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Successive replacement of tending ant species at aggregations of scale insects (Hemiptera: Margarodidae and Eriococcidae) on *Eucalyptus* in south-east Queensland

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Abstract Scale insects generally display enhanced survival rates in the presence of tending ants, but studies of ant and scale–insect interactions typically examine a single tending ant species. This study investigated the successive changes in tending ant species during the lifespan of two species of scale aggregations, a monophlebuline margarodid and an *Eriococcus* sp. (Eriococcidae) on the Plunkett mallee, *Eucalyptus curtisii*. Scale aggregations were also subject to an ant-exclusion experiment to quantify the degree to which ants increased the survival rates of both scale insect species. Tending ants assorted to two categories, dominant and secondary, with a significant bias according to the chronological age of the scale aggregation. Secondary ant species (opportunists and subordinates) tended juvenile-scale aggregations. These were replaced by a dominant species of *Iridomyrmex* (Dolichoderinae), which almost exclusively tended larger (mature) aggregations until the senescent stages of the infestation when secondary ant species returned. Exclusion of the primary tending *Iridomyrmex* ant increased mortality of both species of scale insects by 96% relative to controls.

Key words Ant association, ant exclusion, ant functional groups, Monophlebulini, mutualism.

INTRODUCTION

There are some 7000 species of scale insects worldwide and most form mutualistic associations with ants (Carver *et al*. 1991; McGavin 1993). Ants protect scale insects from predators and parasitoids by reducing the frequency of attacks and allowing the scale-insect population to expand and flourish (Itioka & Inoue 1996; James *et al*. 1997). In return, ants benefit from the stable source of energy in the form of honeydew, lipids and proteins that scale insects exude from their anus (Gullan 1997). The removal of honeydew additionally benefits scale insects by minimising fungal growth associated with the exudate and preventing fouling from excess honeydew (Gullan 1997). Some ant species transport scale insects to new sites, while others are said to exercise control over scale population levels by withholding protection from, or eating the individuals in excess of their needs (Hölldobler & Wilson 1990). While many relationships are facultative for both partners (Way 1963; Gullan 1997), some are obligate (Ward 1991). Numerous ant species have been recorded tending scale insects (for example, Ben-Dov 1990; Buckley *et al*. 1990; Gullan 1997), but Buckley & Gullan (1991) found that aggressive ants provided better protection than relatively inoffensive species.

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Experimental studies of ant–scale interactions typically involve a single ant species (Rosario *et al*. 1993; Itioka & Inoue 1996; 25 additional studies summarised in Gullan 1997). However, many homopteran aggregations have been recorded with multiple ant species in attendance, for example, Membracidae (Del Claro & Oliveira 1999), Coccidae and Pseudococcidae (Buckley & Gullan 1991; Campbell 1995), and Cicadellidae (Moya-Raygoza & Nault 2000). During outbreaks of scale insects on the Nathan campus of Griffith University in 1999, I noticed that different ant species appeared to be associated with infestations of Margarodidae and Eriococcidae at different developmental stages of their aggregations.

My study tested for differences in tending ant species for two scale insects from the families Margarodidae and Eriococcidae at three developmental stages of their aggregations from establishment, through maturation to senescence. An ant-exclusion experiment was run simultaneously to assess the degree to which tending ants improved the survival rate of both scale-insect species and whether there were significant differences in survival rates between the two scale species when ants were excluded.

METHODS

The investigation was carried out during March and April 1999 within the Nathan campus of Griffith University, where two species of scale insects from the families Margarodidae and Eriococcidae were found infesting the Plunkett mallee, *Eucalyptus curtisii* (Myrtaceae). Margarodidae are sap-feeding, soft scale insects usually covered in a fluffy white waxy scale that exudes from their multilocular pores (Bhatti 1990). Adults are extremely sexually dimorphic. Free-living females are a reddish brown colour, apterous and larviform and anchor to the host plant by their stylet (Carver *et al*. 1991). The adult male in contrast is much smaller, lacks functional mouthparts and has only two wings. Dispersal is by the first-instar nymph or crawler, which is highly mobile and sufficiently light to be carried by the wind (Carver *et al*. 1991). Eriococcidae include a diverse group of sedentary gall formers and others that produce a characteristic outer waxy cover or 'test' (Gullan & Vranjic 1991). Eriococcid feeding and dispersal is similar to the Margarodidae. The margarodids in my study were identified as belonging to the tribe Monophlebulini and possibly represent an undescribed genus (P. Gullan pers. comm. 1999). The females are a mottled orange colour up to 15 mm long and covered in white fluffy wax. Eriococcids were identified as a gum tree scale, *Eriococcus* sp., possibly *E. coriaceus* Maskell (P. Gullan pers. comm. 1999). Scale aggregations consisted of groups of scale insects confined to single trees or to a single branch of a Plunkett mallee. They were categorised into three developmental stages, which were identifiable as:

1 Early stages: a few (3–9) scale insects, primarily early instar, and confined to one or a few leaves or small branchlet;

2 Mature: larger numbers (>10) of gregarious scale, various instars, typically heavily attended by ants;

3 Senescent: reduced numbers (<10) of scale with obvious signs of decline including sooty mould build-up, empty puparia (Margarodidae), empty tests (Eriococcidae) and dead scale insects.

