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DIFFERENTIAL EFFECTS OF THE ALLEGHENY MOUND ANT, *FORMICA EXSECTOIDES* FOREL, ON APHID, SCALE AND PREDATOR POPULATIONS AND THEIR INTERACTIONS IN JACK PINE FORESTS

By

Donald Bryan Bishop

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ABSTRACT

DIFFERENTIAL EFFECTS OF THE ALLEGHENY MOUND ANT, *FORMICA EXSECTOIDES* FOREL, ON APHID, SCALE AND PREDATOR POPULATIONS AND THEIR INTERACTIONS IN JACK PINE FOREST

By

Donald Bryan Bishop

The Allegheny mound ant, *Formica exsectoides* Forel (Hymenoptera: Formicidae) is one of the most common mound building ants in the eastern United States. It readily tends honeydew producing Homoptera and is also very aggressive towards non-tended homopterans and other arthropod species, including natural enemies of homopterans. A survey in north central Michigan in 1993 indicated that the homopteran community differed markedly between areas of jack pine (*Pinus banksiana* L.) forests with and without this ant. Tended homopteran species dominated areas with *F. exsectoides* while a non-tended aphid was most common in areas without it. In addition, invertebrate predator populations were generally larger and of different composition, consisting primarily of generalist predators in areas without mound ants. Based on this information, I tested the hypothesis that the presence of *F. exsectoides* alters the homopteran community by 1) providing enemy-free space for tended homopterans against their specialist predators and 2) by preying upon non-tended homopterans.

I tested hypothesis 1 by conducting a combination of ant-exclusion, predator-inclusion studies using the two most common tended homopterans in mound ant areas, *Cinara banksiana* Pepper & Tissot (Aphidae) and the pine tortoise scale,

Toumeyella parvicornis (Cockerell) (Coccidae). Allegheny mound ants provided enemy-free space for the aphid against its specialist mirid (*Pilophorus* spp.) predator.

The pine tortoise scale received less effective enemy-free space from ants against its specialist predator; early instars of *Hyperaspis binotata* Say (Coleoptera: Coccinellidae) hid under gravid scales and escaped ant attack while feeding on scale eggs and crawlers. Later instars feeding in the open used glandular secretions and long, waxy tufts to repel ant attack.

Mound ants readily attacked and removed the most abundant predator in non-mound ant areas, lacewing larvae, when encountered. Since both tended aphids and pine tortoise scales were virtually absent from non-mound ant areas implies that the generalist predators in non-ant areas may play a key role in reducing populations of these homopterans.

Hypothesis 2 was tested using ant-exclusions with the non-tended woolly aphid, *Schizolachnus piniradiatae* (Davidson) (Aphidae). Woolly aphids were attacked by ants virtually every time they were encountered, and by the end of 72 h, woolly aphid numbers on ant-present branches were significantly less than those on ant-excluded branches.

Taken together, these results indicate that the Allegheny mound ant played different roles in shifting the homopteran community from one composed primarily of non-tended species in areas without mound ants to one composed of tended species in mound ant areas. Acting as a predator, it preyed on non-tended aphids and some generalist homopteran predators. Acting as a mutualist, it modified predator-homopteran interactions providing effective enemy-free space for some homopterans.

This dissertation is dedicated to David and Kristen and the pursuit of their dreams.

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CHAPTER 1

Introduction

Theoretical Background

Communities are composed of populations that interact with one another both directly and indirectly (Anderson & Kikkawa 1986, Putman 1994). The definition of a community can be made less inclusive by restricting it to at least one of four levels: trophic, spatial, taxonomic or life form (Roughgarden & Diamond 1986). The restriction placed on a community will usually depend on the questions being asked. One question ecologist ask is what mechanisms determine the shape and structure of a particular community (Kitching 1986). Studying the processes occurring between interacting populations may lead to understanding how these processes determine species richness and eveness, and the mechanisms involved in community structure (Kitching 1986, Wilson 1986, Itioka 1993).

While ecologists have debated for years about what forces help regulate populations, typically negative interactions (i.e. competition, predation, including parasitoids and disease) have been thought of and studied as the principle biotic factors regulating populations (Darwin 1872, Park 1954, Hairston et al. 1960, Connell 1961, MacArthur and Connell 1966, Paine 1966, Diamond 1978, Jeffries & Lawton 1984, Sih et al. 1985). However, positive interactions (i.e. mutualism and commensalism) have been largely overlooked as important forces both in regulating populations and shaping communities (Roughgarden & Diamond 1986, Kawanabe and Iwasaki 1993, Putman 1994, Bronstein 1994a, Price 1997).

One negative interaction model of population regulation is that submitted by Hairston et al. (1960). They proposed that in a three-trophic system, natural enemies (hereafter predators) were posited to suppress herbivore populations below their carrying capacity thus limiting the effects of competition between herbivores. This in turn allowed plant populations to increase to the point where competition for space or nutrients became the limiting factor for plants. This is an example of a three-tiered trophic cascade (Paine 1980, Carpenter et al. 1985): the top level (predators) has a positive effect on the lowest level (producers) by suppressing the intervening level (the primary consumers or herbivores) (Figure 1a).

This model was expanded to four trophic levels by including populations of second level (secondary) predators that prey upon first level (primary) predators (Fretwell 1977, 1987). Intraguild predation (Polis & Myers 1989, Polis & Holt 1992), where potential competitors eat each other, can lead to a different outcome in a trophic cascade. In this case, the reduction of one group of predators by another allows herbivore populations to increase (Power et al. 1992, Rosenheim, et al. 1993, Polis and Holt 1992, Spiller and Schoener 1994) (Figure 1b).

These models predict that the outcome of interactions can shift when other species become involved. Hence, one way to better understand population regulation and communities is to focus on how two-way interactions shift depending on the involvement

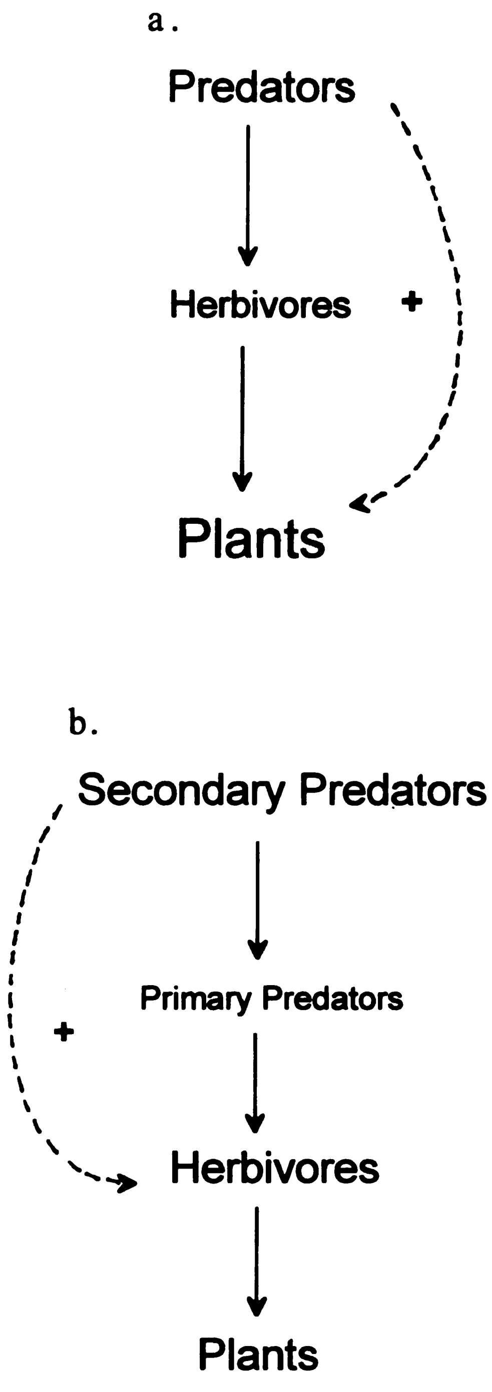


Figure 1. Graphical representation of top-down generated trophic cascades by predators on the trophic levels below them in a (a) three-tiered trophic system and (b) four-tiered trophic system. Dashed line represents indirect effects.

of other species (Price et al. 1980, Wilson 1986, Itioka 1993). Mutualistic interactions involving insects typically involve one species providing a service (e.g. protection or dispersal) to a second species while the second provides food for the first species (Price 1997). By protecting a second species from its enemies, the first species may be altering the predator-prey interaction by providing enemy-free space to the prey species.

The theory of enemy-free space proposes that pressures from predators force potential prey to "find [alternitive] ways of living"; and, further, that this pressure is more important than competition for food in shaping communities (Price et al. 1980, Jeffries & Lawton 1984). A species may “find” enemy-free space by using different feeding sites or hosts (Damman 1987, Ohsaki & Sato 1990, Brown et al. 1995, Hopkins & Dixon 1997), thus allowing species to live in areas previously unavailable to them and causing a shift in species diversity.

Predator-prey-mutualist interactions involve one species that acts as a mutualist (or commensalist) with either the prey or the predator (Addicott & Freedman 1984). By protecting prey species from their enemies and providing enemy-free space, the protector-mutualist could also alter a trophic cascade. However, rather than a top-down suppression of primary predators by secondary predators, this cascade would develop from the horizontal interference by the mutualist of the primary predator-prey interaction (Figure 2).

One particularly interesting model system that could be used to test ideas on the importance of mutualisms in altering predator-prey interactions would be predatory or aggressive, keystone mutualists such as ants.

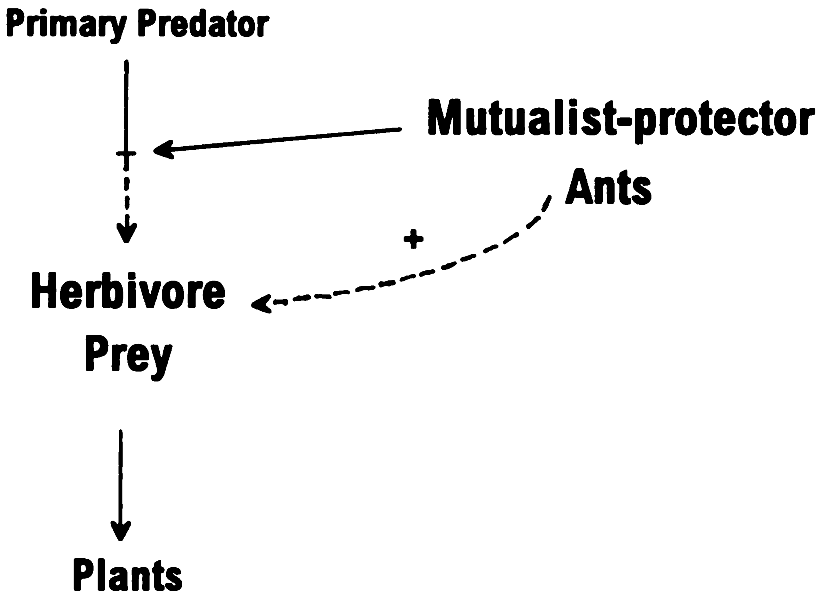


Figure 2. Graphical representation of a trophic cascade caused by the horizontal interference of predator-prey interaction by a mutualist-protector such as homopteran-tending ants. Curved, dashed line represents indirect effect of mutualist on herbivore.

Keystone mutualists (Gilbert, 1980) affect multiple species in a manner analogous to keystone predators (Paine, 1966). Ants, because of the complex social behavior, perennial nature of the colony, and opportunistic feeding behavior, are able to play several roles within a single community by providing enemy-free space for some homopterans, ignoring others, and by acting as predators of still other homopterans. This could, in turn, cause a shift in the species composition of both homopterans and their predators.

Ants as mutualists to homopterans

"The ant ascends the tree that it may milk its cows, the aphids, not kill them." (Linneaus 1758, cited in Jones 1929). For centuries, naturalists have recognized that a relationship exists between ants and honeydew producing Homoptera. Honeydew appears to be an important component of the diet in many ant species (Jones 1929, Way 1963, Bradley & Hinks 1968, Carroll & Janzen 1973, Skinner 1980, Degen et al. 1986). Depending on the relative amounts of carbohydrate verses protein available, ants may also switch to feeding on the tended Homoptera (Way 1954, Pontin 1958, Pontin 1978, Hölldobler & Wilson 1990).

Tended homopterans appear to gain various benefits from ants, including sanitary removal of honeydew (Strickland 1947, Majer, 1982), stimulation of aphids to grow and mature more rapidly (Banks & Nixon 1958, El-Ziady 1960) and a decrease in development time of tended homopterans (Bristow 1984). However, protection from natural enemies, especially when colonies are small, may be the most important benefit (Way 1963, Bradley and Hinks 1968, Bradley 1973, Addicott 1979, Tilles & Wood 1982, Warrington and Whittaker 1985b, Sudd 1987, Bach 1991, Bristow 1991, Seibert 1992, Breton & Addicott 1992), although this idea has not always been universally accepted (Jones 1929). Whether mutualistic ants could play a role in impacting homopteran populations and hence effect community structure remains poorly understood since most field studies on mutualisms have focused on the individual level or as a life history trait of one of only two parties (Addicott 1986, Bronstein 1994a).

Study ant species

I have chosen to use the Allegheny mound ant, *Formica exsectoides* Forel, to examine the role an aggressive mutualist may play in altering predator-prey interactions. It has several properties that make it a good organism for this study. First, *F. exsectoides* forms large, locally abundant populations covering several hectares in jack pine (*Pinus banksiana* L.) forests of north-central Michigan (Bristow et al. 1992). Second, this ant tends a variety of honeydew producing taxa including membracids, aphids and scales (Andrews 1929, Headly 1943, Haviland 1947, Campbell 1990). Third, it is also very aggressive and acts as a predator in several local ecosystems (Allen et al. 1970, Campbell 1990). Lastly, the Allegheny mound ant forms new colonies by budding, a new mound is formed by workers and queen(s) from an older mound (Creighton 1938, 1950). This behavior contributes to populations of *F. exsectoides* becomming very large, in terms of both mound density and individual ants (Cory & Haviland 1938). Taken together, these various traits can allow this ant to suppress other arthropods, including other ant species (Hölldobler & Wilson 1990), while acting as a mutualist with honeydew producing Homoptera. By tending some insects and acting as a predator on others, this ant would appear to fit the role of a mutualist-predator. (See Appendix 2 for biology of this ant).

This research was designed to examine the various roles Allegheny mound ants may play in impacting homopteran populations in jack pine forests. By studying how Allegheny mound ants influence the interactions between homopterans and their predators, and the direct interactions of this ant on other arthropods, we aim to increase our understanding of how a keystone mutualist-predator impacts the homopteran community and potential homopteran predators.

In chapter 2, I present the results of the survey that first indicated that the homopteran and predator communities differed between areas with and without Allegheny mound ants. Tended homopterans reached much higher population sizes in areas where *F. exsectoides* populations were dense, but were less numerous or virtually absent as *F. exsectoides* density fell to zero. However, a non-tended aphid, *Schizolachnus piniradiatae* (Davidson), showed an opposite trend by having the largest populations in areas without Allegheny mound ants. Subsequent experiments indicated that *F. exsectoides* can reduce this aphids population by preying on them.

The hypothesis that *F. exsectoides* provides enemy-free space to homopterans is addressed in chapter 3. Using the two most abundant homopterans, I performed a combination of ant-exclusion and predator-inclusion experiments to determine whether the ants were providing enemy-free space to *Cinara banksiana* Pepper & Tissot (Aphididae) and the pine tortoise scale, *Toumeyella parvicornis* (Cockerell) (Coccidae). The results supported the hypothesis when *C. banksiana* was involved. However, the hypothesis was not supported for the pine tortoise scale. The enemy-free space appeared to be more conditional, perhaps depending partly on the population size of the scales' primary predator, *Hyperaspis binotata* Say (Coccinellidae).

Chapter 4 addresses the possible mechanisms by which *H. binotata* circumvents the protection provided by tending ants. First instar lady beetle larvae virtually always fed under gravid scales on eggs and crawlers. This behavior allowed them to escape detection by the ants. Second and third instar lady beetles also fed under scales when ants were present but shifted to feeding more in the open when ants were excluded. When attacked by aggressive ants, waxy tufts and glandular secretions provided protection for those larvae feeding in the open. However most larvae were simply ignored by scale-tending ants.

The last chapter summarizes the results of the previous chapters and examines the role Allegheny mound ants have in shaping the homopteran and predator communities in jack pine forests.

CHAPTER 2

Effect of Allegheny mound ant, *Formica exsectoides* (Formicidae), presence on homopteran and predator populations in Michigan jack pine forests

Introduction

The tending of honeydew producing Homoptera by ants can provide many benefits to the tended homopterans, including sanitary removal of excess honeydew (Strickland 1947, Majer 1982), increased growth rate (Banks & Nixon 1958), decreased development time (El-Ziady 1960, Bristow 1984), or even a transfer of parental care to the tending ants (Bristow 1983). The primary benefit though appears to be protection from predators and parasitoids (Way 1963, Buckley 1987, Bristow 1991), although this idea was not always accepted (Jones 1929). The positive effect tending ants have upon many honeydew-producing homopterans is well known to fruit tree growers. One method of control for aphid and scale infestations is the removal of ant nests from plantations; removal of nests can allow natural enemies to control successfully the homopterans (Flanders 1945, DeBach et al. 1951, Fleschner 1959, Bartlett 1961, Itioka 1994, Stechmann & Völkl 1996).

In non-agricultural and forest settings, the exclusion of tending ants can also result in an increase of natural enemies and a resulting decrease in homopteran density (Bradley & Hinks 1968, Bradley 1973, Tilles & Wood 1982, Bristow 1984, Nechols & Seibert 1985, Cushman & Whitham 1989, Buckley & Gullan 1991). The effectiveness of ant protection however appears to depend on the aggressiveness of the ants involved; more aggressive ants appear to provide better protection for the tended homopterans (Buckley & Gullan 1991).

While many studies indicate the effect mutualist ants can have on a single homopteran species, fewer studies indicate how ant mutualists can influence homopteran communities (Addicott 1986, Bronstein 1994a). In one example, the removal of two mutualist ants, *Dolichoderus taschenbergi* (Mayer) and *Formica obscuripes* Forel, resulted in the extinction of tended aphid species on jack pines near the destroyed ant nests (Bradley and Hinks 1968).

Many homopterans are not tended by ants; 75% of aphid species do not associate with ants (Bristow 1991). Ants will often prey upon non-tended homopterans (Skinner & Whittaker 1981, Mahdi & Whittaker 1993). This aggressive or predatory nature of ants can also negatively impact both the populations of individual species and community composition (Skinner and Whittaker 1981, Risch and Carroll 1982, Fowler and MacGarvin 1985, Warrington and Whittaker 1985 ab, Grant and Moran 1986, Campbell 1990, Ito and Higashi 1990, Mahdi & Whittaker 1993). By suppressing potential natural enemies and preying on non-tended homopterans, the presence of a large population of aggressive, mutualist ants could cause a shift in a homopteran community, from one dominated by non-tended species to one dominated by tended homopteran species.

In the jack pine (*Pinus banksiana* (L.)) forests of north-central Michigan, Allegheny mound ants, *Formica exsectoides* Forel, form large, locally abundant, but patchy populations (Bristow et al. 1992). These mound ants have been described as "the most common mound building ant in North America" (Andrews, 1926). Where established, they can become extremely numerous (Andrews 1925, Cory & Haviland 1938, Bristow et al. 1992) and dominate the ant fauna (Hölldobler and Wilson, 1990). McCook (1877) estimated 1700 mounds in a 50 acre area near Hollidaysburg, PA. This ant exhibits no colony boundaries (Hölldobler & Wilson, 1990), so trees can be patrolled by a large number of ants from different mounds. These ants are very aggressive, attacking and overpowering almost every arthropod they encounter, including honeydew-seeking yellow jackets (*Vespa* sp., pers. obs.). At the same time, they associate with several species of honeydew producing Homoptera (Cory & Haviland 1938, Haviland 1947, Dimmick 1951).

Preliminary observations documented differences in the homopteran community on jack pine saplings between areas with and without Allegheny mound ants. Two tended homopterans, the aphid *Cinara banksiana* Pepper & Tissot, and the pine tortoise scale, *Toumeyella parvicornis* (Cockerell) appeared to be very common in areas with mound ants but virtually absent from other areas. Conversely, the pine woolly aphid, *Schizolachnus piniradiatae* (Davidson) was more common in areas without mound ants.

