Interactions between ants (Hymonoptera: Formicidae) and Aphis fabae Scop. complex (Hemiptera: Aphididae), on Cirsium arvense L. Scop (Compositae) by Ronald Franklin Lang

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Entomology
Montana State University
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Abstract:
Canada thistle (Cirsium arvense (L.) Scop. (Compositae)) is a widespread weed in Montana. The black bean aphid (Aphis fabae Scop, complex) (Hemiptera: Aphididae) colonizes C. arvense and is tended by ants for the honeydew the aphids provide. It is hypothesized that the presence of ants enhances ft. fabae and survival in the A. fabae colonies established on C. arvense by protecting the aphids from predators.

The study utilized three sites each year for two years. The treatment was to choose, at random, a set number of plants and apply Tangle-footR to those plants to prevent ant access. The control was to leave a set number of plants free of Tangle-foot to allow ant access. Equal numbers of A. fabae were transplanted to plants chosen for the study which lasted seven weeks. Plants from the treatments and the control were cut each week and the A. fabae and predators were counted. The plants to be cut each week were chosen from a random numbers table.

The study indicated that while ants do make a difference in the number of A. fabae in a colony, A. fabae were not effectively protected against predators. Predator numbers increased as the A. fabae numbers increased. The results were not conclusive as to the enhancement or suppression of the development of alates in the colony.
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ON CIRSIMUM ARVENSE L. SCOP (COMPOSITAE)

by

Ronald Franklin Lang

A thesis submitted in partial fulfillment
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Bozeman, Montana

July 1988
ii

APPROVAL

of a thesis submitted by

Ronald F. Lang

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

July 29, 1988
Signature
Chairperson, Graduate Committee

Approved for the Major Department

July 29, 1988
Signature
Head, Major Department

Approved for the College of Graduate Studies

9/8/88
Signature
Graduate Dean
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Dr. Richard Lund recommended the statistical methods for this study.

The aphids captured in this study were identified by Susan Halbert. Representative ants were collected from the study sites and sent to USDA Insect Identification labs in Maryland and determined to species by Dr. D. R. Smith. The coccinellids were determined by Kathy Johnson in consultation with Dr. Michael Ivie. Voucher specimens from this study were submitted to the Montana State University Insect Collection, Bozeman, Montana.

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ABSTRACT

Canada thistle (Cirsium arvense (L.) Scop. (Compositae)) is a widespread weed in Montana. The black bean aphid (Aphis fabae Scop. complex) (Hemiptera: Aphididae) colonizes C. arvense and is tended by ants for the honeydew the aphids provide. It is hypothesized that the presence of ants enhances A. fabae and survival in the A. fabae colonies established on C. arvense by protecting the aphids from predators.

The study utilized three sites each year for two years. The treatment was to choose, at random, a set number of plants and apply Tangle-foot® to those plants to prevent ant access. The control was to leave a set number of plants free of Tangle-foot to allow ant access. Equal numbers of A. fabae were transplanted to plants chosen for the study which lasted seven weeks. Plants from the treatments and the control were cut each week and the A. fabae and predators were counted. The plants to be cut each week were chosen from a random numbers table.

The study indicated that while ants do make a difference in the number of A. fabae in a colony, A. fabae were not effectively protected against predators. Predator numbers increased as the A. fabae numbers increased. The results were not conclusive as to the enhancement or suppression of the development of alates in the colony.
Aphids (Hemiptera: Aphididae) are important plant feeding insects. Aphids are vectors of viruses that cause plant disease, and damage plants by the toxins they inject into the plants when feeding. This liquid diet causes large amounts of "honeydew" to be excreted from their anus as a way to eliminate the excess water, some undigested sugars, and other waste materials. The honeydew is a food source of many insects including some ant species (Borror et al. 1976).

The life cycle of aphids is complex. In temperate zones aphids over-winter as eggs either on a host plant or in a few cases in the nests of ants. The eggs over-winter and in the spring hatch into females which begin to reproduce parthenogenetically. These females are usually wingless, however, after about two generations, a winged generation develops. Aphid dispersal to summer host plants begins as soon as the winged aphids, or alates, become adults. Once an alate female finds an appropriate host plant, she begins to produce female offspring starting a new colony. Aphids reproduce very rapidly and produce large populations in a short time (Bland and Jaques 1978; Borror et al. 1976). They also reproduce at a wider range of temperatures than many of their predators and parasitoids, allowing them to reproduce rapidly (Morrill 1985).
Alates develop in response to crowded conditions in the growing colony (Dixon et al. 1968). The alates mature and disperse to other plants and start new colonies. This phase of the aphids life cycle continues through the summer until fall. In the fall male and female alates are produced, mate, and the females lay eggs on the appropriate overwintering site (Johnson 1959; Dixon 1985).

