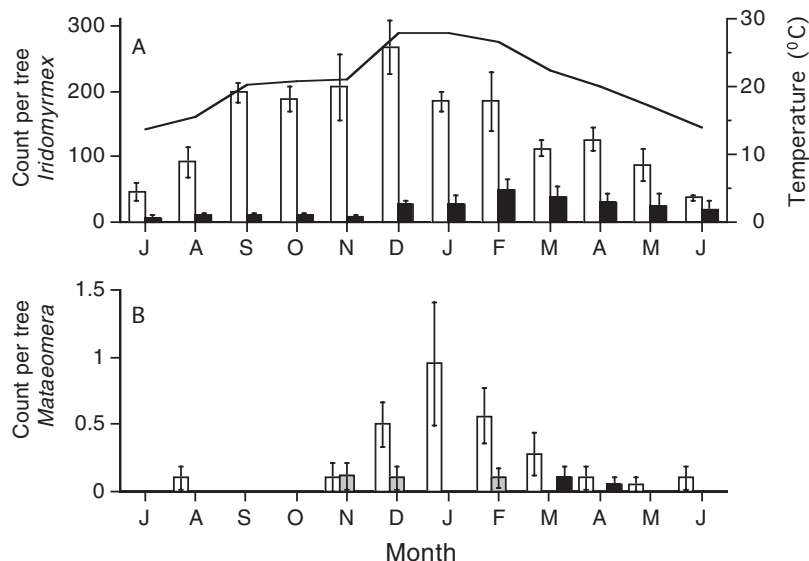
Fig. 1. Seasonal activity levels of the ant *I. rufoniger* and the relative abundance of the scale-eating caterpillar *M. dubia*, the specific predator of black scale, *S. oleae*. (a) The mean number (±SE) of ants per tree moving downwards past a point on the trunk during 4 min of observation. White bars, 'high ant control'; black bars, 'low ant control'; line graph, median ambient shade temperature (°C) during the observation periods. No ants were seen on the 'ant exclusion' trees. (b) Mean number (±SE) of larvae and pupae of the moth *M. dubia* seen in each canopy during 1 min observations per tree on the same day that ant activity was recorded. The 'ant exclusion', 'high ant control' and 'late ant exclusion' treatments represented by grey, white and black bars, respectively.

parasitoid also attacks earlier stages, the resulting larvae survive to complete development in 3M♀ (Richardson, 1978; Forster *et al.*, 1995). The above methods were chosen as a consistent way of making comparisons between treatments with respect to the effectiveness of a given parasitoid. The percentages therefore should not be expected to add up to 100, as they are not based on all scales present.

Predation on red scale

As a result of scale predation by the coccinellids *H. chalybeus* and *O. australasiae*, transient pale scale-sized marks, referred to hereafter as 'footprints', remained for about 2–3 weeks on host plant substrates on which the scales were feeding whereas predation by *Rhyzobius* spp. was indicated by the remains of scale covers with ragged holes. The percentage of red scale suffering recent predation by the coccinellids was estimated as $P_{PRED} = 100(x/(x+y))$ where x = the total number of footprints and damaged scale covers and y = the total number of live red scales.

Data analysis

Total numbers of predators and ants counted in each treatment in each site were calculated. For any given species, the differences between treatments were analysed by one-way ANOVA using these totals with sites as replicates using the program SPSS 18. All data passed Cochran's test for homogeneity of variances. Means for each treatment (i.e. the mean of the three site totals in each case) were separated using the Tukey least significant differences (LSD) method (α = 0.05).

Since the statistical analyses calculated the overall mean for a given treatment that was based on six trees per site, any such

mean is expressed in the text and figures as the equivalent mean per tree (i.e. overall mean/6).

Results

Black scale

Black scale populations on the banded trees declined dramatically after *I. rufoniger* was excluded. On 26 November 2010 (5 months after the trees were banded) a mean of 2.2 nymphs and adults of black scale was found on 'ant exclusion' trees, compared with 12.3 nymphs and adults on the 'high ant control' trees ($F_{1,4} = 32$, $P = 0.005$). Also, by this date, the covering of sooty mould fungi (Capnodiales: Capnodiaceae) that was on the leaves and twigs of heavily infested trees before ant exclusion (due to accumulation of honeydew), had been almost completely removed by wind and rain.