To determine whether a pattern existed between the presence of *F. exsectoides*, aphid and scale species, and potential predators of homopterans, I conducted surveys on jack pine saplings at sites with high Allegheny mound ant densities (hereafter referred to as high-ant density), areas with low mound ant densities (low-ant density) areas that contained no mound ants (no-ants). This survey was conducted during the summer of 1993. In addition to the survey, I performed experiments in 1994 to determine the type of interaction occurring between *F. exsectoides* and the pine woolly aphid. Since other studies have addressed the positive role tending ants have for homoptera (Way 1963, Boucher et al. 1987, Chapter 3), no parallel experiments were conducted to determine the nature of the interaction between mound ants and tended homopterans. I report here the results of the survey and experiments involving pine woolly aphids.

Material and Methods

Survey

Replicate sites and plot selection

Three 30 x 30 m plots, based on Allegheny mound ant abundance, each replicated five times, were selected in the Huron-Manistee National forests of north-central Michigan. Each replicate site was within a 6 x 15 km area of southeast Crawford and southwest Oscoda counties (Figure 1, Table 1). This area has sandy soils, part of the Grayling-Rubicon soil association (MacDonald 1983). All replicate sites (hereafter sites) for plots were in jack pine stands and chosen to be as similar as possible in stand age, plant composition and soil moisture. In selecting sites, I first scouted jack pine forest areas with Allegheny mound ant populations. High-ant plots were then placed in areas where mounds were at a high density (mean mound density per plot ± SE: 15.4 ± 3.8), while low-ant plots were placed near the edges of mound distribution , areas where mound density was decreasing (mean mound density per plot ± SE: 3.8 ± 1.5). If possible, I also marked off a no-ant plot, not closer than 100 m to the nearest ant mound. Two of the no-ant plots were between 2 and 6 km from their paired ant-plots due to a change in stand age. All plot sites had 40-72 year old jack pine as the dominant tree, with blueberry (*Vaccinium angustifolium* Aiton), bracken fern (*Pteridium* sp.) and sweet-fern (*Compotonia peregrina* (L) Coulter) forming the majority of understory plants.

In each ant-density plot, all jack pine seedlings and saplings between 1.5 and 3 meters tall were identified and 15 of these trees were randomly selected. However, site 2 had only seven trees within this size range in the high-ant plot. For this site, all three ant-density plots had seven trees marked for the study. A total of 67 trees were marked for each of the ant-densities. The mean distance (± SE) from each marked tree to the nearest mound in the high-ant and low-ant density plots was 4.38 ± 0.29 m and 12.48 ± 0.73 m, respectively.

Census method and analysis

In order to reduce the time needed to examine 201 trees, a half side of each tree was randomly chosen. I conducted a census of the same side every two weeks, beginning the week of June 8, for a total of 5 sample periods. For each census period, an absolute sample (number of animals per unit habitat, i.e. 1/2 side of tree) was taken of aphids, scales, ants, and any predators. Representative specimens were collected for identification.

Homopteran and predator species having large enough numbers for statistical analysis were analyzed as a split-plot repeated measures ANOVA with ant densities (fixed effect) the among-site factor and census period (fixed effect) the within-site factor (SAS 1995, Zar 1996). Site (random effect) was nested within the ant densities treatment and used to test the ant density effect. Because my main question concerned how these arthropod populations varied between different ant-densities, I took the mean number of each arthropod species found on all the surveyed trees for each ant-density plot at each site and used this mean in the analysis. Data were tested for the main effect of ant-density on homopteran and predator numbers and the ant-density by census period interaction. Mean arthropod numbers were log-transformed to normalize error distributions. Untransformed data is presented in figures.

Since some homopteran and predator species did not appear until the third sampling date (July 8), earlier dates could not be used in the repeated measures since their variance on those dates was zero. An additional census date (September 6) was conducted one month later than the previous sampling date (August 5), and was not used in the repeated measures analysis. A Pearson correlation analysis was also conducted to test for correlation between different homopteran species. The correlation was tested on each sampling date when appropriate.

Woolly aphid experiments

To determine the types of interactions between the untended woolly aphid and Allegheny mound ants, I used the high-ant density areas at three of the survey sites (Sites 1, 4, and 5) to conduct ant-exclusion experiments and timed observations during 1994. I

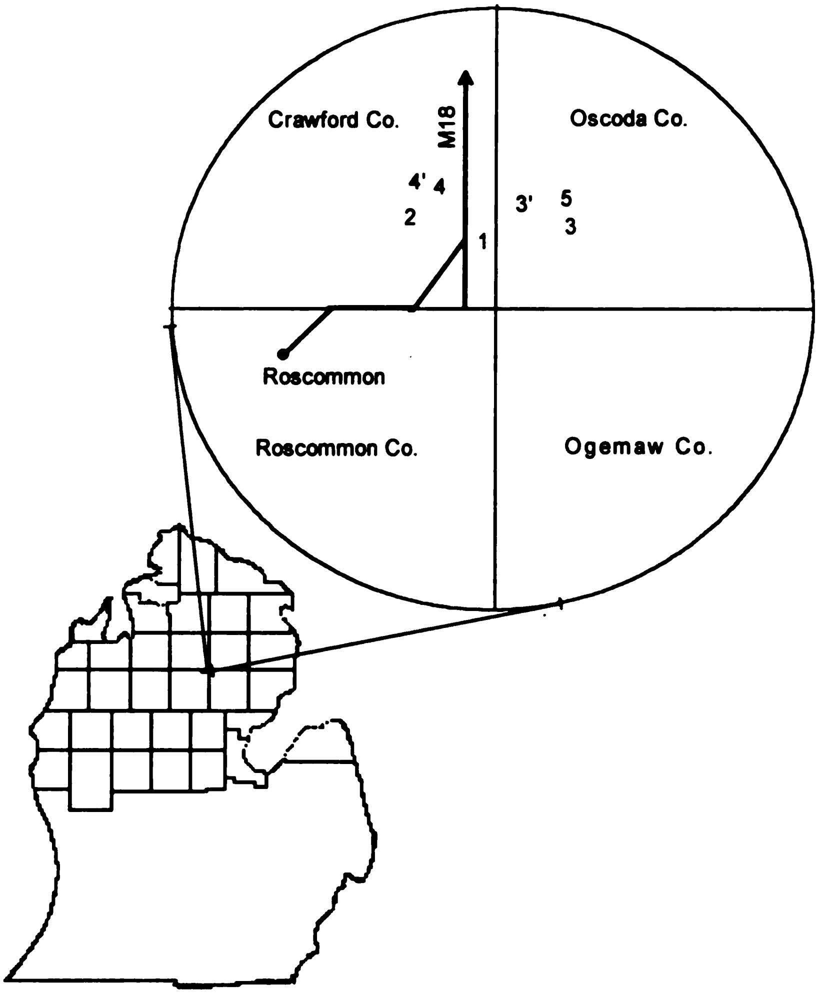


Figure 1. Map of northern Michigan counties. Inset shows replicate sites as numbers and their relative positions to each other and highway M 18. Sites 3' and 4' were no-Allegheny mound ant replicate sites paired with sites 3 and 4.

Table 1. Location of replicate sites and jack pine stand description.[a]

Site	Location[b]	Stand Size (ha)	Age (Years)	SI[c]	Stand Size Density
1	T. 25N. R. 1W. Sec 24	30.7	58	39	Poletimber, >70% stocked
2	T. 25N. R. 1W. Sec 4	29.1	72	49	Poletimber, 40% - 69% stocked
3	T. 25N. R. 1E. Sec 24	48.5	69	50	Poletimber, 40% - 69% stocked
3'*	T. 25N. R. 1E. Sec 8	8.9	61	49	Poletimber, 40% - 69% stocked
4	T. 25N. R. 1W. Sec 11	28.7	60	50	Poletimber, 40% - 69% stocked
4'*	T. 25N. R. 1W. Sec 3	14.9	43	39	Poletimber, 40% - 69% stocked
5	T. 25N. R. 1E. Sec 13	64.7	43	48	Seedling-Sapling, >70% stocked
5[d]	T. 25N. R. 2E. Sec 19	59.1	42	40	Seedling-Sapling, 40% - 69% stocked

a. Based on Huron-Manistee National Forests database inventory. USDA Forest Service Mio, Michigan.

b. 1W sites located in Crawford Co., 1E sites located in Oscoda Co.

c. Site Index: height of dominate and co-dominate trees at 50 years.

d. The no-ant plot for site 5 was located in the adjacent section to the high and low-ant density plots.

* No-Allegheny mound ant sites. Site 3' was approximately 6 km from site 3, and site 4' was approximately 2 km from site 4.

randomly selected 10 trees that had colonies of *C. banksiana* with tending ants on at least two branches at each site. One branch was randomly selected and all ants were removed. A 4 cm band of Tanglefoot® was applied around the base of this branch to exclude ants, and any branches touching this branch were clipped back. The second branch was left as an untreated control. Each branch had three *S. piniradiatae* placed on the tip of the branch, away from the *C. banksiana* colony. For branches with ants, data were gathered on the interactions between woolly aphids and ants for 15 minutes. After 72 h, the numbers of woolly aphids remaining on branches were recorded.

C. banksiana aphids were also placed on other branches with *C. banksiana* colonies and ants as a comparison to the woolly aphids. Newly placed *C. banksiana* aphids were observed for 15 minutes, but since they mixed in with the other aphids I could not assess their survival 72 h later.

A survival analysis was conducted comparing the survival times (time till removal by ants) of woolly aphids to *C. banksiana* for the 15 min. observations. A split-plot ANOVA, with ant treatment (ants present or excluded) and site as fixed effects, was used to test for a difference in the percent change ([woolly aphid number at 72 h - woolly aphid number at start] / woolly aphid number at start) in woolly aphid numbers after 72 h between the two ant treatments. Trees (random effect) were nested within site and used to test the ant treatment effect. All analyses for both the survey and woolly aphid experiments were conducted using the JMP® statistical package (SAS 1995).

Results

Survey

Arthropod diversity fluctuated over the course of the summer and between plots with different ant densities; the greatest diversity occurred in late July and early August in the high-ant density plots (Table 2). In high-ant plots, the overall mean Allegheny mound ant activity (ants encountered on sample side of tree) during the five, two-week census periods was 6.2 ± 1.2 (± SE), and the mean activity in low-ant plots was 2.8 ± 1.1 (± SE) (Figure 2). Other ant species were an order of magnitude less abundant as *F. exsectoides*, even in non-mound ant areas (overall mean ± SE: 0.2 ± 0.04; 0.7 ± 0.14; 0.5 ± 0.15; for high, low and no-*F. exsectoides* areas respectively).

Aphids

I found five aphid species feeding on jack pine during this survey (Table 2). Four were in the genus *Cinara*, three of which were numerous enough to use in statistical comparisons, *C. ontarioensis* Bradley, *C. pergandei* (Wilson), and *C. banksiana*. The other *Cinara* aphid was not identified to species. The 5th aphid species was the woolly aphid, *S. piniradiatae*.

The most common aphid present in high ant areas was *C. banksiana* (Figure 3a). It first was found on second and third year growth very early in the season, but moved to new shoots when they began to elongate. By late-season most aphids moved back to older growth. This aphid was found in all the high-ant plots and four of the low-ant plots (Table 2). *C. banksiana* numbers were significantly larger in high-ant plots than no-ant plots (Table 3). The interaction between census date and ant-density was also significant, indicating an increasing difference in *C. banksiana* numbers between high and no-ant plots (Table 3). *C. banksiana* numbers did not significantly differ for any of the other ant-density comparisons (Table 3).

The second most common aphid in high-ant areas was *C. ontarioensis* (Figure 3b). This is apparently the first record for this species in Michigan (Voegtlin and Bridges 1988). It feeds on needles and their fascicles, causing needle yellowing and senescence. Population numbers increased later in the season than *C. banksiana,* but *C. ontarioensis* never reached the numbers *C. banksiana* attained. Also unlike *C. banksiana*, this aphid had a very patchy distribution both within plots and among plots (Table 2). *C. ontarioensis* numbers did not significantly differ between any of the ant-density plots (Table 4).

The third most abundant aphid in high-ant areas was *C. pergandei* (Figure 4a). This was a large solitary aphid that appeared to be facultatively tended by *F. exsectoides*. This aphid was not abundant, although it was found in all three ant density plots at all sites (Table 2). *C. pergandei* numbers in low-ant density plots were significantly larger than in both the high-ant density and no-ant plots (Table 5), but there was no significant interaction between census date and ant-densities. No significant difference in *C. pergandei* numbers was detected between the high-ant and no-ant density plots.

The last aphid common enough for statistical tests was the pine woolly aphid, *S. piniradiatae*. Woolly aphid populations increased late in the season and were found primarily in non-ant plots (Figure 4b). Population size was significantly larger in no-ant plots compared to the high-ant density plots (Table 6) and this difference increased

Table 2. Number of local populations (i.e. total number of trees with populations) and individuals found on 67 jack pine trees in a 30 X 30 m plot. First numbers are local populations, numbers in parentheses are total individual numbers.

	Early June			Late June		
Populations	High	Low	No	High	Low	No
Aphididae						
Cinara banksiana	13 (247)	3 (160)	1 (15)	30 (1080)	7 (104)	1 (52)
C. ontarioensis	4 (6)	0	0	3 (22)	2 (83)	1 (1)
C. pergandei	3 (6)	7 (8)	5 (9)	5 (9)	17 (26)	5 (9)
Cinara sp. 4	4 (11)	3 (8)	0	1 (1)	0	1 (1)
Schizolachnus piniradiatae	0	0	0	0	0	1 (1)
Coccidae						
Toumeyella parvicornis	13 (153)	8 (13)	4 (22)	16 (121)	5 (7)	4 (20)
Scale sp. 2	3 (4)	2 (3)	2 (2)	3 (3)	5 (5)	2 (2)
Cercopidae						
Aphrophora parallela	0	14 (22)	19 (34)	1 (1)	17 (36)	19 (43)
Miridae	0	0	0	0	0	0
Salticidae	5 (6)	7 (11)	11 (14)	3 (4)	14 (17)	11 (13)
Lacewings	1 (1)	0	3 (3)	0	0	0
Scale parasitoids	0	0	0	0	0	0
Aphid parasitoids	1 (3)	1 (1)	3 (3)	3 (3)	1 (1)	7 (8)
Coccinellidae	0	4 (5)	6 (12)	0	1 (1)	1 (1)
Syrphidae	1 (1)	0	0	0	0	0
Cantheridae	0	0	0	0	0	0
Web spiders	18 (31)	20 (27)	26 (33)	13 (17)	10 (17)	14 (17)
Thomisidae	0	0	0	3 (3)	0	2 (2)

Table 2. cont. Number of local populations (i.e. number of trees with populations) and individuals found on 67 jack pine trees in a 30 X 30 m plot. First numbers are local populations, numbers in parentheses are total individual numbers.

	Early July			Late July			Early August		
Populations	High	Low	No	High	Low	No	High	Low	No
Aphididae									
Cinara banksiana	34 (1128)	9 (156)	1 (3)	26 (1185)	6 (280)	1 (3)	13 (578)	5 (547)	2 (8)
C. ontarioensis	12 (86)	3 (161)	1 (1)	16 (130)	3 (328)	1 (1)	15 (477)	1 (450)	0
C. pergandei	8 (10)	9 (28)	8 (7)	2 (5)	7 (13)	6 (7)	2 (2)	8 (13)	6 (13)
Cinara sp. 4	1 (10)	0	1 (1)	0	0	0	1 (20)	0	0
Schizolachnus piniradiatae	0	1 (15)	0	2 (13)	10 (72)	14 (50)	5 (17)	17 (92)	36 (367)
Coccidae									
Toumeyella parvicornis	10 (1467)	4 (178)	2 (152)	11 (2026)	6 (54)	2 (58)	14 (1496)	5 (245)	0
Scale sp. 2	2 (2)	2 (2)	1 (1)	0	0	0	0	0	0
Cercopidae									
Aphrophora parallela	0	8 (11)	14 (29)	0	1 (1)	6 (7)	1 (1)	0	0
Miridae	7 (10)	1 (1)	5 (9)	23 (32)	7 (14)	5 (11)	20 (35)	15 (17)	6 (10)
Salticidae	13 (17)	18 (23)	25 (29)	12 (15)	20 (27)	17 (27)	9 (9)	21 (25)	13 (19)
Lacewings	0	0	2 (5)	2 (9)	3 (8)	13 (56)	4 (19)	11 (42)	23 (124)
Scale parasitoids	1 (16)	1 (1)	0	5 (21)	1 (1)	0	0	0	0
Aphid parasitoids	2 (2)	6 (6)	5 (8)	3 (4)	2 (2)	1 (1)	3 (8)	3 (3)	3 (3)
Coccinellidae	0	2 (2)	4 (11)	1 (1)	0	6 (6)	0	3 (3)	2 (2)
Syrphidae	0	0	0	0	0	0	2 (2)	0	1 (1)
Cantheridae	0	0	0	2 (4)	2 (2)	1 (1)	1 (1)	0	2 (3)
Web spiders	8 (8)	13 (17)	13 (16)	8 (12)	10 (12)	15 (19)	15 (17)	12 (16)	15 (20)
Thomisidae	3 (3)	2 (2)	4 (5)	2 (2)	2 (2)	4 (4)	1 (1)	2 (2)	4 (4)

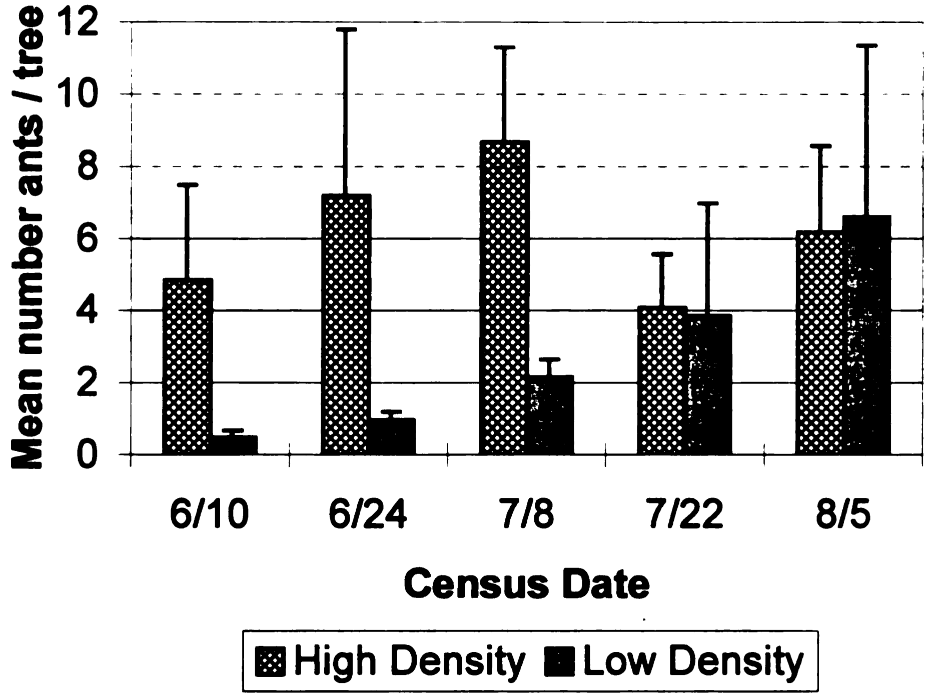
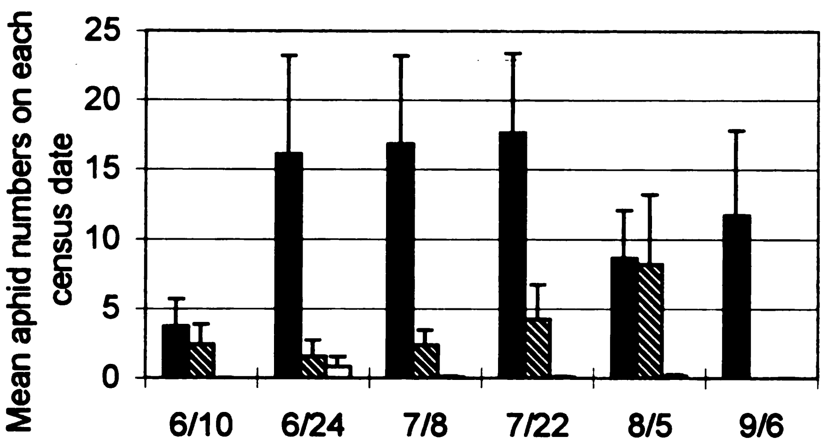


Figure 2. Mean (± SE) number of Allegheny mound ants found per half side of each sampled tree in high-ant areas and low-ant areas. n = 67 trees.

a) *C. banksiana*



b) *C. ontarioensis*

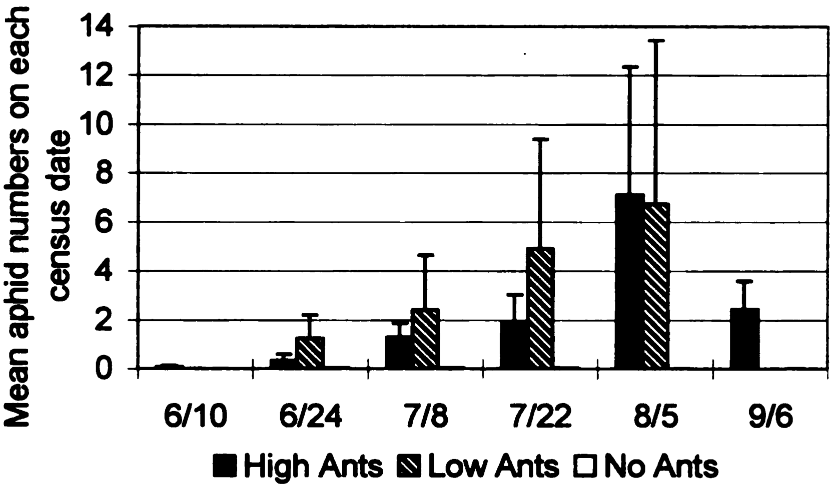


Figure 3. Population trends in high- low- and no- mound ant density plots across six census dates for a) *C. banksiana* and b) *C. pergandei*. Sixty-seven half sides of trees were sampled in 5 plots for each ant density. No data were collected for low-ant density plots on Sept. 6. Bars represent mean aphid numbers per tree (± SE). Note, Y axis is different for each species.