The effect of the presence of ants at A. fabae colonies on C. arvense has not been studied. Studies on other hosts and with other aphid species, suggest that 1) ants may provide protection from predators, 2) protection by ants may increase the colony size, 3) ants may inhibit the development of alates, and 4) ants contribute to the maintenance of the aphid colony in a compact group. These topics are the focus of this study.

Ants (Hymenoptera: Formicidae) tend many families of insects for honeydew and the comparison study of ant behavior with coccids and other honeydew producing insects was beneficial in understanding ant/aphid interactions. Formica obscuripes protect Toumeveella numismaticum (Hemiptera: Coccidae), a pest of Pinus banksiana Lamb from the predator Hyperaspis congressis Chevrolat (Coleoptera: Coccinellidae). The coccinellid does not destroy the coccid populations because of F. obscuripes defense of the coccids. There was some equilibrium established between predator, protector, and protected. The coccid colonies, protected by the F. obscuripes were a reservoir for a continued presence of unguarded coccids that were fed upon by the coccinellids. Therefore there was always a reservoir of
predators to control rapid outbreaks of coccids. If all the coccids were destroyed the coccinellid populations would be too low to control subsequent coccid outbreaks (Bradley 1973).

An experiment was designed to determine the effect of ant tending on *Aphis fabae* colonizing the common weed *Cirsium arvense* in southern Montana. Specifically studied was the effect of ants on predators, aphid development, fecundity (colony size) and colony stabilization.

*Aphis fabae* colonies can survive in the absence of tending ants as they are not dependent on them for the removal of honeydew. If the colony is not ant tended, the aphids forcibly eject the honeydew away from the colony, but the *A. fabae* colonies are usually ant-tended (Banks 1958). Colonies of *A. fabae* are usually in tight clusters, with the nymphs clustered around the parent giving the ants a smaller area to protect and from which to gather honeydew. The colony response to crowding is for individual mature apterae to move to different parts of the plant and establish new satellite colonies. The presence of tending ants delays this dispersal reaction (Banks 1958).

I hypothesized that *A. fabae* colonies tended by ant species in the study sites will have larger colonies due to higher fecundity, lower migration, and less predation than *A. fabae* colonies without ants.
CHAPTER 2

LITERATURE REVIEW

Ants and Aphids

The complex relationships between ants and aphids have been studied in detail on a variety of host plants. Many species of aphids are tended by ants seeking honeydew as a rich food source (Bradley and Hinks 1968; Takeda et al. 1982; Nixon 1951). Honeydew from Myzus persicae (Sulzer) (Hemiptera: Aphididae) contained undigested fructose, glucose, sucrose, free amino acids, and lipids (Strong 1965). Ant species that take advantage of this food source and tend aphids include members of the subfamilies Formicinae, Camponotinae, Dolichoderinae, and Myrmicinae (Flanders 1951).

The General Influence of Ants on Aphid Colonies

Formica cinerea Mayr (Hymenoptera: Formicidae) were found to aid in colony establishment of Aphis variance Patch and Aphis helianthi Monell (Hemiptera: Aphididae) on fire weed, (Epilobium augustifolium L.) (Addicott 1979). The foundress alates of A. variance, A. helianthi, and Cinara gracilis (Wilson)(Hemiptera: Aphididae) were susceptible to predation but survivorship was improved if they were quickly found and tended by Formica obscuripes, Dolichoderus (Hypoclinea) taschenbergi (Mayr), Formica fusca L., F. cinerea
Mayr, *Formica neorufibarbis* Emery or *Tapinoma sessile* (Say) (Addicott 1978; Addicott 1979). Colonies of *Cinara occidentalis* (Davidson) on *Abies concolor* Gord. and Glen. tended by *Camponotus modoc* Mayr (Hymenoptera: Formicidae), exhibited a higher survival rate than those from which ants were excluded. Aphids did not survive if the ants were removed and/or prevented access to the aphid colony (Tilles and Wood 1982). *Aphis fabae* colonies produced more offspring and thus formed larger colonies when tended by *Lasius niger* (L.) (Hymenoptera: Formicidae) (Banks 1962).