Tending ants at every scale aggregation were identified to genus and the primary tending ant identified as the one most commonly encountered tending scale aggregations during the peak of their productivity, i.e., the mature colony. Ants were also categorised into functional groups according to the system proposed by Greenslade (1978, 1979) and modified by Andersen (1995). Chi-square analysis was used to test the null hypothesis that primary (dominant) ant species and other ant species (or functional groups) grouped as secondary tenders were equally likely to be found tending all three categories of scale aggregations. Voucher specimens of ants from this study are held at the South Australian Museum and examples of both scale insect species are lodged in the Griffith University insect collection.

For the exclusion experiment, six mature aggregations of each scale species were selected at random. Tending ants were excluded from access to three aggregations of each species by the application of a 3 cm band of Tangletrap around the base of the host tree branch, and removal of connecting vegetation (The Tanglefoot Co., Grand Rapids, Michigan, USA). The remaining three aggregations of each scale species provided a control. Scale insects of both species were counted at the beginning of the study and again after 1 week. This process was repeated: the following week for eight different aggregations of each scale species, in which four of each were controls; and again for another six aggregations of each species in the third week. In total, there were 10 control groups and 10 experiments for each scale species. The inclusion of spatial and temporal elements in the experimental design served to control for environmental variables within the time frame of the study. Numbers of scale insects surviving at the end of each week were converted to proportions surviving, then arcsine transformed to normalise the data for analysis of variance (ANOVA). These values were used as the dependent variable in a two-factor ANOVA performed in SAS (SAS Institute Inc., Cary, North Carolina, USA) to test for significant differences in survival rates with and without ants for both scale species.

RESULTS

The primary attendant ant for both species of scale insects was a species of *Iridomyrmex* (Dolichoderinae). In total, 11 ant species were found tending the eriococcid aggregations and seven ant species tended the margarodids (Table 1).

Table 1 Ant species tending scale insects at Griffith University, Nathan campus. Numbers include scale aggregations in all developmental categories. Ant functional groups are based on their roles and status in Australian ant communities following a system proposed by Greenslade (1978, 1979) and modified by Andersen (1995)

Tending ant	Functional group	Number of aggregations tended	
		Eriococcidae	Margarodidae
Iridomyrmex sp.	Dominant species	36	39
Papyrius sp.		1	–
Paratrechina sp.	Opportunists	44	12
Rhytidoponera spp.		8	3
Ochetellus sp.		9	1
Crematogaster spp.	Generalised Myrmicinae	4	6
Pheidole sp.		1	1
Polyrhachis spp.	Subordinate Camponotini	19	7
Opisthopsis spp.		3	–
Plagiolepis sp.	Cold-climate specialists	10	–
Dolichoderus sp.		3	–

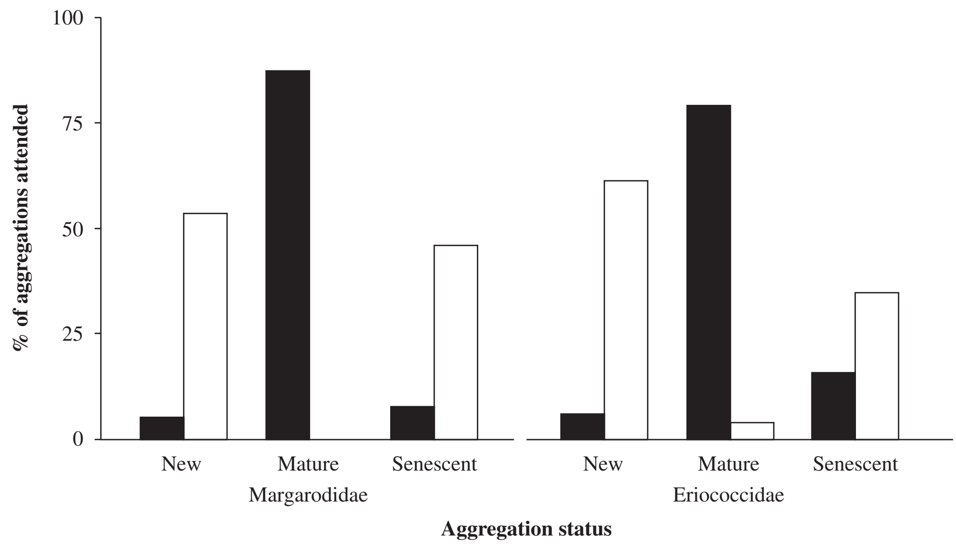

Fig. 1. Tending ant species in the three categories of scale insect aggregations. Percentage of aggregations tended is for primary (*Iridomyrmex* sp., ■) or secondary (other species, □) ants across the three categories, for each species of scale insect. Eriococcidae tended by *Iridomyrmex* ($n = 36$), and other ants ($n = 102$); Margarodidae tended by *Iridomyrmex* ($n = 39$), and other ants ($n = 30$).