Table 3. Repeated measures ANOVA (five census dates) on log-transformed *Cinara banksiana* populations as a function of ant-density (high, low, or no-ants), replicated at five sites.

		Ant densities					
		High vs no ant		High vs low ant		Low vs no ant	
Source	df	MS	F	MS	F	MS	F
Ant density	1	7.08	16.37**	2.87	4.69†	0.94	3.94†
Error a[a]	8	0.43		0.61		0.24	
Date	4	0.25	4.69**	0.33	2.54†	0.01	0.07
Date x ants	4	0.3	5.69**	0.21	1.64	0.04	0.34
Error b[b]	32	0.05		0.13		0.11	

† $P \leq 0.1$; *$P \leq 0.05$; **$P \leq 0.01$

a Site (Ant density) used to test Ant density effect.

b Residual error: used to test Date and Date x Ant density effects.

Table 4. Repeated measures ANOVA (five census dates) on log-transformed *Cinara ontarioensis* populations as a function of ant-density (high, low, or no-ants), replicated at five sites.

		Ant densities					
		High vs no ant		High vs low ant		Low vs no ant	
Source	df	MS	F	MS	F	MS	F
Ant density	1	0.54	2.31	<0.001	0.98	0.5	1.17
Error a[a]	8	0.23		0.66		0.43	
Date	4	0.06	2.38†	0.19	0.03	0.04	1.09
Date x ants	4	0.06	2.39†	0.02	0.91	0.04	1.04
Error b[b]	32	0.03		0.06		0.04	

† $P \leq 0.1$; *$P \leq 0.05$; **$P \leq 0.01$

a Site (Ant density) used to test Ant density effect.

b Residual error: used to test Date and Date x Ant density effects.

Table 5. Repeated measures ANOVA (five census dates) on log-transformed *Cinara pergandei* populations as a function of ant-density (high, low, or no-ants), replicated at five sites.

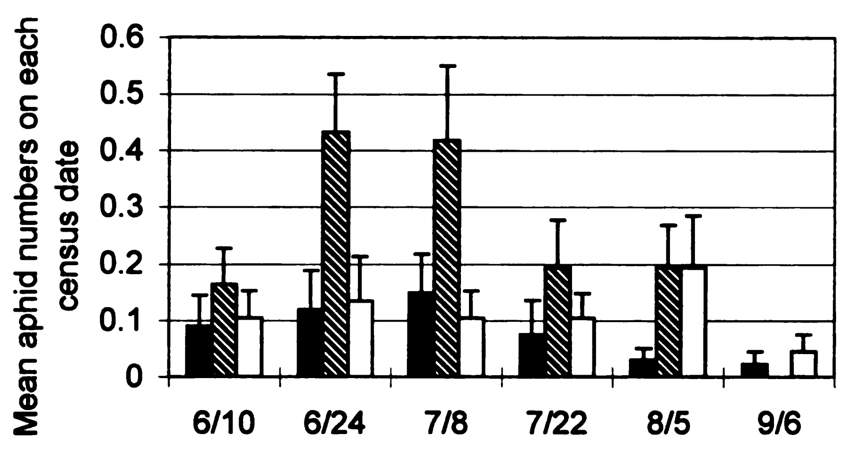
		Ant densities					
		High vs no ant		High vs low ant		Low vs no ant	
Source	df	MS	F	MS	F	MS	F
Ant density	1	0	0.71	0.05	15.42**	0.03	6.39*
Error a[a]	8	0.01		0		0	
Date	4	0	0.45	0.01	1.57	0.01	0.95
Date x ants	4	0	0.39	0	0.53	0	0.75
Error b[b]	32	0		0.01		0.01	

† $P \leq 0.1$; *$P \leq 0.05$; **$P \leq 0.01$

a Site (Ant density) used to test Ant density effect.

b Residual error: used to test Date and Date x Ant density effects.

a) *C. pergandei*



b) *S. piniradiatae*

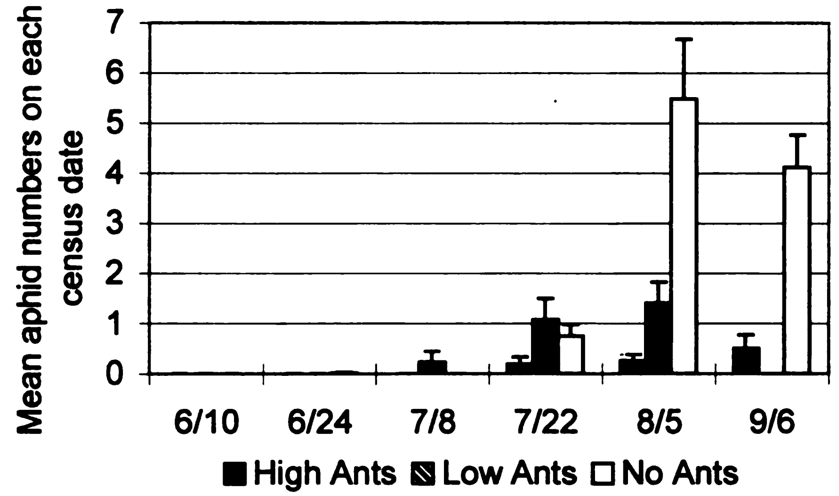


Figure 4. Population trends in high- low- and no- mound ant density plots across six census dates for a) *C. pergandei* and b) *S. ontarioensis*. Sixty-seven half sides of trees were sampled in 5 plots for each ant density. No data were collected for low-ant density plots on Sept. 6. Bars represent mean aphid numbers per tree (± SE). Note, Y axis is different for each species.

Table 6. Repeated measures ANOVA (five census dates) on log-transformed *Schizolachnus piniradiatae* populations as a function of ant-density (high, low, or no-ants), replicated at five sites.

		Ant densities					
		High vs no ant		High vs low ant		Low vs no ant	
Source	df	MS	F	MS	F	MS	F
Ant density	1	0.25	9.13*	0.12	8.22*	0.02	0.59
Error a[a]	8	0.04		0.03		0.04	
Date	2	0.33	9.24**	0.08	4.16*	0.49	12.71**
Date x ants	2	0.22	6.04**	0.02	1.19	0.08	2.09
Error b[b]	16	0.04		0.02		0.04	

† $P \leq 0.1$; *$P \leq 0.05$; **$P \leq 0.01$

a Site (Ant density) used to test Ant density effect.

b Residual error: used to test Date and Date x Ant density effects.

significantly over the five census periods (Table 6). Woolly aphid numbers also differed significantly between the high-ant and low-ant density plots (Table 6), although this difference did not significantly increase over the five census dates (Table 6). No difference in woolly aphid numbers was detected between the low-ant density and no-ant plots (Table 6).

Scales

Toumeyella parvicornis (Cockerell), the pine tortoise scale, was the primary scale involved with ants and was predominately found in the high-ant density plots (Figure 5). Crawlers were released in late June and early July, causing scale numbers to increase greatly in high-ant density plots, and to a lesser extent in the low-ant density and no-ant plots (Figure 5). Ant numbers on trees with scales tended to fluctuate during and after crawler release, whereas in comparison ant numbers remained relatively stable for *C. banksiana* (Figure 6).

Scale numbers were significantly greater in high-ant density plots than in no-ant plots (Table 7); the interaction between census period and ant-density indicated that this difference increased over time (Table 7). No other significant differences in scale numbers were detected between other ant-density comparisons (Table 7).

No significant correlation was detected between any of the homopteran populations.

Predators

Three principle aphid predators were encountered and analyzed in this survey, lacewings, salticid spiders and mirids. Predator ratios differed between high-ant and no-ant plots with mirids being replaced as the more common predator by lacewing larvae in no-ant plots (Figure 7). Lacewings were significantly more common in the no-ant plots than in the high-ant density plots (Table 8) and this difference became greater over the five census periods (Table 8). No other comparisons between ant-density plots were significantly different (Table 8).

Mirid populations were composed of at least two species, *Pilophorus urhlei* Knight and *P. furvus* Knight. These were the only predators I detected that appeared to be more common in the high-ant density plots than in other plots (Figure 7), although none of the ant-density comparisons were significant at the 0.05 level (Table 9).

Salticid spiders were the only predator present at all three ant-densities throughout the summer (Figure 7). On two occasions I witnessed salticid spiders feeding in small, aphid colonies. In both cases, the aphid colony disappeared within 3 d. Salticid numbers were significantly lower in high-ant density plots than in both the low-ant density and no-ant plots (Table 10). The interaction between census dates and ant-density treatments were not significant in either case, indicating that these differences did not increase over time (Table 10).

Woolly aphid experiments.

Observations indicated that, when encountered by ants, woolly aphids were more likely to be attacked and carried off than newly placed *C. banksiana*. Whereas 10% of *C. banksiana* were removed by ants after 15 minutes, 10% of the woolly aphids were removed by 2 1/2 minutes and 24% by 15 minutes (= 5.36, df = 1, p = 0.02; Figure 8). Virtually every woolly aphid that was encountered by an ant (21 of 26 encounters) was

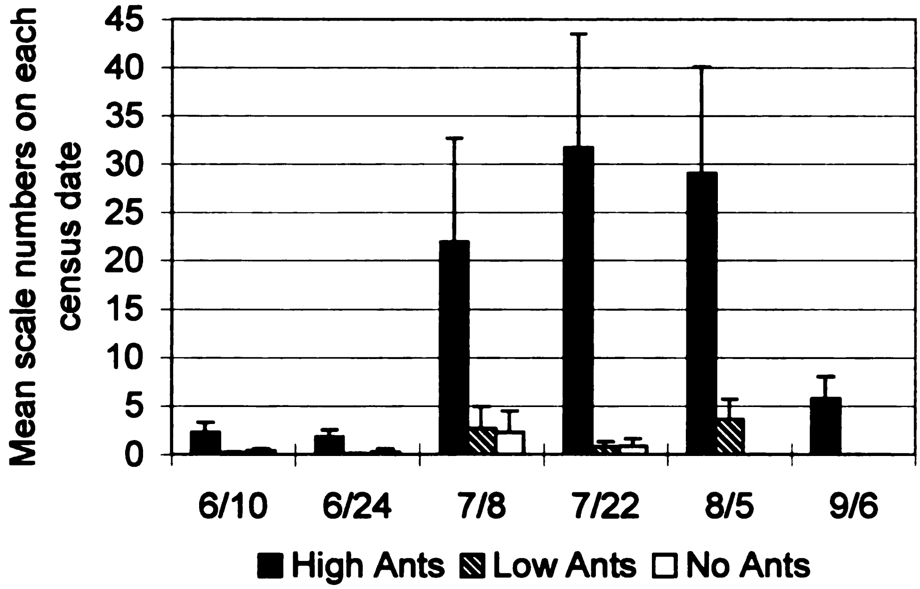


Figure 5. Population trends in high- low- and no- mound ant density plots across six census dates for *T. parvicornis*. Sixty-seven half sides of trees were sampled in 5 plots for each ant density. No data were collected for low-ant density plots on Sept. 6. Bars represent mean scale numbers per tree (± SE).

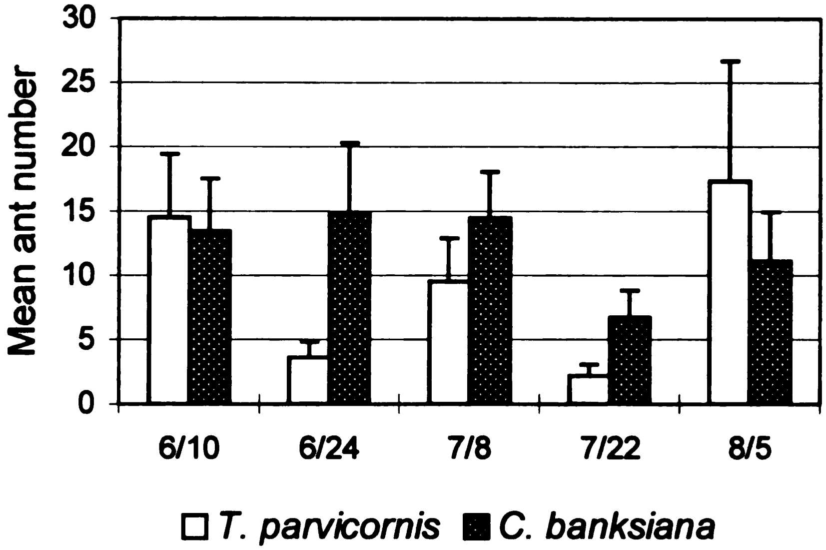


Figure 6. Ants found on half-side of 67 trees that had either *T. parvicornis* colonies or *C. banksiana* colonies but not both. Bars represent mean ant number per tree (± SE).

Table 7. Repeated measures ANOVA (five census dates) on log-transformed *Toumeyella parvicornis* populations as a function of ant-density (high, low, or no-ants), replicated at five sites.

		Ant densities					
		High vs no ant		High vs low ant		Low vs no ant	
Source	df	MS	F	MS	F	MS	F
Ant density	1	5.44	7.37*	4.09	4.87†	0.1	0.39
Error a[a]	8	0.74		0.84		0.25	
Date	4	0.45	6.23**	0.71	7.18**	0.06	0.83
Date x ants	4	0.37	5.21**	0.2	2.03	0.1	1.28
Error b[b]	32	0.07		0.1		0.08	

† $P \leq 0.1$; *$P \leq 0.05$; **$P \leq 0.01$

a Site (Ant density) used to test Ant density effect.

b Residual error: used to test Date and Date x Ant density effects.

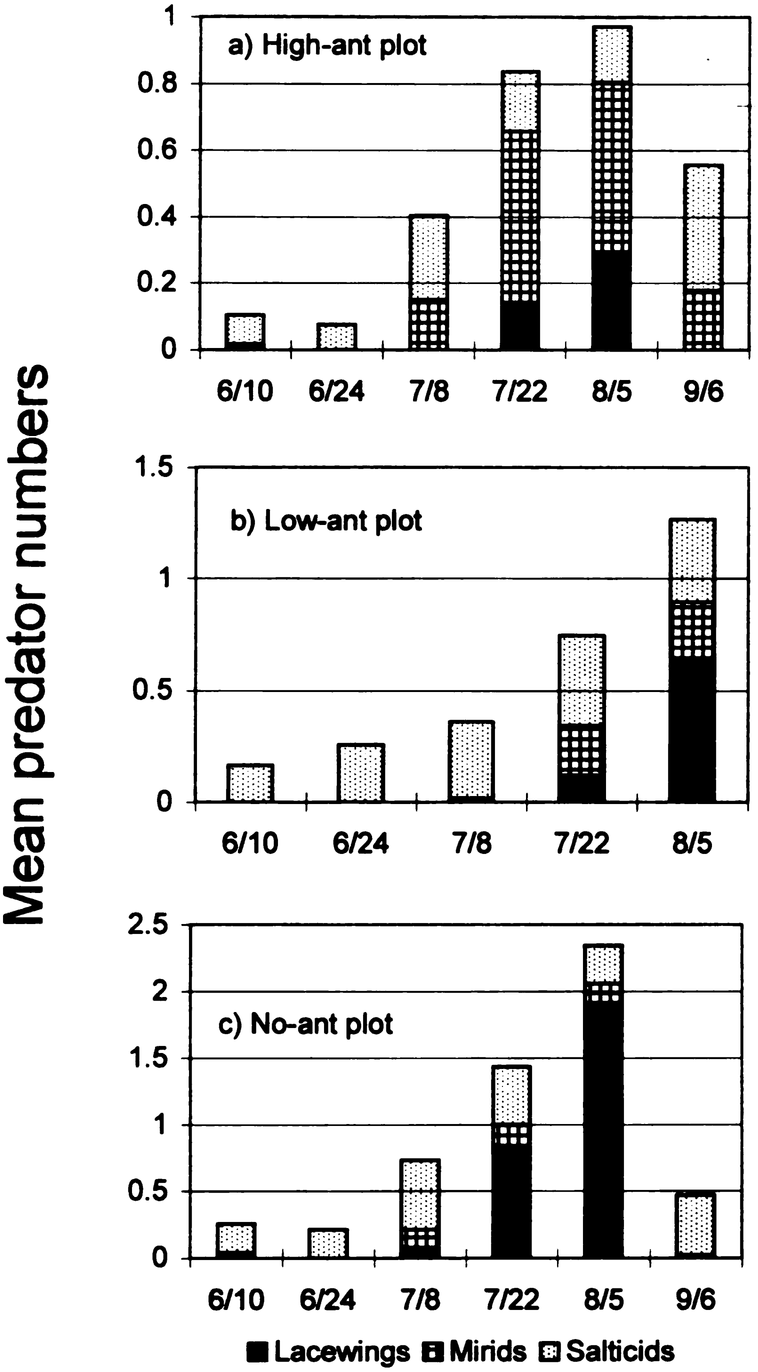


Figure 7. Population trends in high- low- and no- mound ant density plots across six census dates for the three commonest predators observed. Sixty-seven half sides of trees were sampled in 5 plots for each ant density. No data were collected for low-ant density plots on Sept. 6. Bars represent mean predator numbers per tree. Note, Y axis is different for each ant-density.

Table 8. Repeated measures ANOVA (five census dates) on log-transformed lacewing populations as a function of ant-density (high, low, or no-ants), replicated at five sites.

		Ant densities					
		High vs no ant		High vs low ant		Low vs no ant	
Source	df	MS	F	MS	F	MS	F
Ant density	1	0.11	5.91*	0	0.51	0.08	3.83†
Error a[a]	8	0.02		0.01		0.02	
Date	4	0.13	9.94**	0.05	8.61**	0.17	13.06**
Date x ants	4	0.04	2.89*	0	0.71	0.02	1.44
Error b[b]	32	0.01		0.01		0.01	

† $P \leq 0.1$; *$P \leq 0.05$; **$P \leq 0.01$

a Site (Ant density) used to test Ant density effect.

b Residual error: used to test Date and Date x Ant density effects.

Table 9. Repeated measures ANOVA (five census dates) on log-transformed mirid populations as a function of ant-density (high, low, or no-ants), replicated at five sites.

		Ant densities					
		High vs no ant		High vs low ant		Low vs no ant	
Source	df	MS	F	MS	F	MS	F
Ant density	1	0.04	4.38†	0.03	3.49†	0	0.72
Error a[a]	8	0.01		0.01		0	
Date	2	0.01	2.01	0.03	5.19*	0.01	0.18
Date x ants	2	0.01	1.49	0	0.35	0.01	0.24
Error b[b]	16	0.01		0.01		0	

† $P \leq 0.1$; *$P \leq 0.05$; **$P \leq 0.01$

a Site (Ant density) used to test Ant density effect.

b Residual error: used to test Date and Date x Ant density effects.