The survival of some aphid species seems to be ant-dependent and most previous studies would support the hypothesis that ant attendance enhances aphid numbers. It must be noted that this refers only to those aphids that are generally tended by ants. Many aphid species such as *Capitophorus* sp., *Urolecon* spp., and *Macrosiphum valerianace* (Clarke) thrive quite well in the absence of ants (Addicott 1979; Morrill 1978; Stary 1986) and some ant species prey directly upon aphids (Dixon 1985). For example, *Solenopsis invicta* Buren (Hymenoptera: Formicidae) preys on *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae) (Morrill 1978).

**Ant Tending Effects on Aphid Development and Behavior**

Ants may affect the cohesiveness of aphid colonies. When *F. obscuripes* were removed from a colony of *C. gracilis* on Jack pine, the aphids became restless and began to disperse (Bradley and Hinks 1968). *Aphis fabae* tended by *L. niger* on *Vicia fabae* Scopli remained in
compact colonies at the top of the plant. *Aphis fabae* colonies that were not tended by ants dispersed and established smaller colonies on the lower and older leaves of the plant. However, *L. niger* did not prevent individuals from moving to the lower leaves as the colony grew larger. Non-tended colonies were weakened as individuals moved to the lower leaves or left the plant. Thus, the overall effect of the ant *L. niger* on colonies of *A. fabae* feeding on *V. fabae* was formation of larger, more compact, colonies on the younger more nutritious leaves by delaying dispersal to the lower more mature leaves (Banks 1958).

Alate development may be inhibited by the tending of ants, thereby slowing aphid dispersal and causing the development of larger colonies (Johnson 1959; Tilles and Wood 1982). The study by Tilles and Wood (1982) showed that when colonies of *Aphis craccivora* Koch (Hemiptera: Aphididae) were crowded, those tended by *Paratrachina* (Nylanderia) *baveri* Mayr (Hymenoptera: Formicidae) developed fewer alates than non-tended colonies. *Cinara occidentalis* colonies tended by *C. modoc* had significantly fewer alate forms than those colonies that were not tended (Tilles and Wood 1982).

Some aphids are known to secrete an alarm pheromone when disturbed or attacked (Nault and Montgomery 1976). Myrmecophilous aphid species tend to remain in place when the alarm pheromone is released in the presence of tending ants; non-myrmecophilous species tend to drop to the ground. *Aphis fabae* and *Chaitophorus populicola* Thomas (Hemiptera: Aphididae) have an inhibited dispersal response when tended by *Formica subsericea* Say (Hymenoptera: Formicidae).
However, untended aphids responded to the alarm pheromone by dispersing from the feeding cluster. The inhibition of dispersal behavior caused by the release of the alarm pheromone may be a key to the maintenance of a compact myrmecophilous aphid colony (Nault and Montgomery 1976).

**Ant Protection of Aphids From Predation**

Ant tending of aphid colonies may include protection from predators (Flanders 1951); however, authors disagree about the effectiveness of ant tending. The claim of protection was felt to be exaggerated by some (Banks 1962; Nixon 1951). Addicott (1978) found that ants effectively exclude predators and parasites. *Formica cinerea* and *F. fusca* tending *A. varians* kept coccinellid species away from the colonies. A significantly reduced number of coccinellids were found feeding on *A. varians* colonies that were tended by *F. fusca* and *F. cinerea* compared to the colonies which were not tended by ants (Addicott 1979). *Aphis fabae* colonies without *L. niger* in attendance were subject to heavy predation and sometimes complete destruction by *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), *Adalia bipunctata* Mulsant (Coleoptera: Coccinellidae), *Anthocoris nemorum* L. (Hemiptera: Anthocoridae), *Syrphus balteatus* Degeer (Diptera: Syrphidae), *Chrysopa carnea* Stephens (Neuroptera: Chrysopidae), and the parasite *Diaeretus* sp. (Hymenoptera: Braconidae) (Banks 1962).

It was shown that *L. niger* tending *A. fabae* colonies feeding on field beans directly enhanced the growth of the aphid colonies by
preventing A. bipunctata and Platyscheirus albimanus Fabr. (Diptera: Syrphidae) from feeding on the aphids (Banks 1962). It was found that when C. gracilis individuals strayed from the main colony they were subject to predation by Philophorus sp. (Hemiptera: Miridae) (Bradley and Hinks 1968).