Table 2 Mean survival rates (±SD) for two species of scale insects (expressed as arcsine transformed percentage surviving) at the end of three contiguous time periods for exclusion experiments (without ants) and controls (with ants)

	Scale species	With ants	Without ants
Week 1	Eriococcidae	71.9 ± 13.9 ($n = 3$)	41.0 ± 12.0 ($n = 3$)
	Margarodidae	72.6 ± 3.1 ($n = 3$)	53.9 ± 11.6 ($n = 3$)
Week 2	Eriococcidae	79.8 ± 17.7 ($n = 4$)	33.5 ± 19.3 ($n = 4$)
	Margarodidae	55.1 ± 22.8 ($n = 4$)	43.5 ± 20.0 ($n = 4$)
Week 3	Eriococcidae	84.8 ± 7.3 ($n = 3$)	60.4 ± 1.5 ($n = 3$)
	Margarodidae	84.0 ± 8.5 ($n = 3$)	66.0 ± 3.0 ($n = 3$)
Total (±SE)	Eriococcidae	78.9 ± 4.7 ($n = 10$)	43.9 ± 5.7 ($n = 10$)
	Margarodidae	69.0 ± 6.2 ($n = 10$)	53.3 ± 5.4 ($n = 10$)

Tending ant species for both scale insects was significantly dependent on the category of the aggregation (Eriococcidae $\chi^2 = 84.5$, $P < 0.001$; Margarodidae $\chi^2 = 46.6$, $P < 0.001$; Yates correction for small sample size; Fig. 1). *Iridomyrmex* ants almost exclusively tended both species of scale during the most productive stages of their aggregations when scale numbers were at a maximum. In contrast, other ant species almost exclusively tended scale insects in the early stages of their aggregations and to a lesser extent in the senescent stages.

During the study, scale-insect aggregations had a mean overall survival rate of 74% (Eriococcidae 78.9%; Margarodidae 69.0%) when tended by the primary attendant ant (Table 2). This was significantly higher than the 49% (Eriococcidae 43.9%; Margarodidae 53.3%) mean survival rate for aggregations in which ants were excluded ($F_{3,36} = 7.26$, $P < 0.0006$) (Table 2). Exclusion of the primary tending *Iridomyrmex* ant almost doubled mortality of both species of scale insects (96%) relative to controls. The low survival rate of Margarodidae with ants in week 2 resulted from the decimation of one aggregation by an unknown cause. There was no significant difference in the mean survival rates of the two species of scale with and without ants, and there was no significant interaction between ant attendance level and scale insect species.

DISCUSSION

The significant differences in tending ant species at successive developmental stages in scale aggregations suggest there is an ant species replacement process (i.e., succession) occurring. Opportunist ants (and those in other subordinate functional groups) are quickly able to locate new resources, such as juvenile scale aggregations, and exploit them before other ants arrive (Davidson 1998). Dominant ant species are rarely found with solitary females or small nymphal aggregations (see McEvoy 1979; Messina 1981), presumably because the resource is marginal. However, as the scale insect aggregation grows, dominant ant species displace the initial secondary ant tenders. Transition from attendance by secondary to dominant ant species was not observed, but two juvenile aggregations of eriococcids tended by *Crematogaster* were tended by *Iridomyrmex* 2 weeks later when the aggregations had increased in size. The senescent stages of scale aggregations again provided opportunities for less aggressive ants to return to the resource when numbers of *Iridomyrmex* declined, and a few instances of attendance by more than one ant species were observed. *Opisthopsis* sp. was found tending scale insects together with small numbers of *Iridomyrmex*, as was a *Polyrhachis* sp. that may have been attracted to the sooty mould but which opportunistically took honeydew from the scale. It seems that primary attendant species (for example, *Iridomyrmex*) defend the declining honeydew resource with progressively fewer numbers and with less vigour until finally, less aggressive ant species are able to reclaim the resource.

Results of the exclusion experiment support previous findings that survival rates of scale insects are significantly greater when their ant guard is maintained. While no attempt was made to determine all causes of mortality, several natural enemies were observed in contact with the scale aggregations. Early instar larvae of the coccinellid predator *Rodolia cardinalis* (Mulsant) (Coleoptera) were found on untended margarodids, while another coccinellid, *Cryptolaemus montrouzieri* Mulsant, and an unidentified epipyropid larva (Lepidoptera), attacked the eriococcids. These last two predators were active in tended and untended aggregations, apparently immune from ant attack through chemical or mechanical means. At one site, epipyropid moth larvae ate 31 of the 32 untended eriococcids. No obvious enemies were observed in the early stages of scale colonies.

While the results of my study confirm the importance of primary tending ants when scale aggregations are most productive, the protection afforded by secondary tenders may also play an important role in the natural lifespan of a scale infestation when different predator fauna or predation rates could apply. Testing for significant differences, however, in scale-insect survival rates with and without ants during early and senescent stages of their aggregations may be more difficult. Under certain environmental conditions, an increased survival rate for scale insects during the vulnerable early stages, or during the senescent stages of their aggregations, may be an important element of scale insect population dynamics.

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