Table 10. Repeated measures ANOVA (five census dates) on log-transformed salticid populations as a function of ant-density (high, low, or no-ants), replicated at five sites.

		Ant densities					
		High vs no ant		High vs low ant		Low vs no ant	
Source	df	MS	F	MS	F	MS	F
Ant density	1	0.04	11.27**	0.04	7.12*	<0.001	0.03
Error a[a]	8	0		0.01		0	
Date	4	0.01	2.46†	0.01	2.89*	0.02	3.14*
Date x ants	4	0	0.21	0	0.39	0	0.41
Error b[b]	32	0.01		0		0.01	

† $P \leq 0.1$; *$P \leq 0.05$; **$P \leq 0.01$

a Site (Ant density) used to test Ant density effect.

b Residual error: used to test Date and Date x Ant density effects.

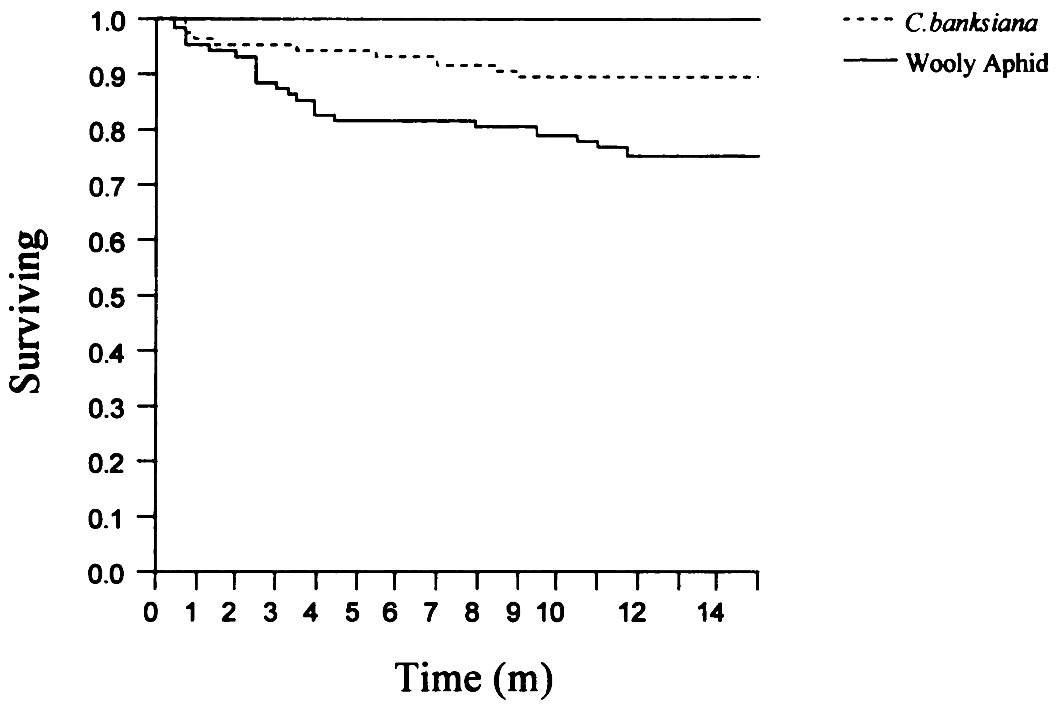


Figure 8. Percentage remaining of woolly aphids and *C. banksiana* for 15 minutes when placed on ant-patrolled jack pine shoot tips.

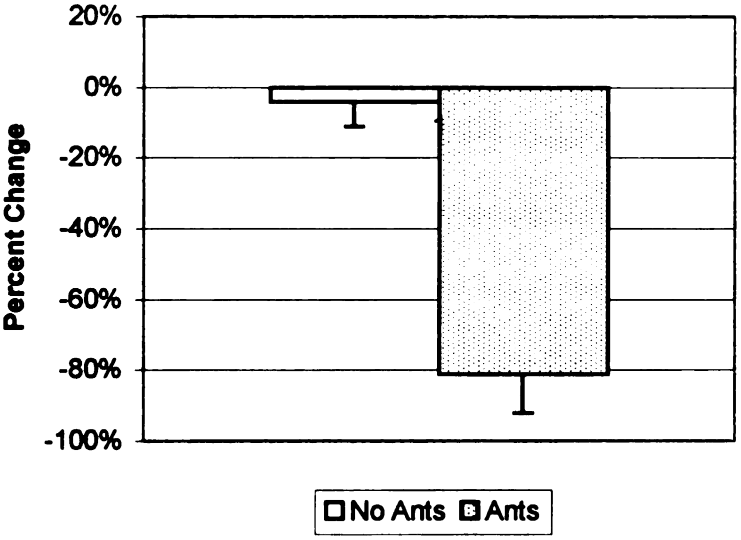


Figure 9. Percent change in woolly aphid numbers after 72 hours on ant patrolled and ant-excluded branches.

attacked and removed by the attacking ant. This compared to only 9 of 63 *C. banksiana* removed by ants after an encounter. Only one woolly aphid was attacked and released by the ant. During this 15 min observation, most woolly aphids were not encountered and removed by ants (Figure 8). These aphids climbed up adjacent needles and remained undetected by ants during the observation.

However, after 72 h woolly aphid number decreased significantly more when ants were present ($F_{1,27}$= 36.60; $P << 0.001$; Figure 9); woolly aphids on branches with ants declined by 81% ± 0.07 (mean ± SE) compared to a decline of only 4% ± 0.11 (mean ±SE) for woolly aphids on branches without ants.

Discussion

The results of this study indicated that a shift occurred in the homopteran community on jack pine saplings, apparently due in part to both the presence and density of *F. exsectoides*. Ant-tended homopterans were the most abundant homopterans in high-Allegheny mound ant density areas, but were gradually replaced by the non-tended pine woolly aphid as *F. exsectoides* density declined to zero. This distribution would be expected if tended homopterans were dependent on ants for certain benefits.

An alternative hypothesis is that Allegheny mound ants were tracking the honeydew producing Homoptera. I reject this hypothesis since *F. exsectoides* colonies are stationary in large mounds, that remain year after year (Andrews 1926, Bristow et. al 1992), even when aphid populations were reduced by late frosts (pers. obs.). Other studies (Chapter 3) have shown that the exclusion of *F. exsectoides* from tended aphid colonies resulted in the disappearance of the aphid colonies. Additionally, Bradley and Hinks (1968) found that while aphids disappeared when *F. obscuripes* mounds were destroyed, the ants survived the destruction of aphid colonies, extending their foraging trails two to three times farther than previous. They suggested that aphids must wait for *F. obscuripes* to colonize new areas prior to aphid populations building up in those areas. I hypothesize the same may be true for *F. exsectoides* and these tended homopterans. In this jack pine ecosystem, it appeared that the small populations of other species of ants would not be able to support such large populations of tended homopterans were *F. exsectoides* removed.

This survey indicated that there appears to be a difference in the way different ant-tended homopterans responded to *F. exsectoides* densities. *C. banksiana* was more abundant in the high-ant density areas than the no-ant areas, but its population size was similar between the low and no-ant areas. A similar pattern was detected for *T. parvicornis*. This suggests that both of these homopterans may need a critical density of *F. exsectoides* for their populations to become large. A larger population of ants should find newly settled homopterans more quickly, insuring their survival (Addicott 1978).

A different pattern was detected for *C. pergandei*. It appeared to do best in areas with low Allegheny mound ant densities. Bradley and Hinks (1968) also detected a similar pattern for this aphid; it was found in the largest numbers on the edges of ant areas (my low-ant areas) for most of the summer. This aphid may be exploiting a niche where other, more obligately tended homopterans don't do as well, and where predator numbers are still more reduced than in the non-ant areas. A direct competitive exclusion effect between tended homopterans and *C. pergandei* may also be occurring in areas with high mound ant densities.

While *C. ontarioensis* was predominately found in the high-ant density areas, its population sizes did not significantly differ between any of the ant-density areas. This may have been due in part to its very patchy distribution both within and between sites. A similar, patchy distribution was also detected by Bradley and Hinks (1968) for this aphid.

The pine woolly aphid showed a pattern opposite *C. banksiana* and *T. parvicornis*. It appeared to be sensitive to high populations of *F. exsectoides*, but could tolerate the lower ant-densities found on the edges of ant areas. Allegheny mound ants were constantly patrolling shoots of trees and would move onto needles apparently to collect fallen honeydew. The large number of ants would insure that many alate woolly aphids (or their offspring) that settled in ant areas would be found and removed.

The decrease observed in late July of ant numbers on trees with only scales may be a reponse of the ants in part to the biology of pine tortoise scales. Rabkin & Lejeune (1954) report that female pine tortoise scales don't begin producing honeydew until after mating, 2-3 weeks after the crawler stage. This decline in honeydew production for these few weeks could result in the abandoning of scales by ants, exposing scales to their natural enemies.

The lower population sizes of tended homopteran in the non-ant areas was probably partly due to the larger populations of predators, in particular generalist predators. Like the homopterans, predators appeared to differ in their sensitivity to ant-densities and in their response to ants. Lacewing populations were significantly larger in the non-ant areas than in high-ant areas and were marginally significantly larger than in the low-ant areas. This may indicate that even low numbers of *F. exsectoides* can be successful at reducing lacewing populations, as has been shown with other predators (Rosenheim et al 1993). Slow moving lacewing larvae were easily caught by *F. exsectoides* workers (Appendix 3).

Unlike lacewings, salticid spiders appeared to tolerate low Allegheny mound ant densities, but were negatively impacted by the higher ant-densities. This may be due in part to exploitative competition for prey by *F. exsectoides* rather than the spiders being captured by ants since their good eyesight and speed should allow them to avoid capture.

While none of the population sizes of mirids differed between any ant-density areas, the high and no-ant density plots had a marginal significant difference ($P = 0.07$). A larger sample size may have indicated that unlike lacewings and salticids, mirids could benefit from the larger populations of aphids supported by tending Allegheny mound ants. Various mirid species that feed on aphids, including *P. furvus* and *P. uhrlei*, have been reported to associate with ant-tended aphid colonies (Bradley & Hinks 1968, Wheeler 1991). This association may be due to a larger population of aphids present in the ant areas (Wheeler 1991), whereas the non-ant areas had small, sporadic aphid populations that did not increase until late in the season. Mirids were observed close to aphid colonies, rushing in when ants were not present, and piercing an aphid and feeding until an ant appeared. Mirids would run up needles or shoots to escape any ants that got too close (~ 3 cm).

In conclusion, the low numbers of other ant species suggests that where established, *F. exsectoides* may play a keystone role as a mutualist-predator for homopterans and their natural enemies in jack pine forests. Those homopterans that have a mutualistic relation with Allegheny mound ants appeared to benefit from its large numbers and aggressiveness. As a predator, *F. exsectoides* preyed on both non-mutualist homopterans and homopteran predators such as lacewings. But other predators may benefit from its tending of homopterans. I speculate that the presence of the Allegheny mound ant shifts the composition of the Homoptera community from one dominated by non-tended homopterans and generalist predators to one dominated by ant-tended homopterans and specialist predators. These results, along with others (e.g. Bradley and Hinks 1968, Skinner and Whittaker 1981, Warrington and Whittaker 1985ab, Campbell 1990, Mahdi & Whittaker 1993) imply that large populations of aggressive mound or wood ants play important roles in shaping both herbivore and predator communities in forest systems.

CHAPTER 3

Differential response of specialist predators to ant-generated enemy-free space for mutualist homopterans

Introduction

In their model for the organization of terrestrial communities, Hairston et al. (1960) proposed that predators suppress herbivore populations below their carrying capacity, allowing plant populations to increase to the point where competition for space or nutrients becomes the limiting factor. This is an example of a three-tiered trophic cascade (Paine, 1980; Carpenter et. al., 1985): the top level (predators) has a positive effect on the lowest level (producers) by suppressing the intervening level (the primary consumers or herbivores). This model was expanded to four trophic levels by including populations of second level (secondary) predators that prey upon first level (primary) predators (Fretwell, 1977; 1987). This relationship, known as intraguild predation (Polis & Myers, 1989), could cause a shift in the trophic cascade, now allowing herbivore populations to increase (Power et. al., 1992; Rosenheim et. al., 1993; Spiller and Schoener, 1994). Thus, suppression of primary predators by secondary predators could provide enemy-free space (*sensu* Jeffries & Lawton, 1984) for herbivores.

Species that co-exist and survive in a community, by definition, have found sufficient enemy-free niche space to support their populations (Jeffries & Lawton, 1984). Competition for enemy-free space has been proposed to be more important in shaping communities than competition for food (Price et al., 1980; Jeffries and Lawton, 1984). However, few studies have actually evaluated the existence and importance of enemy-free space (Berdegue et al., 1996).

Keystone mutualists (Gilbert, 1980) affect multiple species in a manner analogous to keystone predators (Paine, 1966). Many ant species form mutualisms with honeydew-producing homopterans (Way, 1963; Buckley, 1987). The homopterans may receive various benefits including sanitary removal of honeydew (Strickland, 1947; Majer, 1982), a decrease in development time of tended homopterans (Bristow, 1984); and, of primary importance, protection from natural enemies (Bach, 1991; Tilles & Wood, 1982). The ants in return have access to a defensible and renewable food source (Carroll & Janzen, 1973). Such ant-hompteran systems could be used to test the importance of enemy-free space provided by ants for tended homopterans.

In the jack pine (*Pinus banksiana* (L.)) forests of north-central Michigan, Allegheny mound ants, *Formica exsectoides* Forel, form large, locally abundant but patchy populations (Bristow et al. 1992). These ants tend honeydew-producing Homoptera and will aggressively attack other arthropods, including the homopteran's predators, potentially providing enemy-free space. Two tended homopterans, the pine tortoise scale, *Toumeyella parvicornis* (Cockerell), and the aphid, *Cinara banksiana* Pepper and Tissot, were found almost exclusively in areas with the mound ant, and were virtually absent from areas without mound ants (Chapter 2). Predators preying upon *C. banksiana* were *Pilophorus* spp. (Heteroptera: Miridae) and larvae of an unidentified lacewing, while the pine tortoise scale was attacked by the specialist predator, lady beetle *Hyperaspis binotata* (Say). I postulate that mound ants provide enemy-free space for these homopterans by preying upon or interfering with their predators.

I tested three predictions (based on Berdegue et al., 1996) that must be accepted if ant-provided enemy-free space is of primary importance in affecting these aphid and scale populations: (1) Homopteran fitness should be lower in the presence of natural enemies without ants than homopteran fitness without both natural enemies and ants. (2) Homopteran fitness needs to be greater in the presence of natural enemies and ants than homopteran fitness in the presence of natural enemies alone. (3) Homopteran fitness in the presence of ants without natural enemies cannot exceed homopteran fitness without both ants and natural enemies. Prediction (1) tests the importance of natural enemies as mortality factors of homopterans; prediction (2) tests whether mound ants provide enemy-free space to tended homopterans and prediction (3) tests if the protection mound ants provide is greater than any other benefits (e.g. sanitation) they may provide to the homopterans.

Using population size and survivorship as estimates of fitness, my objective was to determine if *F. exsectoides* provides enemy-free space for the aphid, *C. banksiana,* and the pine tortoise scale, *T. parvicornis.*

Materials and Methods

Study sites

Field experiments were conducted at three sites in north-central Michigan in the Huron-Manistee National Forests of Crawford and Oscoda counties in 1994 and 1995 (Table 1). This area has sandy soils and is part of the Grayling-Rubicon soil association (MacDonald 1983). Jack pine was the dominant canopy tree at all sites (Table 1). Ground cover was composed primarily of low bush blueberry (*Vaccinium angustifolium* Aiton), sweetfern (*Comptonia peregrina* (L) Coulter) and several grass species in the more open areas. The distribution of *F. exsectoides* mounds covered several hectares at each site. Scale experiments were conducted only at Site 1.

Experimental methods

Exclusion experiments

For each site, I selected 20 trees for the aphid study in 1994 and 10 trees in 1994 and 1995 for the scale study. I selected the first 20 (10 for scales) trees that were healthy (>50% live needles or branches) with at least two branches on each tree that were similar in appearance to each other and to branches on other selected trees. Trees used in the pine tortoise scale experiments had the added requirement that both branches have equal size scale colonies on them. If more that one tree meeting the requirements was located around the same ant mound, I picked one using a randomization method. Branches on each tree were paired to be as similar as possible in terms of vigor, diameter and length.

Table 1. Location of study sites and jack pine stand description[a]

Site	Location	Stand Size (ha)	Age (Years)	SI[b]	Stand Size Density
	Crawford Co.				
1	T. 25N. R. 1W. Sec 24	30.7	59	39	Poletimber, >70% stocked
2	T. 25N. R. 1W. Sec 11	28.7	61	50	Poletimber, 40% - 69% stocked
	Oscoda Co.				
3	T. 25N. R. 1E. Sec 13	64.8	44	48	Seedling-Sapling, >70% stocked

a. Based on Huron-Manistee National Forests database inventory. USDA Forest Service Mio, Michigan.

b. Site Index: height of dominate and co-dominate trees at 50 years.

The following methods were the same for aphid and scale experiments. For each tree, ants (and natural enemies) were excluded from experimental branches by one of two methods: barrier method excluded ants and other crawling insects, and sleeve cages excluded all crawling and flying insects. For the barrier exclusion I placed a 4 cm band of Tanglefoot (The Tanglefoot Co. Grand Rapids, MI, USA) around the base of the experimental branch. I reapplied Tanglefoot as necessary to keep ants excluded from colonies. Any shoots touching either the experimental (ants excluded) or control branches (ants present) were clipped back. I made sleeve cages (35 x 70 cm) out of tulle with a 0.8 mm hole size. Sleeve cages (hereafter nets) on experimental branches were placed around the branch and tightly tied, excluding both ants and natural enemies. Control branches had loose strings (~1 cm gap) holding the nets to the branch, allowing access to the homopteran colony.

Aphids were collected from trees in a nearby stand of jack pine by placing collecting containers (18.5 x 9 cm) directly under a branch with aphids and lightly tapping the branch, causing aphids to fall in the container. I removed any predators and ants from the container. Aphids could survive for at least 96 h in the container if refrigerated, but new aphids were acquired every 48 h or as needed.

For both Tanglefoot and netting exclusion methods, I placed 15-20 late instar or adult aphids on each treatment branch, and a net was placed around the branch and tied at its basal end. Any observed predators were removed. Aphids settled and began feeding within a few h.

After 24 h, I randomly picked 10 of the 20 trees to serve as Tanglefoot trees, the remaining trees as netting trees. For Tanglefoot barrier branches, I slowly removed nets and an experimental (ants excluded) or control (ants present) treatment was randomly assigned to each branch. I also randomly assigned branches as either experimental (ants excluded) or control (ants present) for the net exclusion method. Since nets were already in place, I kept the net tight for the experimental treatment and loosened the net (~1 cm) for the control treatment. Previous pilot studies and observations indicated that ants patrolling the trees would find newly placed aphids within a few hours, usually sooner. I recorded the aphid and ant numbers on each branch at the initiation of the experiment and every 7 to 10 d thereafter. These exclusion experiments ran from July 7 to August 16 1994, for a total of 5 sample periods.

In late June 1994, I began the Tanglefoot barrier exclusion experiments with the pine tortoise scale. I randomly assigned a treatment of either experimental (ants excluded, removed any ants tending scales) or control (ants present, allowed ants to continue tending scales) to each paired branch on 10 trees. Once crawlers appeared, I estimated the number of crawlers (and subsequent instars) on new growth every 14 d for 3 sample periods beginning July 3. Crawler numbers below 100 were counted, numbers greater than this were placed into the categories of 101-250, 251-500, 501-750, 751-1000, >1000. I recorded additional data on the number of any *Hyperaspis binotata* present.

In 1995, I conducted exclusion experiments using nets to exclude mound ants from scale colonies. I placed nets around scale colonies and randomly assigned either experimental (ants excluded) or control (ants present) treatments to each branch, loosening strings around control branches as before. I made initial counts of mound ants, lady beetles, and female scales. I used a different method of couting scales than in the previous year to lessen the time involved. Once crawlers appeared, I measured the highest density of crawler populations on a given shoot by finding the length of shoot with the greatest number of crawlers, counting those crawlers, and dividing the crawler number by the length of shoot the counted crawlers occupied. This gave an average density of crawlers per cm for that section of shoot but did not measure the density for the entire shoot. After crawlers appeared, I made counts of all study organisms on July 13 and 19.