Other studies show that ants do not show a consistent beneficial effect on aphid colonies. There is evidence that Formica polycrana Forst (Hymenoptera: Formicidae) may actually help some coccinellids find colonies of Sypydobius oblongus (Hemiptera: Aphididae) (Bhatkar 1982). Coccinella septempunctata L., Coccinella undecimpunctata L., and A. bipunctata (Coleoptera: Coccinellidae) have been observed gathering around the mounds of F. polycrana and following chemical trails left by the ants to locate aphid colonies. The use of ant trails by these coccinellids was especially noticeable in the spring. Coccinella septempunctata was able to determine how far and in what direction the colonies of S. oblongus were to be found. This information was detected from the F. polycrana odor trails that mark the way to the aphid colony (Bhatkar 1982).

Effects of Ants on Parasitoids

Ants discouraging parasitoids of aphids have been reported. The reported protection by ants from parasitoids on coccoidea may give insight into possible effects on parasitoids of aphids. The parasitoid Coccophagus capensis Comp. (Hymenoptera: Aphelinidae), which attacks Saissetia oleae (Hemiptera: Coccoidae), parasitized more
coccoidae when *Iridomyrmex humilis* Wheeler (Hymenoptera: Formicidae) were restricted. However *Coccophagus trifasciatus* Comp. (Hymenoptera: Aphelinidae) success was enhanced by the presence of *I. humilis*. *Iridomyrmex humilis* increased egg deposition of *C. trifasciatus* by driving away more efficient parasites (Flanders 1951).

**Aphid and Ant Species associated with Cirsium arvense**

The thistle *Cirsium arvense*, a native of Eurasia, has been introduced into North America where it is a noxious weed. Several studies of the entomofauna give an idea of the aphids utilizing this species.

In Saskatchewan, 4 species of aphids were found inhabiting this plant: *Capitophorus bragii* (Gillette), *Capitophorus carduinus* (Walk), *Capitophorus elaeagni* (del Guericio) and *Dactynotus cirsii* (L.) (Maw 1976). Four were also found in southern Montana: *A. fabae*, *Brachycaurus cardui* (L.), *C. carduinus* and *Dactynotus* sp. (Story et al. 1985). In central Europe the aphids *A. fabae cirsiiacanthoidis* and *B. cardui* were tended by a *Lasius* species (Stary 1986).
CHAPTER 3

MATERIALS AND METHODS

Study Site Description

Three study sites were selected the first season (1986). Site I was located along the west side of 11th Avenue, south of Kagy Boulevard in Bozeman, Montana. It was a narrow strip of land measuring 145 m X 6 m, between a hayfield and grass parking area, with electric poles down the middle. The area was old field vegetation consisting of Bromus spp., and C. arvense, with a small patch of wild rose (Rosa woodsii Lindl.) and a clump of chokecherry (Prunus virginiana L.).

Site II was in a pasture of Bromus spp., Carduus nutans L., and C. arvense, 3.2 km south of Four Corners, Montana (near Bozeman), measuring 75 m X 8 m.

Site III was in Bozeman, perpendicular at the north end to site I along the south side of Kagy Boulevard, west of 11th Avenue, measuring 45m X 30m. It was a drainage ditch, between the street and a hay field. The site vegetation consisted of Bromus spp. and C. arvense. Sites II and III were abandoned in the second year, due to unfavorable terrain, mowing, drought, and heavy grazing by dairy cows.

Four new sites were chosen for the second year study (1987) and each site was renumbered. Site I was located 6.4 km south of Amsterdam, Montana in an experimental enclosure fenced to check growth
and survival of C. nutans. The site, which measured 65 m X 8 m consisted of grass, C. nutans and C. arvense.

Site II and III are located at the 1986 Site I, extending further to the south. Site II measured 65 m X 6 m. Site III was located to the south of Site II and measured 168 m X 6 m and extended to a stand of young Populus sp. trees at the south end.

There were some problems in getting the A. fabae colonies to establish in year 2 (1987). One potential site was not used due to lack of colony establishment. A possible explanation for the differences in total aphid numbers in the two study years is the early and heavy presence of predators. At the beginning of 1986 two coccinellid adults were observed in Site I. But in the same area in 1987 coccinellid adults were seen throughout the site and one A. fabae transplant was lost to a coccinellid within 20 minutes of the aphids being placed on the thistle.