Seasonal activity of I. rufoniger

The lowest activity score on 'high ant control' trees was 39.6 in June 2010. Activity increased as median ambient temperatures rose and reached the highest average number of 271 in December 2010. Activity then fell to 185 in January and remained at similar levels in February before declining to an average of 100 in March and April 2011 (fig. 1a). Ant activity was higher on 'high ant control' trees than on trees selected for the 'low ant control' treatment ($F_{1,4} = 37$, $P = 0.004$). *I. rufoniger* was not found on the ant exclusion trees.

Parasitism and predation of red scale

Parasitism rates on 7 April 2010 (3 days before the ant exclusion treatment started) were as follows. On the trees
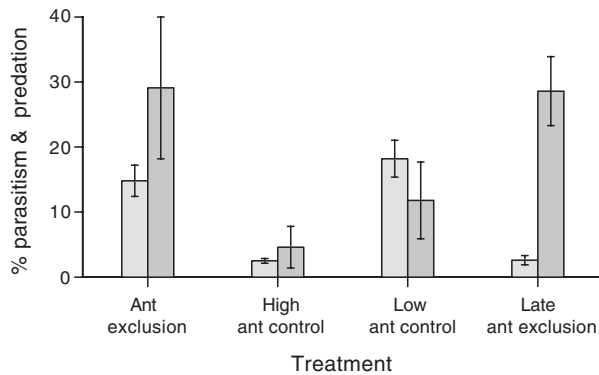
Fig. 2. Parasitism and predation of red scale, *Aonidiella aurantii*, in April 2011 towards the end of ant exclusion experiment in the Hamlin orange orchard blocks. (a) Percentage (±SE) of susceptible stages of red scale parasitized by *Encarsia* spp. (dark bars). (b) Percentage (±SE) of red scale recently removed by predation estimated on the same date (light bars).

Fig. 3. Seasonal trends in prevalence of three types of coccinellid predator during ant exclusion experiment (June 2010 – June 2011). Means (±SE) of numbers of predators per tree counted in 1 min observations per tree. The 'ant exclusion', 'high ant control' and 'late ant exclusion' treatments represented by grey, white and black bars, respectively. (a–c) Adults and larvae of *H. chalybeus*, *Rhyzobius* spp. and *O. australasiae*, respectively. Median ambient shade temperature during the observation periods as in fig. 1a.

selected for the 'ant exclusion' treatment, average percent parasitism by *Aphytis* spp., *C. bifasciata* and *Encarsia* spp. was 2.7, 4.3 and 0.1%, respectively. The percentage recently removed by predators was 7.3%. On the trees selected for the 'high ant control' treatment, equivalent figures were 5.8, 10.2, 10.2 and 0%, respectively, and on those intended for the 'low ant control' treatment they were, 3.3, 22.8, 7.5 and 9.2%, respectively. Differences between the 'high ant control', 'ant exclusion' and 'low ant control' treatments were not significant ($F_{2,6} = 0.14$, $P = 0.869$ for *Encarsia* spp.; $F_{2,6} = 1.3$, $P = 0.35$ for *Aphytis* spp.; $F_{2,6} = 1.2$, $P = 0.37$ for *C. bifasciata*).

In early April 2011 average percent parasitism by *Encarsia* spp. was 14.8, 2.5, 18.2 and 2.6% in the 'ant exclusion', 'high ant control', 'low ant control' and 'late ant exclusion' treatments, respectively (fig. 2). Differences among treatments were significant ($F_{3,8} = 4.5$, $P = 0.04$). Percent parasitism on 'ant exclusion' trees was significantly higher than on 'high ant control' and 'late ant exclusion' trees but not significantly different from 'low ant control' trees (mean differences > LSD, > LSD, < LSD, respectively, α = 0.05). Parasitism rates by *Aphytis* spp. and *C. bifasciata* were extremely low in all treatments. These parasitoids suffer high mortality in heatwaves (Smith *et al.*, 1997) so this result is probably due to the record hot summer (January–February 2011).