Inclusion/exclusion experiments

These experiments were conducted in 1995 to test the impact of mirids on aphids in the presence/absence of ants. The same 3 sites and tree selection method used for exclusion experiments were used again. However, I selected trees with 4 branches instead of 2, one on each 1/4 side of tree and similar in diameter and size. Tanglefoot was not used. Each branch was examined for mirids (and other predators) and ants; these were removed prior to placement of aphids. I collected *C. banksïana* as before and placed 10-15 late instars on each of four branches per tree using nets as previously described.

After 24 h, I randomly assigned each branch to one of four treatments: 1) aphids only-netting closed, 2) aphids only-netting open, 3) aphids with a single late instar mirid-netting closed, and 4) aphids with a single late instar mirid-netting open. To place mirids into nets, I made a small tear (2-3 cm in length) in the distal (branch tip) portion of each net and the mirid was introduced through this tear. As in the previous net experiments, the strings attaching nets to branches were loosened ~ 1 cm, allowing ants into and out of the nets for the treatments involving ants. I counted the number of aphids, ants and mirids in each net at 24 and 72 h later.

Statistical analyses

I used the JMP® statistical package (SAS Institute, 1995) to perform all statistical analyses. For the 1994 exclusion experiments with aphids, I conducted a split-plot repeated measures analysis of variance (ANOVA; SAS 1995). Trees and sites were random effects with trees nested within site and treated as plots. Ant treatment (fixed effect) was the whole plot factor, and census period (fixed effect) the subplot factor. The ant treatment x tree(nested in site) interaction was used to test the ant treatment effect on aphid numbers (Zar 1996). Aphid numbers were transformed ($\log_{10}$ [number + 1]) to normalize error distribution for the statistical analyses (Sokal & Rolth, 1981). For the inclusion/exclusion experiments with aphids, aphid numbers were analyzed using a planned, one-tailed, paired t-test comparing the aphid numbers between treatments at 24 and 72 h. A priori comparisons were made between the following pairs: 1) aphids only and aphids with mirid treatments, 2) the aphids with mirid and ants treatment and aphids with mirid treatment, and 3) aphids only and aphids with ants treatments. Since these were paired comparisons on each tree, analyses were conducted using only those treatment pairs on the same tree. A treatment that had no corresponding comparison treatment on the same tree (e.g. no ants tending aphids at 24 or 72 h) was not used for that paired analysis. Means in text are presented as mean aphid numbers ± SE.

For the exclusion experiments with pine tortoise scales in 1994 and 1995, I also used a split-plot repeated measures ANOVA to test the effect of ant treatment (ants excluded, ants present). Ant treatment (fixed effect) was the whole-plot factor with trees (random effect) treated as blocks, and census period was the sub-plot factor. The 1994 scale numbers were square-root transformed $\left(\sqrt{\text{crawler number} + \frac{1}{2}}\right)$, and for 1995, scale densities were log transformed ($\log_{10}$ crawler density + 1) to normalize error distribution.

Results

Tests of enemy-free space hypotheses--*C. banksiana*

Test of prediction 1: Importance of natural enemies

In the inclusion/exclusion studies, aphid numbers needed to be significantly larger in the aphids only treatment than in the aphids with mirids treatment if mirids were truly a significant source of mortality for aphids. At 24 h, mean aphid number in the aphids only treatment (13.5 ± 2.4) were significantly larger than that in the aphids with mirids treatment (4.7 ± 1.6, Table 2). This difference was still significant at 72 h (aphids only: 14.8 ± 4.7, aphids with mirids: 4.3 ± 2.3, Table 2).

Test of prediction 2: Importance of ant protection from natural enemies for aphids

Tanglefoot exclusion experiments indicated that when ants were excluded, aphid populations exposed to predators were significantly smaller than those still tended by ants (Table 3). The treatment x time interaction was also significant, indicating this difference increased over time (Figure 1, Table 3). Additionally, the number of aphid populations that went extinct on ant-excluded branches were twice as high as on ant-present branches, 26 to 13 respectively (Figure 1).

For the inclusion/exclusion experiments, aphids with both ants and mirids needed to have larger numbers than aphids with mirids to indicate if ants were providing enemy-free space for the aphids. At 24 h, mean aphid number in the aphids with ants and mirids treatment (7.6 ± 1.9) were not significantly greater than the mean aphid number in the aphids with mirids treatment (5.3 ± 1.8, Table 2). By the 72 h census the mean number of aphids with ants and mirids was significantly larger (18.6 ± 2.8) than that observed in the aphids with mirids treatment (4.1 ± 2.0, Table 2).

Test of prediction 3: Importance of ant tending without natural enemies for aphids

No significant difference in aphid population sizes was detected between aphid populations with ants but without predators and the aphid populations without both ants and predators (Table 4). The interaction between ant treatment and time was also not significant (Table 4, Figure 2). The number of populations going extinct between treatments was similar, and by sample period 5 both treatments had 16 extinct populations (Figure 2).

For the inclusion/exclusion studies (Table 2), if aphid numbers in the aphid only treatment were significantly less than the aphid number in the aphids with ants treatment would indicate that ants were providing other significant benefits to aphids besides enemy-free space. The mean number of aphids in the aphids only treatment (9.0 ± 2.0) was significantly smaller than the mean aphid number with ants at 24 h (14.5 ± 1.8, Table 2), indicating other benefits. However by 72 h, there was no difference in aphid numbers between the two treatments (aphids only: 16.4 ± 4.8, aphids with ants: 14.2 ± 4.3, Table 2).

Table 2. Difference between mean population numbers of C. *banksiana* under four treatments at 24 and 72 h

Relation predicted by enemy-free space	Mean population numbers Observed relation	df	*t*	Do results support enemy-free space?[a]
	Mean ± SE at 24 h			
Tmt 1 > Tmt 3	13.5 ± 2.4 > 4.7 ± 1.6	10	3.75**	Yes
Tmt 4 > Tmt 3	7.6 ± 1.9 > 5.3 ± 1.8	8	1.14	No
Tmt 1 ≥ Tmt 2	9.0 ± 2.0 < 14.5 ± 1.8	11	-2.63*	No
	Mean ± SE at 72 h			
Tmt 1 > Tmt 3	14.8 ± 4.7 > 4.3 ± 2.3	11	2.07*	Yes
Tmt 4 > Tmt 3	18.6 ± 2.8 > 4.1 ± 2.0	13	5.79**	Yes
Tmt 1 ≥ Tmt 2	16.4 ± 4.8 = 14.2 ± 4.3	7	0.34	Yes

* $P < 0.05$; ** $P < 0.001$

- Treatment 1: aphids only, no ants or mirid present.
- Treatment 2: aphids and ants present, no mirid.
- Treatment 3: aphids and mirid present, no ants.
- Treatment 4: aphids, ants and mirid present.

[a] Population differences were analyzed using paired, 1-tailed t-tests. For the enemy-free space hypothesis to be supported, each predicted relation between treatments must be true.

Table 3. Repeated measures ANOVA of *Cinara banksiana* numbers[a] on ant-present and ant-excluded branches: ants excluded with tanglefoot

Source of variation	df	Mean Square	F Ratio	P-value
Site	2	1.8567	1.64	0.212
Trees(Site)[b]	27	1.1303	1.9076	0.0496
Treatment[c]	1	11.5214	19.44	0.0001
Treatment x Site	2	1.0332	1.74	0.194
Error a[d]	27	0.5925		
Time[e]	4	4.7715	29.2758	<0.0001
Time x Site	8	0.5218	3.2019	0.0027
Time x Treatment	4	1.1814	7.2487	<0.0001
Time x Treatment x Site	8	0.1261	0.7734	0.627
Error b[g]	108	0.1629		

a Transformed for analysis: Log_{10} (aphid numbers + 1).

b Trees nested within site.

c Treatment: Ants excluded with tanglefoot and ants present (control).

d Treatment x Trees(Site): used to test Treatment effect.

e Aphid populations sampled every 7-10 days from July 7 to August 16 for 5 periods.

f Residual error: used to test Time x Treatment

Table 4. Repeated measures ANOVA of *Cinara banksiana* numbers[a] on ant-present and ant-excluded branches: ants excluded with netting

Source of variation	df	Mean Square	F Ratio	P-value
Site	2	7.9476	11.9254	0.002
Trees(Site)[b]	27	1.3269	1.9911	0.0475
Treatment[c]	1	0.2756	0.4136	0.5256
Treatment x Site	2	0.0324	0.0486	0.9526
Error a[d]	27	0.6664		
Time[e]	4	1.9031	9.2063	<0.0001
Time x Site	8	0.4214	2.0387	0.0484
Time x Treatment	4	0.0852	0.4122	0.7996
Time x Treatment x Site	8	0.1451	0.7018	0.6893
Error b[f]	108	0.2067		

a Transformed for analysis: Log_{10} (aphid numbers + 1).

b Trees nested within Site.

c Treatments: Ants excluded with netting and ants present (control).

d Treatment x Trees(Site): used to test treatment effect.

e Aphid populations sampled every 7-10 days from July 7 to August 16 for 5 periods.

f Residual error: used to test Time x Treatment

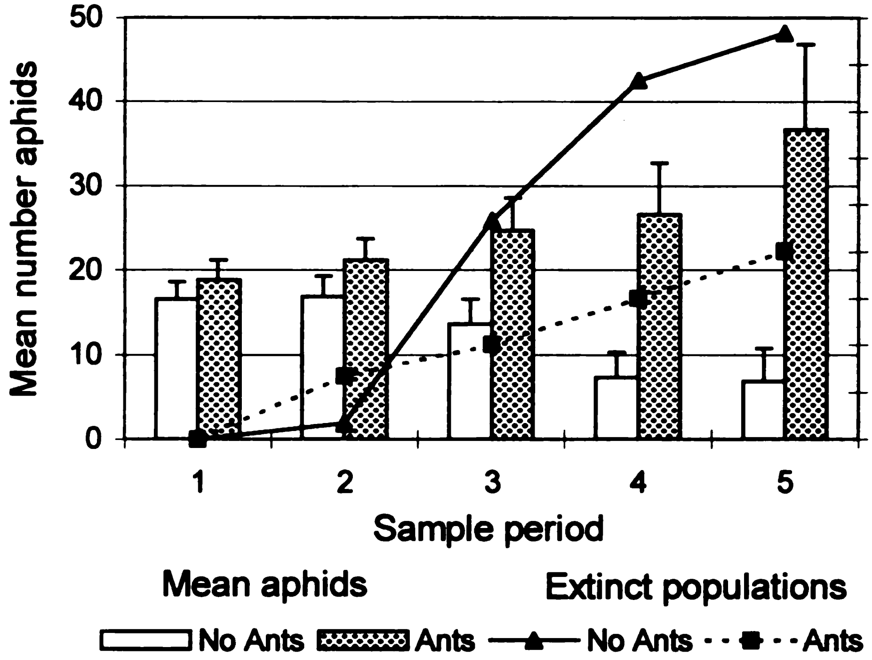


Figure 1. Mean (± SE) *C. banksiana* numbers per branch (bars) across all three sites using tanglefoot to exclude ants and other crawling insects. Lines represent percentage of aphid populations that went extinct during course of experiment. n = 30 colonies for each treatment. Sample periods were 7-10 days apart starting July 7.

Table 5. Repeated measures ANOVA of *Toumeyella parvicornis* numbers[a] in 1994 on ant-present and ant-excluded branches: ants excluded with tanglefoot

Source of variation	df	Mean Square	F Ratio	P-value
Trees[b]	9	155.363	1.214	0.389
Treatment	1	455.939	3.563	0.092
Error a[c]	9	127.969		
Time	2	21.715	0.758	0.476
Time x Treatment	2	21.406	0.747	0.481
Error b[d]	36	28.639		

a Transformed for analysis: $\sqrt{\text{scale numbers} + 0.5}$

b Trees treated as blocks.

c Treatment x Tree, used to test Treatment effect.

d Residual error used to test Time x Treatment effect.

Table 6. Repeated measures ANOVA of *Toumeyella parvicornis* densities/cm[a] in 1995 on ant-present and ant-excluded branches: ants excluded with netting

Source of variation	df	Mean Square	F Ratio	P-value
Trees[b]	9	0.435	1.753	0.208
Treatment	1	0.701	2.826	0.127
Error a[c]	9	0.248		
Time	1	0.498	15.656	0.001
Time x Treatment	1	0.005	0.155	0.698
Error b[d]	18	0.032		

a transformed for analysis: $\log_{10}$ (scale density + 1)

b Trees treated as blocks.

c Treatment x Tree, used to test Treatment effect.

d Residual error used to test Time x Treatment effect.

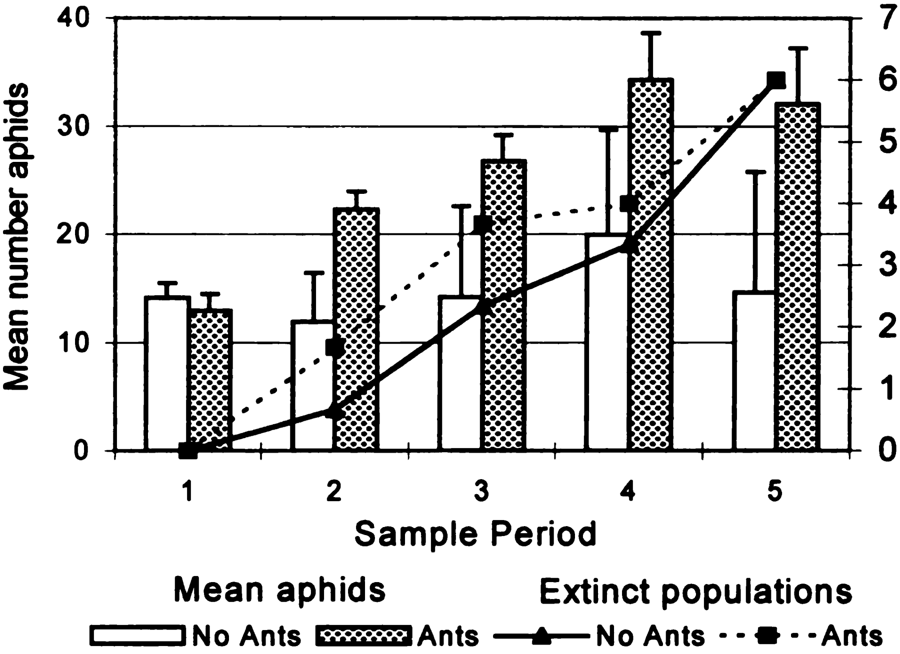


Figure 2. Mean (± SE) *C. banksiana* numbers per branch (bars) across all three sites using netting to excluded all arthropods, including ants. Lines represent percentage of aphid populations that went extinct during course of experiment. n = 30 colonies for each treatment. Sample periods were 7-10 days apart starting July 7.

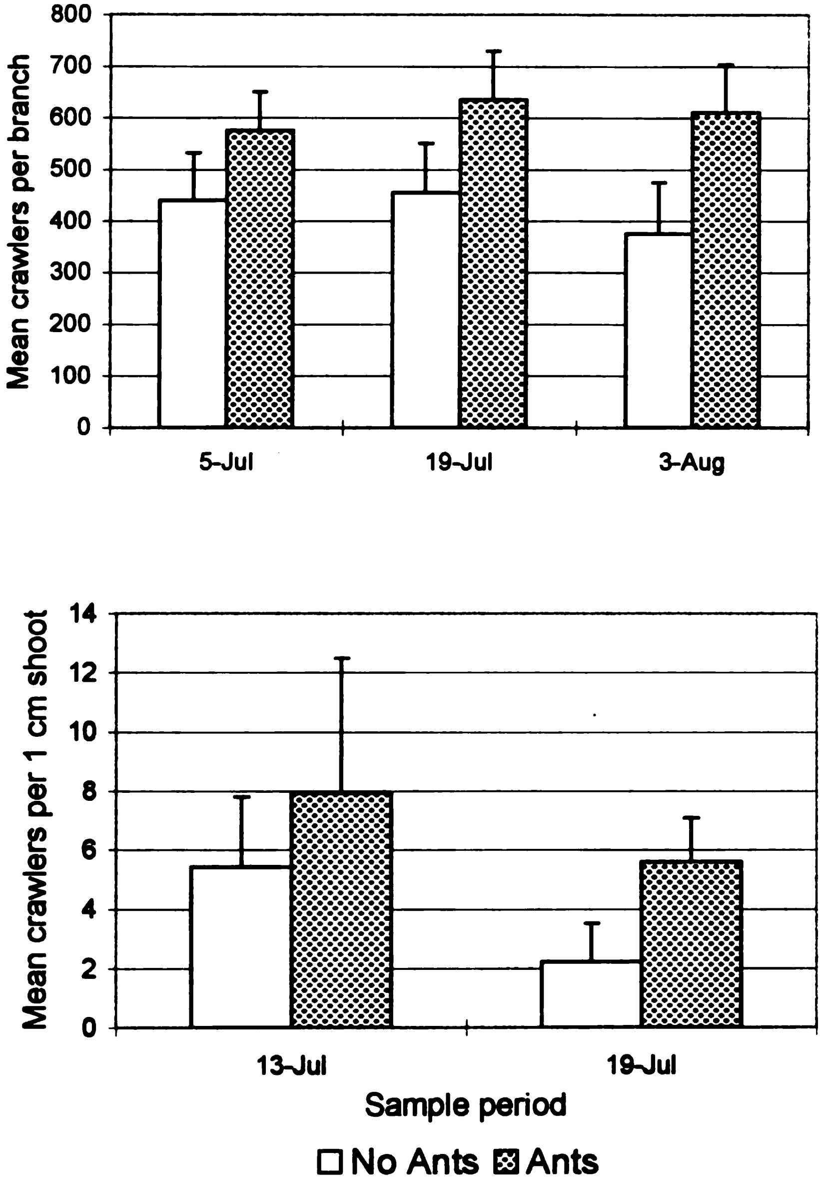


Figure 3. Mean number (± SE) of *T. parvicornis* crawlers per treatment (ants excluded, ants present) for (a) 1994 and (b) 1995. n = 10 scale colonies per treatment. Note Y axis is using a different scale between the 2 years.

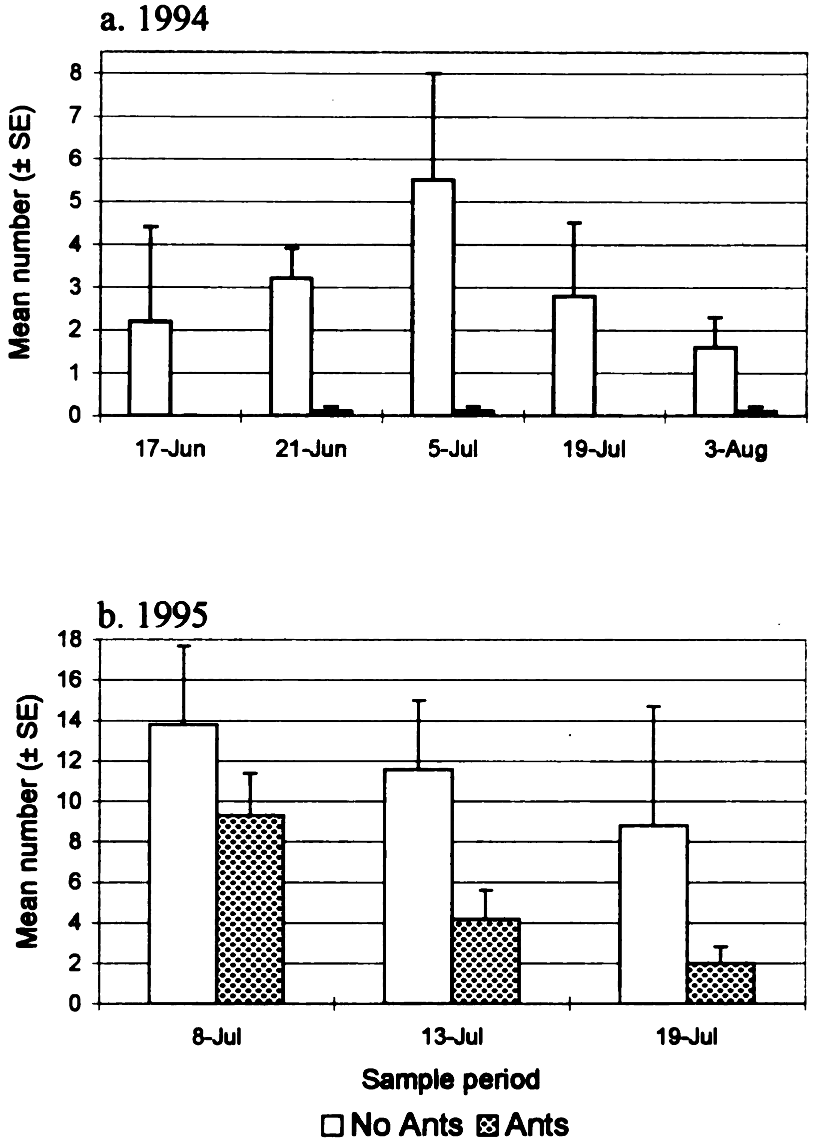


Figure 4. Mean *H. binotata* numbers observed on treatment branches in (a) 1994 and (b) 1995. Sample periods June 17 & 21 (1994) and July 8 (1995) indicate dates before scale crawlers were apparent. n = 10 branches per treatment.