Choice of Sites and Study Plants

Before the study sites were chosen, thistle patches were surveyed in the Gallatin Valley to check how extensively A. fabae colonized C. arvense patches in the area. Nineteen patches were investigated in and around the Bozeman area. Plastic tubes filled with a honey-water mixture were taped to thistle plants to verify that foraging ants would find the food source within 24 hours. The tubes were packed three-fourths with cotton to prevent the ants from drowning.
Thistle plants were selected in each location by walking through the patch and randomly assigning them to control or treatment status, and numbered 1-25. The treatment plants were those A. fabae colonies to which ants would be allowed access; the control those from which they were excluded. The following requirements for including individual plants in the study were: 1) absence of aphids or treehoppers (Hemiptera: Membracidae), 2) plant mature enough to have a flower bud cluster, and 3) apparent freedom from diseases.

All the thistles used in the study were prepared by clipping leaves about one-third the way up the stem to form a leafless 7 cm band. The surrounding vegetation, that touched or might touch the thistle plant above the clipped area, was cut to prevent bridges from forming. Tangle-foot® (1) was then applied in 5 cm bands on the leafless stem area of the 25 thistles selected for control.

Establishing A. fabae Colonies

The A. fabae colonies were established each season on June 15th transplanting four apterous aphids onto each plant. The aphids were collected from naturally established colonies by taking a portion of the original A. fabae infested plant and placing it into a plastic bag for one-half hour. After this time, the aphids became scattered over the plant, and a small piece of thistle branch with four apterous aphids was cut. The thistle pieces were then secured on or near the buds of each selected study plant. The plants were checked after 7
days to determine presence or absence of an aphid colony. Only plants with an established colony were used for the study.

Materials Used

Ant species tending the *A. fabae* colonies on *C. arvense* were *Formica oreas comptula* Wheeler (Hymenoptera: Formicidae), *F. obscuripes*, *F. podzelica*, *F. neoclera*, *F. subnuda*, *Formica sp. rufa* group and *L. sitkaensis*. These ant species will hereafter be referred to simply as "ants" unless otherwise designated. The predators noted were *Coccinella transversoquattata richardsoni* Brown and *Coccinella novemnotata* Nerbst (Coleoptera: Coccinellidae), Syrphid flies (Diptera: Syrphidae) and *Orius insidiosus* say (Hemiptera: Anthocordiae).

Collecting and Recording Data

Once the colonies of *A. fabae* in each site had been established for 14 days, and at 7 day intervals, thereafter, 5 each treatment and control plants were cut at each site at random using a table of random numbers. Each collection was placed in a plastic bag and transferred to a refrigerator until the aphids cooled and became inactive to facilitate counting. Aphids and ants were collected, preserved in 70% alcohol, and later determined to species. Records were kept on the number of 1) apterous *A. fabae*, 2) nymphs with developing wing pads, 3) alate aphids, and 4) predators. Plants that did not meet the standard because of the failure of the aphids to establish in the
first 7 days, the death of the plant, or the presence of ants on
plants that were supposed to be ant-free were rejected for data
collection.

In the second year the following changes were instituted. At
Site I and II, A. fabae colonies were established in the same week as
above with Site III established 14 days after the initial sites using
naturally established A. fabae colonies. The selected colonies had
<200 aphids and were estimated to be 14 days old. Any ants tending
control colonies were removed. This was necessitated by loss of an
intended site.

Statistical Analysis
The statistical method used for comparison of aphid and predator
numbers was the Wilcoxon non-parametric paired sample test (Snedecor
and Cochrane 1980). A non-parametric test was used because of the
inconsistent numbers over the five weeks due to loss of treatment and
control plants.

The 2 X 2 Chi-square contingency analysis was used to compare
ant-tended and non-tended A. fabae colonies for colony establishment
after transplant and to determine if ant tending inhibited alate
production (Snedecor and Cochrane 1980). Probability values < 0.05
were considered to be significant.
CHAPTER 4

RESULTS AND DISCUSSION

A. fabae Distribution

A cursory survey of C. arvense patches in Gallation County, Montana resulted in finding 14 of 19 surveyed patches infested with A. fabae. The infested patches were larger (X = 152.2 stems, N = 14) than the uninfested patches (X = 76.0 stems, N = 5).