If the footprints of red scale removed or otherwise killed by predators are included in the total red scale count of 5 April 2011, they represented 29.1, 4.6, 11.8 and 28.6% of scale recently removed by predation in 'ant exclusion', 'high ant control', 'low ant control' and 'late ant exclusion' treatments, respectively (fig. 2). Differences were significant ($F_{3,8} = 9.2$, $P = 0.006$) because predation rates in the 'ant exclusion' and 'late ant exclusion' trees were significantly higher than in the other treatments (mean differences > LSD, α = 0.05).

Seasonal activity of predators

Predators were present in all months of the study. *H. chalybeus* was most abundant over the summer months December–January (fig. 3a) and *Rhyzobius* spp. (almost all *R. lophanthae*) were seen between August and November and April and June (fig. 3b), whereas *O. australasiae* (which was
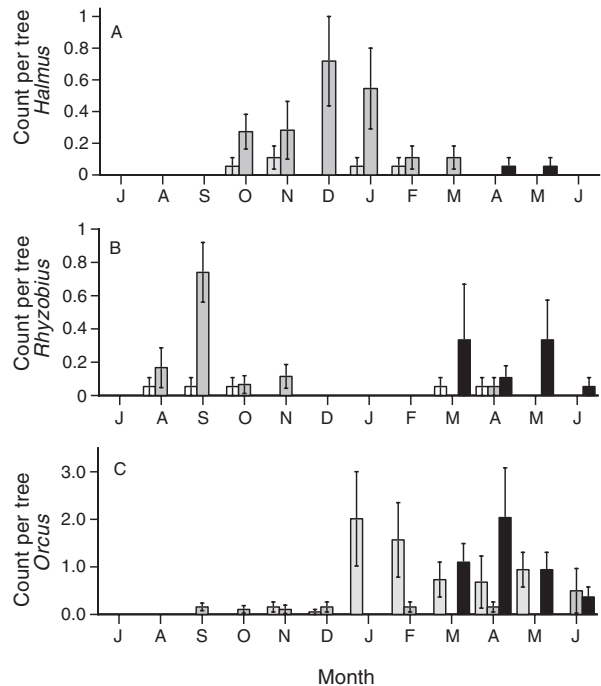
seen attacking both red and black scale) was active between January and June (fig. 3c) and larvae and pupae of the moth *M. dubia* were most abundant between December and March. *M. dubia* larvae were seen attacking only black scale.

H. chalybeus adults and larvae per tree over 12 months from April 2010 averaged 1.7, 0.1 and 0.3 in the 'ant exclusion' 'high ant control' and 'low ant control' treatments, respectively. These differences were significant ($F_{2,6} = 57$, $P < 0.0001$) because the mean for the 'ant exclusion' treatment was significantly higher than the other two (mean differences > LSD, α = 0.05).

Rhyzobius spp. and *O. australasiae* adults and larvae per tree averaged over 12 months were not significantly different ($F_{2,6} = 1.4$, $P = 0.33$ and $F_{2,6} = 1.6$, $P = 0.27$, respectively).

M. dubia larvae and pupae per tree over the 12 months averaged 0.2, 2.0 and 0.28 in the 'ant exclusion', 'high ant control' and 'low ant control' treatments, respectively. Differences were significant ($F_{2,6} = 44.3$; $P < 0.001$) because means on 'high ant control' trees were significantly higher than on 'ant exclusion' and 'low ant control' trees (mean differences > LSD, α = 0.05)

Discussion

Ant numbers were generally highest in summer and lowest in winter. This is the pattern reported for other ant species (Sanders, 1972; Briese & Macauley, 1980; Stevens *et al.*, 1998). Spatial variation appeared to be relatively consistent because

the numbers seen on the 'low ant control' trees (chosen before the experiment started on the criterion of low ant density) were consistently lower than on the high ant control trees (and markedly so from September and February inclusive).