Tests of enemy-free space hypothesis--*T. parvicornis*

Prediction 2: Importance of ant protection from natural enemies for scales

When comparing the cralwer number of July 5 to August 3, crawler populations in the presence of ant had increased slightly by 9% and decreased 16% on ant-excluded branches (Figure 3a). Both treatments showed a decline in cralwer populations from July 19 to August 3 (ant-excluded: -21%; ant-present: -4%; Figure 3a). Repeated measures analysis indicated no significant difference between crawler populations for both the ant treatment effect and ant treatment x time interaction (Table 5). In 1995, crawler populations in both treatments declined, 44% on ant-present branches and 60% on ant-excluded branches (Figure 3b). No significant difference was detected between treatments (Table 6).

In 1994, lady beetle larvae were much more abundant on ant-excluded branches than on the ant-present branches during the study period (Figure 4a). However, in 1995 a larger number of larvae were found on both ant-excluded and ant-present branches than in 1994 (Fig 4b).

Discussion

Berdegue et al. (1996) proposed three testable hypothesis to determine whether enemy-free space is important in a system. My results indicate that the Allegheny mound ant provided enemy-free space for the aphid, *C. banksiana*, but suggests that the pine tortoise scale, *T. parvicornis*, received less protection from ant attendance.

Importance of natural enemies

Natural enemies, and specifically mirid predators, significantly reduced aphid numbers, indicating the importance of natural enemies in this system. Natural enemies of aphids appeared to consist primarily of predators since aphid mummies (indicating parasitoids) were rarely encountered. I observed mirids, salticid spiders, cantharid beetles and syrphid larvae preying on aphids; mirids were the most abundant predator associated with predators (Chapter 2).

Natural enemies may not be the only cause of aphid disappearance. Aphids would drop from branches if disturbed. However, usually late instars dropped, leaving the early instars. Additionally, aphids could have walked from their branch when ants were excluded, but examination of Tanglefoot barriers indicated that few aphids attempted to walk off the branch.

Importance of ant protection from natural enemies

Mound ants were important in protecting aphids from predators, thus providing enemy-free space. The exclusion of ants with tanglefoot resulted in a steady decline of aphid populations over the summer compared to a slight increase in aphid populations in cages (Figures 1, 2). Other studies have suggested that ants may provide enemy-free space to tended homopterans and lycaenid caterpillars (Atsatt, 1981; Buckley, 1987). For example the exclusion of *Camponotus modoc* results in more predators occurring in *Cinara occidentalis* colonies (Tilles and Wood 1982). Untended *C. occidentalis* colonies are more likely to become extinct during the summer than ant-tended colonies (Tilles and Wood 1982). The exclusion of ants results in significantly higher mortality rates from parasitoids and predators for myremecophilous lycaenid larvae (Atsatt, 1981; Pierce & Mead, 1981).

The enemy-free space provided by ants to aphids was not perfect. Mirids would ambush aphids on the periphery of the colony, and a few syrphid larvae were seen feeding on aphids with no interference from ants. Ants occasionally abandoned aphid colonies; both mirids and salticid spiders were seen feeding in these untended aphid colonies.

The inclusion/exclusion experiments indicated that while mirids reduced aphid numbers without ants, *F. exsectoides* was able to provide enemy-free space for aphids in the presence of mirids. This enemy-free space appears to be due to ant interference with mirids rather than the actual removal of mirids by ants since mirids were still in nets with ant-tended aphids at 72 h. My observations indicated that mirids avoided capture by running up shoots and needles, a behavior seen in other mirid species associating with ant-tended aphids (Bradley & Hinks, 1969; Wheeler, 1991). Mirids that can decimate untended aphid colonies are much less successful at attacking aphids in ant-tended colonies (Bradley & Hinks, 1969; Wheeler 1991).

The hypothesis that mound ants provide enemy-free space to the pine tortoise scale from the lady beetle, *H. binotata,* was not supported by this study. These results differed from Bradley (1973) who found that exclusion of *F. obscuripes* from jack pine trees allowed *H. congressis* to eliminate crawlers from those trees.

While it appeared that lady beetle numbers differed between ant treatments, subsequent studies (Chapter 4) have indicated that lady beetle larvae alter their behavior in the presence of ants and will hide under scales, suggesting more larvae were present in ant-tended scale populations than actually seen. These hidden larvae could consume hundreds of scale eggs and crawlers without interference from ants.

The larvae that were observed feeding in the open increased from 56 in 1994 to 231 in 1995 (Figure 3). Even when including only visible larvae from ant-present treatments, peak larval number increased from 1 in 1994 to 93 in 1995. While not directly comparible between years, trends were similar with c This suggests that unlike other mutualisms involving predators (Cushman & Whitham, 1989; Bronstein, 1994b), this ant-scale mutualism may be stronger when *H. binotata* populations are small (or mainly feeding under scales), and weakens as lady beetle populations increase.

Outbreaks of pine tortoise scale have been reduced to non-outbreak status within a single year by *Hyperaspis* spp. A 1957 outbreak in Maryland was eliminated the next year by *H. binotata* and *H. signata* (McIntyre, 1960). The closely related striped pine scale, *T. pini,* was eradicated from 70 of 78 scotch pine trees (*Pinus sylvestris*) in a single season by *H. signata* (Orr & Hall, 1931). Hence, *H. binotata* (and other *Hyperaspis* spp.) appear to be efficient predators of pine tortoise scale, and even protection by aggressive ants does not totally suppress these predators.

Importance of ant tending without natural enemies

Enemy-free space appeared to be the primary benefit aphids received from mound ant presence. During the long term ant-exclusion study (1994), nets developed a black sooty mold on the bottom, indicating honeydew from untended aphids had dropped on the nets. I saw no incidence of fungal contamination on untended aphids. However, other possible indirect impacts of sooty mold formation on aphid colonies were not measured (e.g. decrease of photosynthesis by sooty mold on needles). It is possible the presence of ants enhanced aphid population growth, independent of their protective role. However, as long as the aphids' benefits arising from protection outweigh these other benefits, enemy-free space would remain of primary importance to aphids.

In conclusion, this study demonstrates that the Allegheny mound ant provided enemy-free space for one honeydew producing homopteran but not another. *T. parvicornis* appeared not to gain enemy-free space from its primary predator, *H. binotata*, via its association with Allegheny mound ants. The outcome of this mutualism may depend on the population size of *H. binotata*. Other benefits or protection from other enemies may be provided by mound ants to the pine tortoise scale. *C. banksiana* did experience enemy-free space as its primary benefit from its association with Allegheny mound ants. Berdegue et. al (1996) reported 3 cases of enemy-free space developing through interspecific interactions. In all three cases reported, ants provided the enemy-free space to a second species. The *C. banksiana-F. exsectoides* mutualism adds a fourth case. These four cases suggest that ants play an important role in terrestrial communities, altering predator-prey interactions and influencing population levels of some species by providing enemy-free space.

CHAPTER 4

Multiple defenses of *Hyperaspis binotata* (Coleoptera: Coccinellidae) repel aggressive ants in soft scale colonies

Introduction

The pine tortoise scale, *Toumeyella parvicornis* (Cockerell) is found almost exclusively in the presence of homopteran-tending ant species in jack pine (*Pinus banksiana* (L.)) forests (Bradley 1973, Chapter 2). The presence of tending ants can contribute to homopteran outbreaks by reducing the effectiveness of natural enemies (Flanders 1951, Bartlett 1961, Bradley 1973, Nechols & Seibert 1985, Buckley & Gullan 1991).

In jack pine forests of north-central Michigan, pine tortoise scales were associated with the presence of Allegheny mound ants, *Formica exsectoides* Forel (Chapter 2). These ants form large, locally abundant but patchy populations (Bristow et al. 1992). In areas with mound ants, pine tortoise scale colonies were large, numbering in the hundreds of individuals per branch (Chapter 2) and the stunting or killing young jack pine trees (Rabkin & Lejeune, 1954, Wilkinson & Chellman 1979). Areas without *F. exsectoides* were virtually absent of pine tortoise scales (Chapter 2). Those few scales that were present in non-mound ant areas were eliminated at least in part by the lady beetle

Hyperaspis binotata Say (Chapter 2). Pine tortoise scales overwinter as second instar gravid females and the following spring begin to feed and produce honeydew (Rabkin & Lejeune 1954). Beginning in late June, each female produces up to 500 eggs (Rabkin & Lejeune 1954). Eggs are released into the body cavity and then extruded into the anal cleft where they hatch into the crawler stage after a few hours (Rabkin & Lejeune 1954). Crawlers may spend up to 1/2 the day under the scale before dispersing, settling primarily on current shoot growth.

Hyperaspis spp. are important predators of *Toumeyella* scales in North America (Simanton 1916, Orr & Hall 1931, Bradley 1973), and can regulate their populations (McIntyre 1960, Bradley 1973). In Manitoba, the removal of *F. obscuripes* Forel from pine tortoise scale colonies resulted in female lady beetles, *Hyperaspis congressis* Watson, ovipositing eggs and the subsequent elimination of scale colonies by *H. congressis* larvae (Bradley 1973). One of this most common species of this genus in eastern North America is *Hyperaspis binotata* Say (Dobzhansky 1941). First and second *H. binotata* instars primarily stay under female scales in the anal cleft, feeding on eggs and new crawlers (Simanton 1916). Later instars may also feed under the anal cleft, dislodging the scale from the branch during the course of feeding (Simanton 1916).

While ant-provided protection is very important for ant-tended homopterans (Way 1963, Buckly 1983, Bristow 1991), recent studies have indicated that the protection provided by ants is not complete. Predators (Pierce 1987, Völkol 1995) and parasitoids (Völkol & Mackauer 1993) use various morphological and behavioral adaptations or chemical camouflage to feed on ant protected insects (see also Eisner et al. 1978).

A survey I conducted in 1993 detected no *H. binotata* larvae feeding in the open in ant-tended scale colonies (Chapter 2). However, subsequent studies indicated that *H. binotata* larvae will feed in the open and become common in pine tortoise scale colonies even when mound ants are present (Chapter 3). During experiments in 1994 and 1995, the number of *H. binotata* feeding in the open in ant-tended scale conlonies increased from 1 to 93, respectively (Chapter 3). I noted that ants usually ignored lady beetle larvae, an observation similar to Bradley's (1973) for *H. congressis* and *F. obscuripes*. As the number of lady beetle larvae feeding in the open increased, ants may have become habituated to larval presence and ceased attacking them when encountered.

Since *H. binotata* larvae were numerous and feeding apparently unmolested in ant-tended scale colonies (Chapter 3), I suspected that they may employ one or more traits (behavioral, morphological or chemical) to remain in these scale colonies. First, except for the 1st instar, larvae are covered by tufts of long, pure white, waxy material exuded from 3 rows of dorsal depressions on each side of the body (Bőving 1917), similar to larvae of other *Hyperaspis* spp. (Pope 1979, Nsiama She et al. 1984). These tufts are sticky and may act as mechanical defenses against ants and other potential natural enemies (Pope 1979). Second, larvae have dorsally placed repugnatorial glands on each side of the first 8 abdominal segments that emit a secretion when larvae are disturbed (Bőving 1917). Together with the feeding under scales by early instars, *H. binotata* has three possible means to avoid or repel ant attack while feeding in scale colonies. However, not all of these traits may be equally effective in protecting the different instars (e.g. 1st instars do not have waxy tufts).

Other studies have indicated that larval defenses such as reflex-bleeding (Hagen 1961, Eisner et al. 1994) and waxy tufts (Pope 1979, Völkl and Vohland 1996, but see Bach 1991) can protect lady beetle larvae from attack by ants. Hence I primarily focused my attention on how ants respond to the presence of larvae (e.g. attacking or ignoring), and whether ant presence or absence alters larval feeding location. I observed ant-larvae interactions and addressed the following two questions: first, do ants primarily attack or ignore larvae and is this behavior dependent upon beetle instar? Second, does the presence or absence of ants alter the behavior of larvae? Specifically, do larvae feed under scales (covert feeding) in the presence of ants and in the open (overt feeding) in the absence of ants, or is this behavior more a function of age? I also recorded data on the effectiveness of the waxy covering and glandular secretion in protecting overt larvae from aggressive ants.

Material and Methods

During the summers of 1995 and 1996, I studied the interactions of *H. binotata* and *F. exsectoides* with pine tortoise scales on jack pine in north-central Michigan. Virtually all naturally occurring scales are tended by Allegheny mound ants in the study area (Bristow et al. 1992, Chapter 2).

For behavior studies of ants and lady beetle larvae in 1995, I used 2 field sites, both in jack pine stands of the Huron-Manistee National Forests (Table 1). Site 1 was approximately 8 km east of Roscommon, MI, and Site 2 was about 5 km northwest of Site 1, both in Crawford Co. The larval feeding location study was conducted at Site 1 in

1996. This area has sandy soils, part of the Grayling-Rubicon soil association (MacDonald 1983). Ground cover was composed primarily of lowbush blueberry (*Vaccinium angustifolium* Aiton), sweetfern (*Compotonia peregrina* (L) Coulter) and several grass species in the more open areas.

Interactions: behavior of ants and beetle larvae response

On 27 June 1995, a total of 10 trees were selected at Site 1 and 5 trees at Site 2. For each site, trees between 2 and 5 m tall and within 10 m of an ant mound were selected. Healthy trees (>50% live crowns) were picked with at least 2 branches on each tree that appeared similar in size and vigor to each other and to branches on other selected trees. Additionally, I limited selection of trees to those with at least 2 branches with roughly equal numbers of scales on them. For this and other experiments I used exclusion cages constructed of tulle (0.8 mm hole size) to exclude ants and lady beetle adults from scale colonies. All ants were removed from branches and a sleeve cage (35 x 70 cm) was placed around each branch and tied closed. I had previously determined that tulle cages did not alter the temperature of enclosed branches at mid-day both in the sun (branch surface inside cage: 31.62 C° ± 1.82; outside cage: 31.36 C° ± 1.79, mean ± SE; n = 5) and in the shade (branch surface inside cage: 26.16 C° ± 0.89; outside cage: 26.44 C° ± 0.97, mean ± SE; n = 5).

On 6 July, I randomly picked 1 branch on each tree and slowly removed that net and recorded the number of lady beetle instars seen. Once one ant encountered a larva, I recorded the responses of ants and larvae for the next 15 min. I recorded the number of times the different lady beetle instars were antennated by ants (tapped with antennae

Table 1. Location of replicate sites and jack pine stand description.[a]

Site	Location	Stand Size (ha)	Age (Years)	SI[c]	Stand Size Density
1	T. 25N. R. 1W. Sec 24	30.7	60	39	Poletimber, >70% stocked
2	T. 25N. R. 1W. Sec 11	28.7	62	50	Poletimber, 40% - 69% stocked

a. Based on Huron-Manistee National Forests database inventory. USDA Forest Service Mio, Michigan.

b. Site Index: height of dominate and co-dominate trees at 50 years.

longer than 1s). If an ant antennated a larva, the subsequent behavior of the ant was recorded and assigned to one of the following categories: ignored (ant no longer interacted with larva) or attacked (ant bit larva). If the ant attacked the larva, I recorded whether the ant released or removed the larva. I also recorded whether or not larvae emitted glandular secretions in response either to ant antennation or attack.

Larval feeding positions

Since crawlers typically settle on the years current growth, the following year's adult scales wll be found on 1 year old terminal and side shoots of branches. Hence, I randomly selected 24 trees (1.5 to 5 m tall) that had scale colonies on at least 2 separate shoots on 25 June, 1996. Shoots may or may not have been on the same branch of a tree. A shoot was then randomly picked for ant-exclusion treatments. I placed a tulle sleeve cage (10 x 25 cm) around each of these shoots and its scale colony. Cages were tied off at the basal end, keeping any ants and predators out. The remaining shoot had a string attached to its base to identify it as the control or uncaged treatment (ants present). An initial count of scales, presence of crawlers, and overt *H. binotata* instars (i.e. not hiding under scales) was made on 29 June.

Living adult scales are brownish-red and smooth and turn dark brown and shriveled when dead (pers. obs.). On 3 July, I counted the number of living adult scales and the overt instars of *H. binotata* on each shoot. On 5 July, I destructively removed scales from each shoot and recorded the number of covert *H. binotata* instars under scales, the number of overt larvae, and the number of living adult scales.

Statistical analysis

The relationship between initial scale population size and number of lady beetle larvae on treatment shoots on 29 June and 5 July 1996 was evaluated using a product-moment correlation analysis (Sokal & Rohlf, 1981). A one-way ANOVA was used to test for differences between the number of overt verses covert larvae ($\log_{10}$ [number overt (covert) larvae] + 1) within each treatment (caged or uncaged shoots) on 5 July. Treatments were fixed effects and trees (treated as blocks) were random effects. All analyses were conducted with the JMP® statistical package (SAS Institute, 1995)

Results

Interactions: behavior of ants and beetle larvae

My 1995 observations indicated that 2nd to 4th instar lady beetles were usually ignored by ants; ants would walk over larvae without appearing to investigate them (Table 2). I never observed larvae emit glandular secretions in response to ants walking over them. The 48 larvae antennated by ants were then ignored 75% of the time (Table 2). A higher proportion of 2nd instars were attacked by ants after antennation than either 3rd or 4th instars (Table 2), although this is not conclusive due to the small number of 2nd instars antennated. In 10 of the 12 attacks, larvae responded by emiting a glandular secretion; a 3rd and a 4th instar did not emit a secretion when attack. This secretion caused the attacking ant to release the larva and begin cleaning its mandibles and antennae. However two third instars were not released by the attacking ant and were eventually carried off. All three 2nd instars emited secretions when attacked and were not removed by ants. In

Table 2. Number of overt *H. binotata* instars antennated and subsequently attacked by *F. exsectoides*

	Instar		
	Second	Third	Fourth
Total no. each instar	46	59	52
No. antennated	7	22	19
No. attacked	3	5	4
No. removed	0	2	0

the two cases where no glandular secretion was observed, the attacking ant pulled off waxy tufts from the instar and then withdrew and cleaned its mandibles.

Larval feeding positions

On 25 June 1996, I saw four 1st instars and one 2nd instar *H. binotata* (n = 48 examined shoots on 24 trees) during my placement of sleeve cages. By 29 June I saw a total of 148 first instars and two 2nd instars on the 24 pairs of treatment shoots. The number of overt 1st instar beetle larvae (those instars not under scales) for each treatment was the same uncaged: 3.52 ± 0.60; caged: 3.62 ± 0.35 (mean ± SE; $\chi^2 = 0.19$, df = 1, P = 0.66). However, I do not know how well these numbers reflect the true population of larvae since I could not count those early instars feeding under scales. Gravid scale numbers were roughly equal for both treatments at the start of the experiment, caged: 14.10 ± 1.17; uncaged: 17.33 ± 1.54 (mean ± SE; $\chi^2 = 2.11$, df = 1, P = 0.15). Very few scale crawlers were seen on these 2 dates; one of 15 scales examined had crawlers under it on 25 June and no crawlers were seen on treatment shoots as of 29 June. By 3 July, scale crawlers were abundant and only 2 overt 1st instar lady beetles were observed, both on caged shoots. Significantly more overt larvae were observed on caged than uncaged shoots on 3 July, caged: 6.00 ± 0.78; uncaged: 2.50 ± 0.58 (mean ± SE; $\chi^2 = 11.32$, df = 1, $P < 0.001$). The majority of larvae seen on caged shoots was composed of 3rd instars (Table 3a).

The destructive sampling of 5 July indicated that when ants were excluded, significantly more overt lady beetle larvae (5.69 ±0.71, mean ± SE) were present than covert larvae (0.95 ± 0.39, mean ± SE; Tables 3b, 4a). In the presence of ants, covert larvae (3.32 ± 0.66, mean ± SE) were not significantly more common than overt larvae (1.82 ± 4.48, mean ± SE; Tables 3b, 4b).