Ant Species and Aphid Predators

Aphis fabae feeds on Cirsium arvense in Montana. The colonies are tended by the ant species F. oreas comptula, F. obscuripes Forel, F. podzelica Francouer, F. neoclara Emery, F. subnuda Emery, Formica sp. rufa group, and Lasius sitkaensis Perg. (Hymenoptera: Formicidae).

With few exceptions, A. fabae colonies were tended by one species of ant. A few colonies tended by F. obscuripes had L. sitkaensis present. In the one case where F. obscuripes and F. podzelica were both present at an A. fabae colony, F. obscuripes attempted to drive off F. podzelica, but were not successful in the three weeks that particular colony was under observation.
Effects of Ants on A. fabae Numbers

The data show that the total size of A. fabae colonies was significantly larger when tended by ants with significantly lower numbers of nymphs developing wing pads. Thus the presence of ants appeared to inhibit the development of alate nymphs. Both the 1986 and 1987 seasons included four weeks where alate nymph numbers were significantly greater in the treatment colonies (Table 1). Comparison of the numbers of alate adults was less clear-cut. In 1986, tended colonies had more than twice the number of alate adults, while the difference was not significant in 1987. In both years the numbers of predators also increased when the ants were present.

Both tended and untended colonies of A. fabae tended to stay in fairly compact groups at the apical part of the thistle plant. As the colonies grew larger, individual A. fabae moved away from the main colony to the lower leaves regardless of whether ants were in attendance.
Table 1. Comparison of percent alate nymphs to apterous aphids in ant tended and non-tended aphid colonies.

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<th>N</th>
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<th>% Alate</th>
<th>Nymph</th>
<th>Total Aphids</th>
<th>% Alate</th>
<th>Nymph</th>
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* denotes numbers are statistically different (P<0.05; Chi-square contingency table). N = 30 plants per week.

**Predator-Ant Interactions**

Coccinellids and syrphids are important predators of *A. fabae* (Tilles 1982, Bhatkar 1982). Ants did not prevent coccinellid adults from feeding on or laying their eggs near the *A. fabae* colony. Syrphid larvae found on the study thistles indicated that the syrphids were successful and that the ants did not provide full protection to the aphids. This incomplete protection may occur because the syrphid larvae were beneath the cluster of *A. fabae*. In addition, when the fly larvae grew too large to be under the aphids, they blended very well with the thistle. Their light green color and brown spots provided apparently effective camouflage. The syrphid larvae moved...
rather slowly, possibly not attracting attention of the tending ants. Syrphid pupae were also found on plants with ants and aphids indicating that both larvae and pupae were not destroyed by the tending ants. Spiders may be more important as predators than recorded. Spiders did not seem to be predators of the established colonies, but were a threat to alates attempting to establish colonies. Both alates and ants were frequently found in the spider webs on the bud clusters. The potential of spiders as predators of A. fabae needs further study, especially as it relates to the prevention of colony establishment and whether spiders prey upon the colonies after they are established.

Other signs of possible predators were the presence of unidentified oblong, white eggs within the colonies which were found throughout the sites. The eggs were among the A. fabae or very nearby on the stems, leaves, or buds. The eggs demonstrate that the parent had time to lay the eggs before the ants could chase them away.

Parasitoid wasps that cause aphid mummies did not appear to be a major problem for A. fabae during this study. In all the thistle patches surveyed in Gallatin County only one had a reasonably high number of mummies. Unfortunately that patch was destroyed by the Montana State University ground crew one week after it was discovered.

Ant Species Differences

The seven species of ants that were found tending A. fabae on C. arvense exhibited varying degrees of aggressiveness. The aggression
in all species except *Lasius sitkaensis* was greatest early in the season and declined as the season progressed. The ants could be ranked from most to least aggressive as follows: *F. obscuripes*, *F. oreas* comptula, *F. podzelica*, *F. neoclara*, *F. subnuda*, *Formica* sp. *rufa* group, and *Lasius sitkaensis*. This ranking was arrived at subjectively by disturbing the ants with a blade of grass and observing their attack reactions. *Lasius sitkaensis* did not exhibit aggressive or defensive behavior when disturbed or attacked. The *F. obscuripes* were the most aggressive and usually had the least number of individuals tending per aphid colony. The *F. podzelica* were almost as aggressive as the *F. obscuripes*. The *F. neoclara*, *F. subnuda*, and *Formica* sp. *rufa* group were aggressive some days and sluggish on others. The *L. sitkaensis* were scavengers and if disturbed, abandoned the *A. fabae* colony. The numbers of individual ants tending *A. fabae* colonies seems to be related to the ant species aggressiveness.