Black scale self-asphyxiation

S. oleae suffered high mortality through asphyxiation by its own honeydew in the absence of *I. rufoniger*. Similar experimental results were obtained for *S. zanzibarensis* in the absence of the African weaver ant, *O. longinoda* (Way, 1954) and for *Coccus viridis* in the absence of *Pheidole megacephala* F. (Bach, 1991). Gullan (1997) was uncertain whether such mortality was due to asphyxiation or the effect of fungal growth on honeydew contamination. However, the presence of sooty mould before ant exclusion and rapid mortality of black scale after ant exclusion suggests asphyxiation. This view is supported by observations made by Flanders (1942) who noted that black scale cultures on sprouts of potato, *Solanum tuberosum* L. (Solanales: Solanaceae), were subject to asphyxiation from excess deposits of honeydew in the absence of sooty mould and that washing scale-infested potato tubers every week kept scale healthy.

Ants and parasitoids

Interactions of ants and parasitoids have been studied in laboratory and semi-natural conditions (Barzman & Daane, 2001; Martinez-Ferrer *et al.*, 2002) but are difficult to observe directly in field experiments where the parasitoids are expected to arrive on their own accord. However, the interactions can be inferred from differences in parasitism rates between an ant exclusion treatment and controls just as ant exclusion has been related to lower infestation rates of red scale (Pekas *et al.*, 2010) or increased survival rates of other pests (Flanders, 1945; Bach, 1991; Chong *et al.*, 2010).

In the case of the experiment reported here, the difference on 5 April 2011 between the ant exclusion and 'high ant control' treatments in terms of parasitism rates on red scale can be attributed to the exclusion of ants from the first treatment. Similarly, the high parasitism rate in the low ant control treatment can be attributed to the low density of ants. However, the reason for the low parasitism rate in the late ant exclusion treatment is not immediately obvious. It would have been reasonable to expect that parasitism rates would be high after ant exclusion but the fact that it was low could be due to the short time (48 days) between the late exclusion (16 February) and the census on 5 April. The development time of *E. perniciosi* from oviposition to adult emergence is about 20–24 days (Debach & Sundby, 1963) so some increase in parasitism would have been possible but further research is needed to quantify the parasitoid's ability to build up population density over time.

Ants and predators

Differences between treatments suggest that *I. rufoniger* did not deter the presence of the coccinellid *O. australasiae* and the larva of the noctuid moth *M. dubia*. Their relative rarity in the 'ant exclusion' treatment is associated with the low numbers of their prey (black scale) due to self-asphyxiation after banding. However, levels of the two predators were high in the unbanded treatment, apparently because of their invulnerability to ants. Here, *I. rufoniger* foragers moved over and

around *O. australasiae* adults and larvae but they did not disturb them. Furthermore, *O. australasiae* adults and larvae did not appear to take evasive action in order to avoid encounters with ants.

There are no previous reports of ants attacking *O. australasiae* and *M. dubia*. The apparent invulnerability of *O. australasiae* to ants may be partly a function of its larger size. Lengths of larvae of *O. australasiae*, *H. chalybeus* and *R. lophanthae* range from 6 to 8, 3 to 5 and 3 to 4 mm, respectively (Ślipiński, 2007). The larvae of some coccinellids are not deterred by ants associated with honeydew producers. Their defence can be in the form of thick dense wax filaments (Kaneko, 2007; Liere & Perfect, 2008) or a dorso-ventrally flattened shape fringed by bristles (Völkl, 1995). Here, *M. dubia* could have been invulnerable to ants because larvae and pupae of this moth are protected by the integuments of the black scale that they have eaten and these may mimic the scale physically and chemically. Similarly, ants did not prevent predation of *S. zanzibarensis* by carnivorous larvae of noctuid moths (Way, 1954).

Aggregation of predators

The estimates of predation rates upon red scale in April 2011 show that the 'late ant exclusion' was followed by higher predation rates than those seen in all the other treatments. This can be related to the fact that more coccinellid predators (chiefly *Rhyzobius* spp. and *O. australasiae*) were seen in the 'late ant exclusion' treatment than any other. This may have been due to an aggregative functional response of the kind that has been recorded for other coccinellids (Turchin, 1987; Turchin & Kareiva, 1989; Agarwala & Bardhanroy, 1999; Evans & Toler, 2007) and warrants further investigation.

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