When comparing the number of overt instars to the total number of instars found, virtually no difference was observed in 1st and 4th instars between the 2 treatments (Figure 1). Regardless of ant presence, 1st instars were rarely overt, 0 of 6 on caged shoots and 2 of 16 on uncaged shoots, while 4th instars were primarily overt, 61 of 61 on caged shoots and 10 of 11 on uncaged shoots (Figure 1). However, a shift from overt feeding to covert feeding occured in 2nd and 3rd instars when ants were present on shoots (Figure 1). On caged shoots overt 2nd instars accounted for 11 of 21 total 2nd instars found, and 53 of 58 third instars were observed feeding overtly (Figure 1a). On uncaged shoots, only 17 overt 2nd instars were found out of a total of 62 instars, and 11 of 21 third instars were overt (Figure 1b).

In examining the relationship of starting scale population sizes with the number of lady beetle larvae present for both the starting and ending dates of the study, I found that the number of overt larvae seen on 29 June was not correlated with gravid-scale colony sizes for either caged (r = 0.25, df = 19, P = 0.27) or the uncaged treatments (r = 0.10, df = 19, P = 0.67). However, the total number of lady beetle larvae (overt + covert) found on 5 July was positively correlated with the number of scales on the branches at the start of the experiment both for caged and uncaged treatments (Figure 2).

The presence of these *H. binotata* larvae appeared to have drastic consequences for the scale population, regardless of the presence of tending mound ants. A census of all

Table 3. Mean (± SE) number of *H. binotata* instars observed on a) 3 July feeding in the open (overt feeding) and on b) 5 July feeding in the open and under scales (covert feeding) on caged (ant-excluded) and uncaged (ants-present) branches

		Caged shoots-ants excluded				Uncaged shoots-ants present			
	Instar	First	Second	Third	Fourth	First	Second	Third	Fourth
a) 3 July	Overt	0	0.85 ± 0.28	3.25 ± 0.57	1.95 ± 0.46	0.10 ± 0.07	1.05 ± 0.24	1.2 ± 0.39	0.15 ± 0.11
	Covert*	–	–	–	–	–	–	–	–
b) 5 July	Overt	0	0.50 ± 0.17	2.41 ± 0.48	2.77 ± 0.39	0.09 ± 0.06	0.77 ± 0.24	0.50 ± 0.20	0.45 ± 0.19
	Covert	0.27 ± 0.15	0.45 ± 0.21	0.23 ± 0.15	0	0.77 ± 0.19	2.04 ± 0.49	0.45 ± 0.19	0.04 ± 0.04

* No covert larvae observed until destructive sampling on 5 July.

Table 4. ANOVA results comparing the feeding position (overt- in the open, covert- under gravid scales) of *H. binotata* larvae with respect to a) caged (ants excluded) or b) uncaged (ants present) treatments.

a. Caged (ants absent)

Source of variation	df	SS	F	P
Trees[a]	21	2.157	1.417	0.216
Feeding position	1	3.509	48.388	<0.001
Error	21	1.191		

b. Uncaged (ants present)

Source of variation	df	SS	F	P
Trees[a]	21	2.336	1.181	0.354
Feeding position	1	0.343	3.644	0.07
Error	21	1.979		

[a] Trees treated as blocks (random effect).

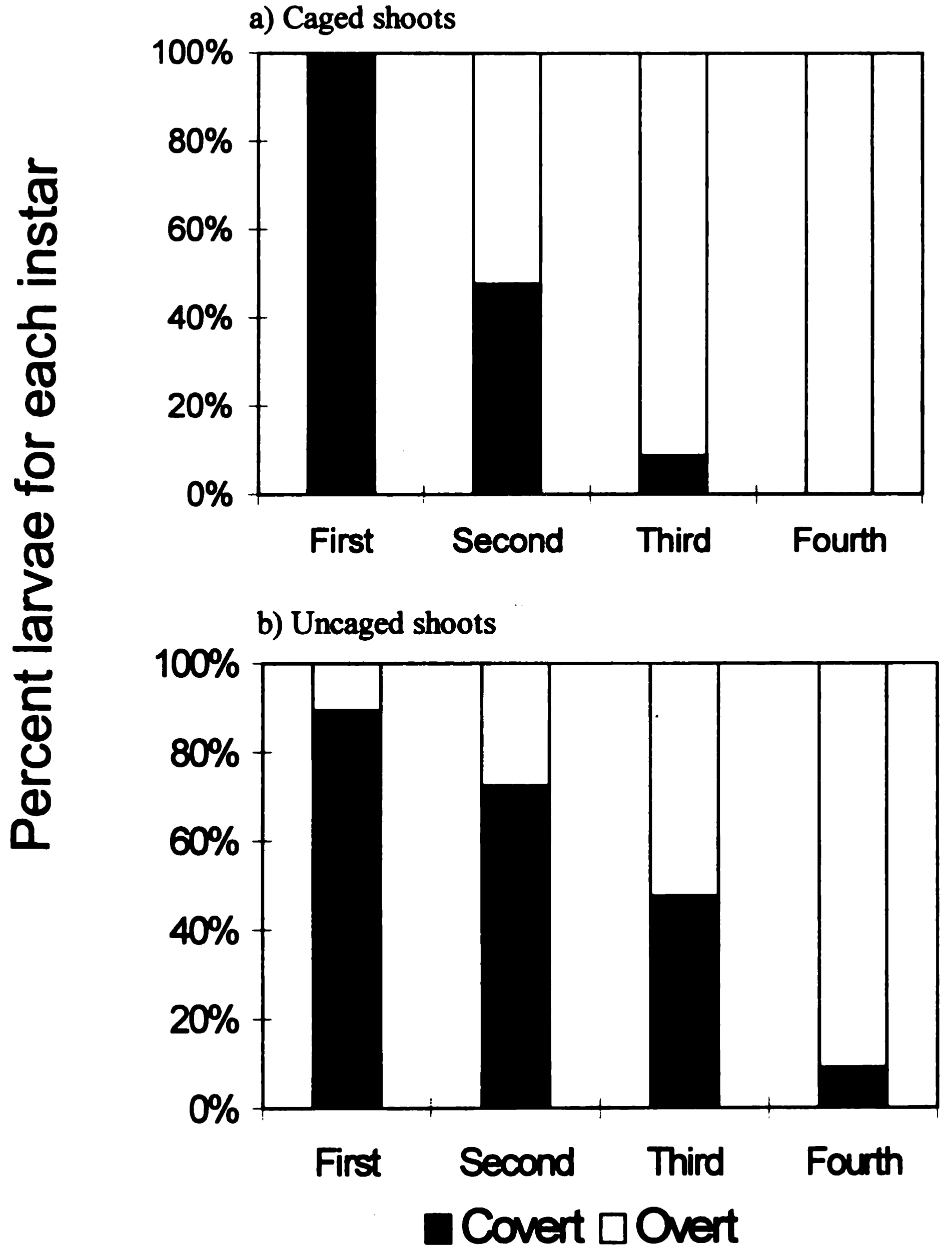
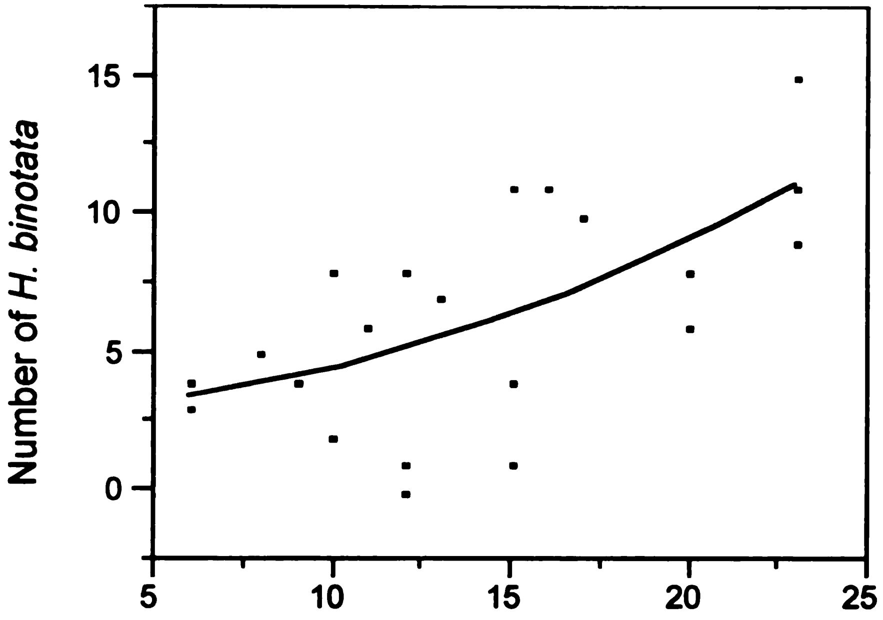


Figure 1. Percent of larvae of each *H. binotata* instar found either in the open (overt) or under scales (covert) in (a) caged (ants absent) or (b) uncaged (ants present) shoots for 1995.

a) Caged shoots



b) Uncaged shoots

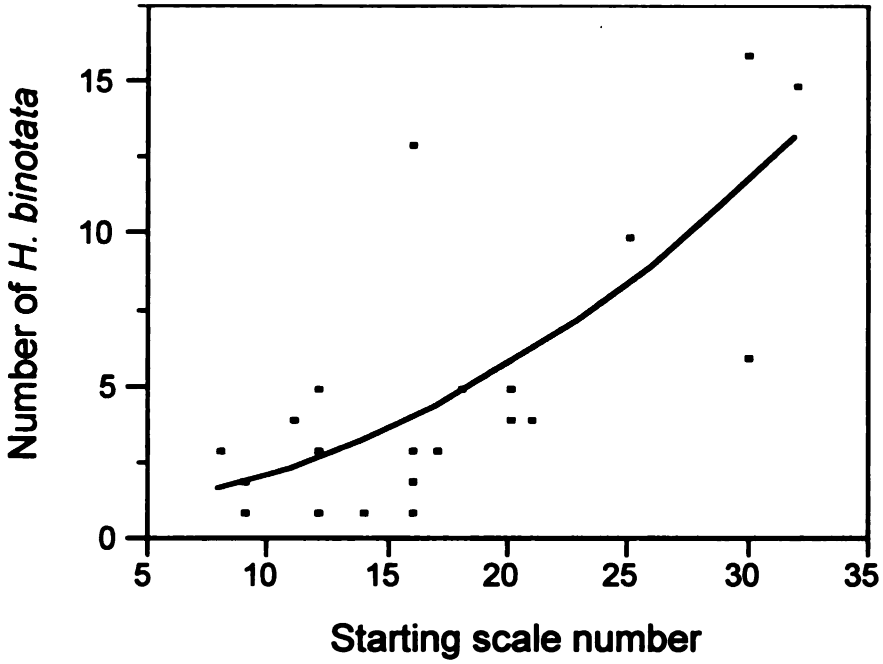


Figure 2. Relationship between the total number of *H. binotata* larvae (covert + overt) and the number of gravid scales at the start of the experiment for a) caged (ants absent) and b) uncaged (ants present) treatment shoots on 5 July, 1996. *r* is the product-moment correlation coefficient. Starting scale numbers did not go below 5.

24 pairs of treatment shoots on 8 Aug found a total of only 12 second instar scales, all on a formely caged shoot.

Discussion

Previous studies indicate that ant-tended scale colonies persist longer and become larger than unattended colonies, apparently due to ant interference with the scales' natural enemies (Bradley 1973, Jutsum et al. 1981, Buckley & Gullan 1991, Itioka 1993). Indeed, when ants are not present, pine tortoise scale populations are usually extremely rare in the jack pine understory (McIntyre 1960, Bradley, 1973, Chapter 3). The primary reason for the absence of pine tortoise scales in non-ant areas appears to be very effective predation by its enemies, *Hyperaspis* spp. (Orr and Hall 1931, McIntyre 1960, Bradley 1973).

My study indicated larvae of *H. binotata* have traits or behaviors that allowed them to feed in ant-tended scale colonies. Some larvae were cryptic, feeding under scales, when ants were present. When ants were excluded, 2nd and 3rd instar beetles shifted to more of an overt feeding habit, feeding in the open on crawlers and 2nd instar scales. However, 1st instar lady beetles remained primarily covert in behavior and 4th instars remained primarily overt in behavior. If attacked by ants, waxy-tufts or glandular secretions usually repelled the attacking ant, but the majority of overt larvae were ignored by the tending ants.

While remaining under gravid scales would certainly be beneficial to the larvae in terms of hiding from ants, I cannot rule out the possibility that this covert behavior is a pre-adapted behavior for early instars, allowing them to find their prey. I first observed *H.*

binotata larvae several days before crawlers appeared, and am unsure what these larvae fed upon. Simanton (1916) reported that adults will feed upon aphids, scales, honeydew, and their own eggs, while larvae appeared to feed only upon crawlers and young scales. I did see 1 case of cannibalism involving a 4th instar feeding upon a 2nd instar. The behavior of feeding under scales by *H. binotata* may be more of a response by early instars to the location of initial high densities of scale eggs and crawlers than ant presence. Whereas a large number of overt 1st instars were observed in the open prior to crawlers appearing, 1st instars virtually disappeared when crawlers began appearing on shoots, indicating eggs were being laid by gravid scales. Presumably, 1st instars had moved under these scales to feed on the high concentrations of eggs or crawlers found there. Early instars of other *Hyperaspis* spp. also feed under or within a "host" on eggs and hatching larvae (McKenzie 1932, Nsiama She et al. 1984, Sullivan et al. 1991, Booth et al. 1995).

After antennating a late larval instar, ants usually ignored it. Larvae observed on other branches at the study site were also feeding in the open unmolested by ants. This same behavior was observed between *H. congressis* and *F. obscuripes* (Bradley 1973). Larvae did not appear to be chemically camouflaged as seen in larvae of the coccinellid *Platynaspis luteorubra* (Goeze) (Völkol 1995) since some *H. binotata* larvae were attacked by ants. Additionally, during previous pilot studies, 3rd and 4th instars newly placed on shoot tips were almost always attacked when encountered by tending ants. I suggest the possibility that the ants may have become habituated or "gave up" to the presence of *H. binotata*, similar to that seen with adult *P. luteorubra*. Adult *P. luteorubra* are aggressively attacked by ants for about 45 s, then the ants give up their attack and leave the beetles alone for at least 20 minutes (Völkol 1995). I hypothesize also that this ant behaivor may be dependent on the population size of overt *H. binotata* larvae present. At low larval numbers, enough naive ants may be present that the attack rate on the few overt beetle larvae is high enough that the ants either succeed in removing them or drive the larvae under scales. At larger numbers, ants would encounter so many larvae that they begin ignoring the overt larvae. If so, this would present an interesting case where an ant-homopteran mutualism becomes less important for the homopteran as predator numbers increase, unlike that seen in other ant-homopteran mutualisms (Cushman & Whitham 1989). Additional studies need to be conducted to determine whether encounters between larvae and naive ants would elicit an attack by the ants and to identify if a critical number of contacts between ants and larvae are needed for habituation to occur.

The large numbers of larvae found on both caged and uncaged branches indicates that female beetles were successful in ovipositing on branches in the presence of ants, unlike Bradley's (1973) findings with *H. congressis* and *F. obscuripes*. He reported that ants constantly harassed female beetles, keeping them from ovipositing on scale infested branches. While I rarely observed adult beetles in the field, I did observe a few cases where ants charged at adult beetles. In all cases the beetles either avoided the ant by falling off the branch or moving to the other side of the branch or up a needle. Similar observances have been seen in other lady beetle adults when attacked by ants (Bradley 1973, Völkol 1995). Apparently though, this aggressive behavior by ants towards female beetles did not keep them from ovipositing in scale colonies. My results also imply that female beetles cue on scale numbers (Figure 2) and oviposit more eggs in larger scale colonies, or that more female beetles are attracted to larger scale colonies than to smaller colonies.

The ability of *H. binotata* larvae to feed in ant-tended scale colonies plus the large number of larvae observed apparently eliminated the scale population from all but 1of the 48 treatment shoots by August. Each *H. binotata* larva is estimated to consume some 3000 scale eggs or young scales before pupation (Simanton 1916), the reproductive output of six adult scales (Rabkin & Lejeune 1954). A census of about 20 other trees in the area known to have had scale colonies revealed similar results. All that remained of 2nd instar scales were indentations or scars on shoots where they had attached. I had observed previously similar scars left on shoots after watching *H. binotata* larvae feed on 2nd instar scales.

In conclusion, *H. binotata* larvae appeared to use a shifting defensive strategy against scale-tending ants, moving from a more covert behavior as 1st instars to a more overt behavior as 4th instars. When ants were excluded, 2nd and 3rd *H. binotata* instars shifted from covertly feeding to overtly feeding. Both waxy-tufts and glandular secretions were used by overtly feeding larvae when attacked by tending ants. However ants usually ignored later instars. Taken together, these behaviors and defenses allowed *H. binotata* to infiltrate ant-tended *T. parvicornis* colonies, altering the dynamics of this ant-scale mutualism in favor of *H. binotata*. This success of *H. binotata* apparently contributed to a collapse of the scale population in this Allegheny mound ant area.

CHAPTER 5

Summary and Conclusions

This study indicated that the presence of large populations of ants, acting as both mutualists and predators, can have strong modifying effects on predator-homopteran interactions. These modifying effects in turn can alter the species composition and population densities of homopteran and predator communities.

On jack pine of north-central Michigan, the distribution of various homopteran and homopteran predators was associated with the presence of the Allegheny mound ant, *Formica exsectoides*. On a gradient from no-ant density to high-ant density, the homopteran community shifted from one made up predominately of the non-tended pine woolly aphid *Schizolachnus piniradiatae*, to one composed primarily of three tended homopterans, the aphids *Cinara banksiana* and *C. ontarioensis*, and the pine tortoise scale *Toumeyella parvicornis* (Chapter 2). A third aphid, *C. pergandei*, did best in areas where *F. exsectoides* densities were low (Chapter 2).

Experiments involving some of these homopterans and their potential predators indicated Allegheny mound ants (hereafter mound ants) impacted them by playing at least two different roles. As a predator of non-tended pine woolly aphids, mound ants appeared to suppress these populations. This same predatory or aggressive behavior also contributed to mound ants providing enemy-free space for some homopterans. Generalist predators such as lacewings were attacked and removed from branches by mound ants (Appendix 3), probably contributing to the low lacewing numbers found in mound ant areas (Chapter 2). Mound ants also interfered with the predator-prey interactions of *C. banksiana* and its specialist mirid predators *Pilophorus furvus* and *P. urhlei* (Chapter 3). However, the type of interaction between mound ants, the pine tortoise scale and its specialist predator, *Hyperaspis binotata* (Coccinellidae) is less clear (Chapters 3, 4).

Population impacts of *F. exsectoides*

In modifying top-down regulation of *C. banksiana* populations by mirids, mound ants allowed *C. banksiana* populations to become much larger in mound ant areas than in the non-mound ant areas (Chapters 2,3). My observations indicated that ants interfered with mirid activity rather than preying directly on them. This interference was sufficient to generate enemy-free space for the aphids when ants were present (Chapter 3). Mirids appeared to be very visual and agile, easily escaping any approaching ants (pers. obs.). However, this behavior may have resulted in mirids spending more time on needles and shoots away from aphids, when ants were present, thus reducing their success at capturing prey. The presence of mound ants allowed aphid colonies to become much larger than untended colonies. Other studies have indicated similar patterns (Bradley & Hinks, 1969; Wheeler 1991).

This mound ant interference with the predator-prey interaction of mirids and aphids stands in contrast an apparent lack of effective interference by mound ants of the predator-prey interaction involving pine tortoise scales and their specialist predator, *H. binotata*. While pine tortoise scales were virtually absent from areas without mound ants, indicating ants may provide protection against generalist predators, experiments indicated that tending mound ants provided little protection to scales against *H. binotata*. Scale populations declined equally whether mound ants were present or not (Chapters 3,4). A reason mound ants were not successful at providing protection to scales against *H. binotata* may derive from the way *H. binotata* escaped removal by tending ants. Unlike mirids, *H. binotata* remained in and continued to feed in scale colonies, despite tending mound ants (Chapters 3,4). Larvae of *H. binotata* were cryptic, hiding and feeding under gravid scales as early instars, and as late instars used waxy tufts and glandular secretions to repel any attacking ants while feeding in the open (Chapter 4). One other observation that may have contributed to the lack of protection for scales was an apparent window of vulnerability for young scales. The literature states that young pine tortoise scales don't begin producing honeydew until after they mate, and then only the females produce it (Rabkin & Lejeune 1954). This would leave a window where young scales were not producing honeydew for about 3 weeks (Rabkin & Lejeune 1954), and could result in ants abandoning these scales for this time period. While the mean number of ants dropped on trees with both pine tortoise scale and *C. banksiana,* their numbers and from about 10 to 2 ratio of ants to tended homopterans, this ratio on July 22, 1993 (Figure 1), the same time young scales were numerous (Chapter 2).

The interactions between mound ants, mirids, and *H. binotata* may actually be of a more positive nature than one would first predict. Using different traits to overcome ant protection, both of these specialist predators had access to large populations of their

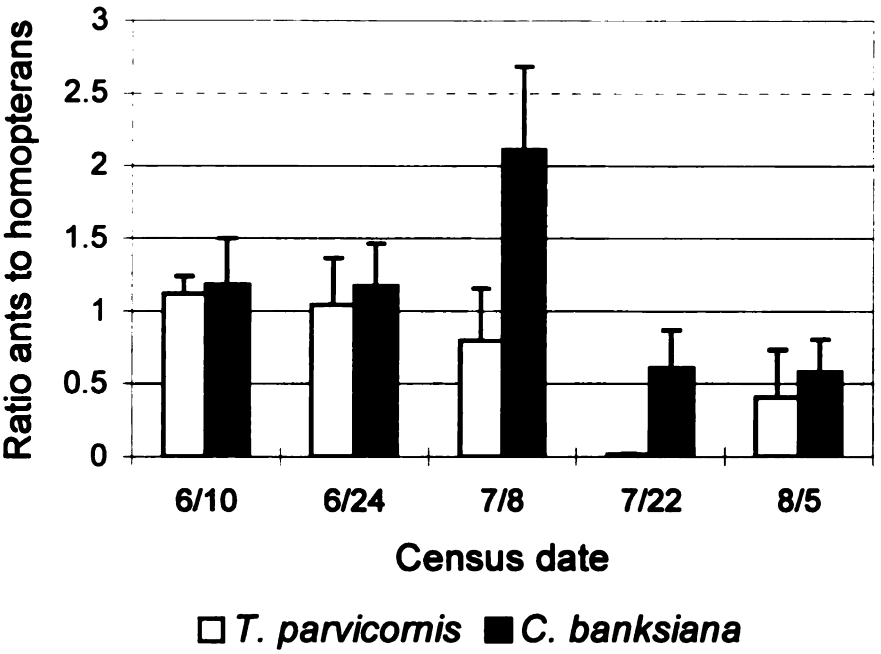


Figure 1. Ratio of ants to tended homopterans (*T. parvicornis* or *C. banksiana*) observed on a seedling or sapling jack pine. Error bars represent 1 SE.

respective prey. Compared to the very low numbers of these aphids and scales found in non-mound ant areas, these large prey populations may have served as a predator refuge for mirids and *H. binotata*, maintaining the larger populations of these specialist predator populations than observed in areas without mound ants.

The one generalist predator examined, lacewing larvae, did not do well in the presence of ants (Chapter 2, Appendix 3). Experiments indicated that mound ants attacked and removed lacewings from branches, probably for food. This predation by mound ants may account for the lower numbers of lacewings found in mound ant areas than the non-mound ants areas. Salticid spiders also had smaller populations in areas with mound ants; the reason for this smaller population is unknown and may be more related to competition between ants and salticids than to direct predation of salticids by ants. The reduction of these generalist predator populations could also contribute to enemy-free space for tended aphids and pine tortoise scales.

Direct predation by mound ants also may have contributed to the lower numbers of pine woolly aphids in mound ant areas than non-mound ant areas. Pine woolly aphids were attacked and removed by mound ants, significantly reducing there numbers on ant patrolled branches (Chapter 2). Although the number of generalist predators was reduced in mound ant areas (Chapter 2), the pine woolly aphids appeared not to have benefited from this reduction since these ants were so numerous. Although not examined, I also cannot rule out the impact of competition between tended homopterans and pine woolly aphids.

The one aphid apparently least influenced by mound ant presence was *C. pergandei*. It was found at low numbers in all mound ant-density areas but was most abundant in the low mound ant-density areas (Chapter 2). *C. pergandei* lived as a solitary aphid and was quick to run if disturbed (Chapter 2, pers. obs.). In areas with mound ants, I observed some individuals tended by ants and others run from approaching ants. This aphid may be exploiting an edge effect of mound ant distribution. *C. pergandei* in these areas benefited from the lower predator numbers found here than found in the non-mound ant areas, where they could remain untended by ants, depending on their own defenses (e.g. running) to avoid any predators.

Allegheny mound ants were the most abundant ants encountered on jack pine seedling/saplings in 1993 (Chapter 2). A result of this dominance appears to be that Allegheny mound ants occupy a key position in this jack pine ecosystem (Figure 2). Similar patterns may also be observed for other ant species, such as *F. rufa*, that occupy such a dominant position in an ecosystem.

In conclusion, this study illustrated that large populations of aggressive-mutualist ants, such as Allegheny mound ants, can allow larger populations of tended homopterans and some of their specialist predators to exist than observed in areas without these ant populations (Figures 2,3). The presence of such ants also appears to impact this community by reducing some generalist predators and non-tended aphids (Figure 2) compared to the areas without mound ants (Figure 3).

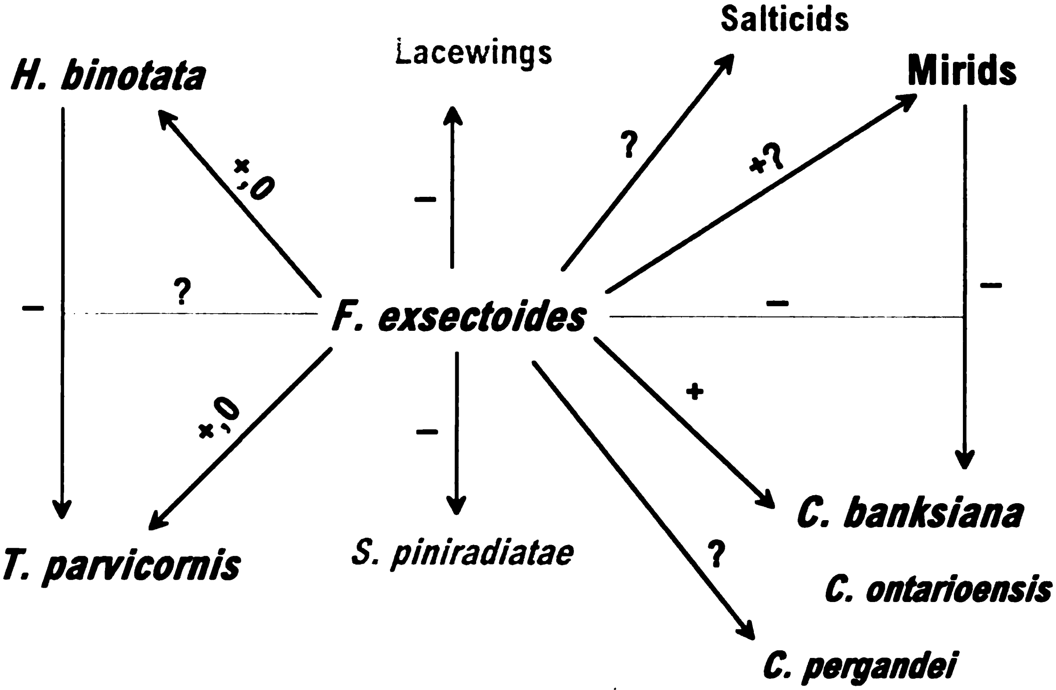


Figure 2. Diagram illustrating top-down interactions of a homopteran-predator community in a jack pine forest and the central role *F. exsectoides* plays in interacting with various populations. Lighter shades represent those populations that declined in *F. exsectoides* areas. Dashed lines represent interference of predator-prey interaction by *F. exsectoides*. Other interactions are not illustrated for clarity.

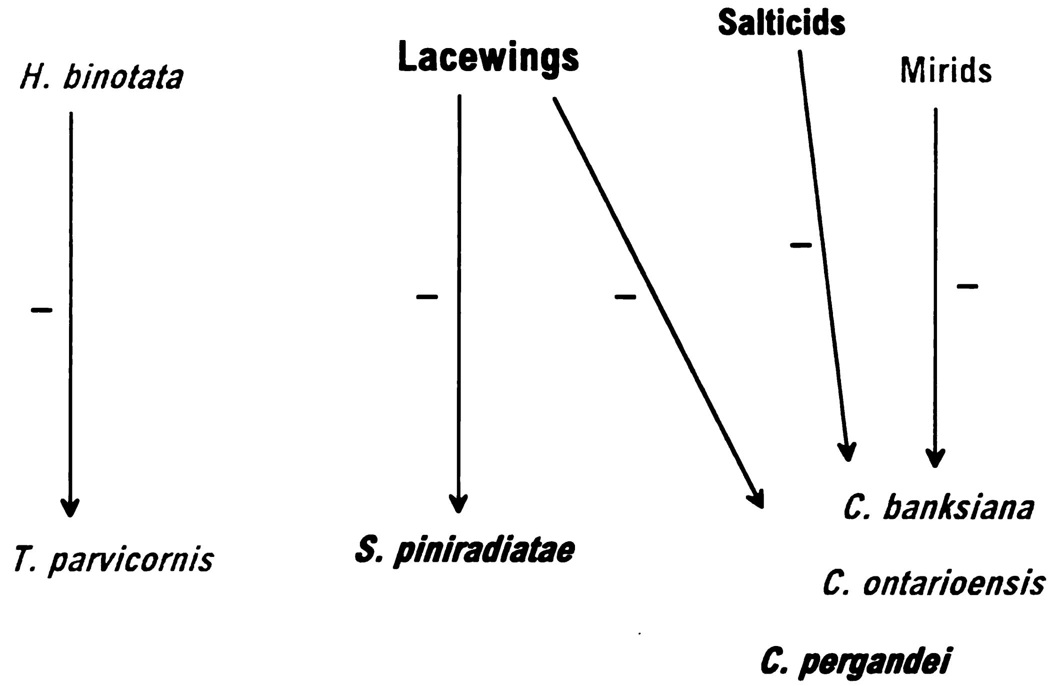


Figure 3. Diagram illustrating top-down interactions homopteran-predator community without *F. exsectoides*. Lighter shades represent those populations that declined in areas without *F. exsectoides*. Other interactions are not illustrated for clarity.

APPENDICES

APPENDIX 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 1998-4

Title of thesis or dissertation (or other research projects):
Differential effects of the Allegheny mound ant, Formica exsectoides Forel, on aphid, scale, and predator populations and their interactions in jack pine forests

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name (s) (typed)
D. Bryan Bishop

Date July 20, 1998

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24:141-42.

Deposit as follows:

Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.
Copies: Included as Appendix 1 in copies of thesis or dissertation.
Museum(s) files.
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

APPENDIX 1.1

Voucher Specimen Data

Page 1 of 2 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Hyperaspis binotata Say	Mich: Crawford Co. Huron Nat'l Forest T.25.N R.1.W Sec 24 on jack pine								
	21-VII-1996					2	1		MSU
	28-VI-1998		5						MSU
Pilophorus uhleri Knight	Mich: Crawford Co. Huron Nat'l Forest on jack pine T.25.N R.1.W Sec 11								
	21-VII-1996					1			MSU
	T.25.N R.1.W Sec 24 25-VII-1993					1			MSU
Pilophorus furvus Knight	Mich: Crawford Co. T.25.N R.1.W Sec 24 Huron Nat'l Forest on jack pine 21-VII-1996					1			MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

D. Bryan Bishop

Date July 20, 1998

Voucher No. 1998-4

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

20 July 1998

Curator Date

APPENDIX 1.1

Voucher Specimen Data

Page 2 of 2 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Cinara banksiana Pepper & Tissot	Mich: Crawford Co. Huron Nat'l Forest C-79 T.25.N R.1.W Sec 24 on jack pine stems 28-VI-1998			11		3			MSU
Cinara pergandei (Wilson)	same on jack pine stems 28-VI-1998			5					MSU
Cinara ontarioensis Bradley	same on jack pine needles 28-VI-1998			30					MSU
Schizolachnus piniradiatae (Davidson)	same, on jack pine needles 28-VI-1998			15		1			MSU
Toumeyella parvicornis (Cockerell)	same, on jack pine stems 28-VI-1998			35		12			MSU
Formica exsectoides Forel	same, on jack pine 21-VII-1996					2	1		MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

D. Bryan Bishop

Date July 20, 1998

Voucher No. 1998-4

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

20 July 1998

Curator Date

APPENDIX 2

Biology of *Formica exsectoides*

The Allegheny mound ant, *Formica exsectoides* Forel, belongs to the *F. exsecta* group of mound building ants. This group contains two other North American species: the western *F. opaciventris* Emery, and the western to mid-west *F. ulkei* Emery (Creighton 1950, Scherba 1961, Gregg 1963). *F. exsectoides* has the widest geographic rangeof all three ants, from Nova Scotia, south to Georgia, and west to Wisconsin, Iowa, Colorado, and northern New Mexico (Creighton 1950, Gregg 1963), although the more western populations may not represent contiguous populations with the eastern and midwest populations (Gregg 1963). It is described as the only ant building large mounds east of the Mississippi river in North America (Forel 1901, Pierson 1922).

Mounds have been found in ecosystems ranging from meadows to oak-hickory, ponderosa and jack pine forests (McCook 1877, Pierson 1922, Andrews 1926, Headly 1943, Haviland 1947, Dimmick 1951, Gregg 1963, Allen et al. 1970, Campbell 1990, Bristow et al. 1992). The main requirements for nesting appear to be well drained soils with good sunshine or numerous open spaces (Pierson 1922, Headly 1943, Haviland 1947, Dimmik 1951). This requisite for sun shine (Andrews 1927) has resulted in *F. exsectoides* receiving a pest status in forest systems since it has been reported to kill young trees encroaching on its mounds (Pierson 1922, Andrews 1928, Wilson 1977).

Individual mounds of this ant are polygynous, containing multiple queens, (Andrews 1929, Cory & Haviland 1938, Bristow et al. 1992). This allows mounds to be long-lived, up to 30 years (Andrews 1926), since new queens are available to replace lost ones. *F. exsectoides* acts as a unicolonial species, exhibiting no colony boundaries (Hölldobler & Wilson 1990); workers from different mounds in an area treat each other as nestmates.

New colonies are formed by one of two ways. Both *F. exsectoides* and *F. ulkei* queens act as temporary social parasites of *F. fusca*; mixed colonies containing workers of the parasite species and *F. fusca* have been observed (Wheeler 1913, Creighton 1934, Creighton 1950, pers. obs.). A nuptial queens apparently enters a *F. fusca* nest either by stealth or else by permiting herself to be carried into the nest by *F. fusca* workers (Creighton 1950, Hölldobler & Wilson 1990). Later, she disposes of the *F. fusca* queen and takes over the reproductive role (Hölldobler & Wilson 1990). The host of *F. opaciventris* is unknown and temporary social parasitism may not occur in this species (Creighton 1950, Scherba 1961).

Budding or colony fission appears to be the commonest way of new nest formation for all three species (Andrews 1926, Haviland 1947, Creighton 1938, Creighton 1950). A new mound is formed from a few meters to tens of meters away from the parent mound (Haviland 1947). Shading of mounds appears to be partly responsible for triggering budding in *F. ulkei* (Scherba 1958).

Colony formation by budding can result in populations of *F. exsectoides* becoming very large, both in terms of mounds and individual ants. McCook (1877) estimated 1700 mounds in a 50 acre area near Hollidaysburg, PA. Other workers have reported mound densities ranging from a low of about 7 mounds per acre in Maryland (Cory and Haviland 1938) to over 100 per acre in Alcona County, Michigan (Allen et al. 1970, see also Andrews 1925, Price 1945, Dimmick 1951). Bristow et al. (1992) reported mound densities of 7 per 1000^2 m in Crawford Co., Michigan. These high mound densities can also translate into large populations of individual ants. Cory and Haviland (1938) estimated that in 10 acres, 73 mounds would contain 11 to 12 million ants, or about 27 ants for every square foot.

F. exsectoides shows several traits that may make it a good biological agent in forest systems (Campbell 1990). These include having long-lived colonies, polygyny and unicolonial behavior (based on Finnegan 1971). These traits lead to the large populations that can allow this ant to suppress some herbivore populations (Campbell 1990, Campbell et al. 1991), and other ant species (Hölldobler & Wilson 1990). Additionally, Allegheny mound ants readily tend various honeydew producing Homoptera (Cory & Haviland 1938, Haviland 1947, Dimmick 1951). Its high densities and aggressive behavior sets the stage for it to also affect the honeydew producing homopteran community.

APPENDIX 3

Lacewing-Ant Interactions

Design

Experiments were conducted in 1995 at Sites 1 and 2 to determine the type of interactions occurring between lacewings and *F. exsectoides*. Eleven trees with aphid colonies and ants were randomly selected. Two second or third instar lacewings were placed on the tip of a branch. I made observations of these lacewings for 15 min or until they were removed from the branch by an ant. Data were also collected on the outcomes of ant-lacewing interactions and a survival analysis was conducted on the time untill encounter data.

Outcome

Eleven of the initial 44 lacewings did not establish on branches due to other factors such as wind. These were not included in the analysis. Within the first 30 s of this experiment, 37% of the remaining 33 lacewings were discovered by ants and had either been removed by the attacking ant or fell off the branch due to the attack (Figure 1). At the 60 s mark, over half (52%) of the lacewings had been taken off the branch. From 1 min. to 15 min. only an additional 8% of the lacewings had been discovered. The remaining 13 lacewings remained stationary or near the distal end of shoots, several cm from the aphid colonies.

In every case (20) that an ant discovered a lacewing, the ant attacked the lacewing. Four of these attacked lacewings fell from the branch during the attack, the others were carried off by the ant. These results indicated that lacewing larvae were very vulnerable to ant attack, unlike *H. binotata* and mirids. Mirids were much more agile than lacewing larvae and avoided any ants that came within their vision (Chapter 2). *H. binotata* either hid from ants or used mechanical and chemical defenses to repel ant attack (Chapter 4).

The removal of lacewings (and subsequent suppression of lacewing populations) by *F. exsectoides* would further contribute to these ants providing enemy-free space for aphids in this jack pine forest (Chapter 3).

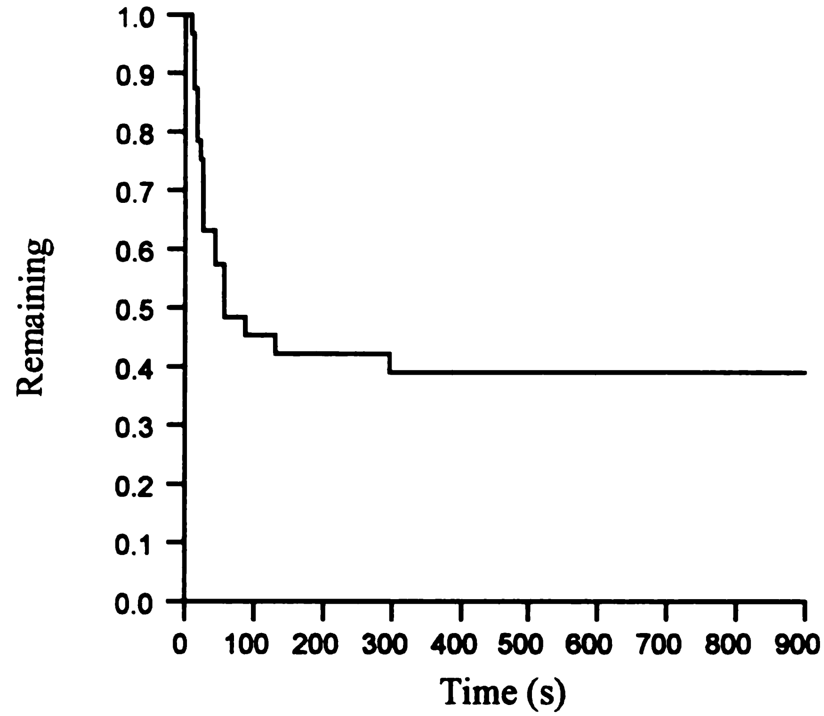


Figure 1. Residence time of second and third instar lacewings placed on branch tips patrolled by *F. exsecotides*.

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