The Spearman rank correlation test was used to check ant species and their numbers as related to aphid numbers. In general, the ant species sample were not large enough to be treated statistically (Snedecor and Cochrane 1980). However, three species had sufficient samples from the two seasons examined: *F. neoclara* in 1986 and 1987 and *L. sitkaensis* in 1986. The *F. neoclara* found tending 12 *A. fabae* colonies in 1987 were the only group to show a positive correlation between ant number and aphid number with a *p* value of 0.0288. But when all the ants species were taken as one group for the season, there was a positive correlation between ant numbers and aphid numbers.
correlation raises the question as to whether there may be species differences and this needs to be studied further.

The incomplete protection provided by ants was evident late each season when coccinellid egg clusters appeared. Clusters of coccinellid eggs were found on the ribbons used to mark the thistles, on the thistle buds near the A. fabae colony, and on thistle leaves next to aphid colonies. There appeared to be no damage to the eggs by the ants. The emergence of coccinellid larvae later in the season indicates that the ants did not destroy the egg masses. These egg clusters began to appear midway through the season when the A. fabae colonies were quite large.

Coccinellids appeared to be a major factor in 1987 in preventing establishment of A. fabae colonies. The reason for colonies failing to establish may be attributed to the early presence of C. transversoguttata richardsoni and C. novemnotata adults.

The ants were most aggressive when the A. fabae colony was being established. During colony establishment under natural conditions, tending ants would remain with the alate or foundress of the colony. When the ants were excluded from the colony, this protection against coccinellid predation was lost and it was difficult for foundresses to survive and establish a colony.

<table>
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* denotes numbers are statistically different (P<0.05; Chi-square contingency table). N = 50 plants per site.

Factors Influencing Colony Establishment

It was noted that where Publilia modesta Uhler (Hemiptera: Membracidae) colonies were well established and tended by ants A. fabae would not establish. Formica obscuripes may have preferred P. modesta to A. fabae for honeydew because in the late season observations in 1987, F. obscuripes were defending the P. modesta colonies and not the A. fabae colonies.
There were no significant differences in 1986 among the three sites in the success rate of establishment of A. fabae colonies, comparing those that were allowed access by ants and those that were not. There was a significant difference between tended and non-tended A. fabae colonies in the post transplant establishment success in Sites II and III in 1987 (Table 2).

Site I had 52% establishment rate of the number of colonies established seven days after the transplant data on A. fabae colonies on 52% of the plants that were restricted and 60% of the plants without ant restriction. Site II had the lowest establishment of A. fabae colonies on restricted and nonrestricted plants. The restricted plants had 8% establishment of A. fabae and the nonrestricted plants had 32% establishment of A. fabae colonies. Site III had a 32% rate of establishment of A. fabae on restricted plants and a 68% establishment of A. fabae on nonrestricted plants.

**Effect of Ant Presence on Predator Activity**

The data show that the presence of those ant species referred to earlier enhance the survival and size of A. fabae colonies on C. arvense. The data collected do not support the hypothesis that colony size increases because of predator absence due to ant predation. The data do lend some support to the hypothesis that ants aid in the early establishment of the aphid colony. Ants may provide better protection against predators while the colony is small (Addicott 1979). It was shown that with more A. fabae individuals present there were more
predators. Behavioral observations and censuses indicate that tending ants do not deter predators such as C. *transversoguttata richardsoni*, C. *novemnotata* and syrphid flies. In fact, the predator numbers were significantly greater on colonies with ants present than where ants were excluded; consequently, predator presence may have persisted because of the increase in aphid density (Addicott 1979). It appears that the protection that *A. fabae* receives at the beginning of colony establishment is the most important. The significant differences among colonies with and without ants indicates that *A. fabae* colonies benefit from ant tending. However, the mechanism responsible for this effect has not been determined.

There was evidence that alate production was inhibited by the ant species tending *A. fabae* colonies. It did not appear to make any real difference in whether the aphid colony remained in a compact group or eventually dispersed on the plant. Individuals in the aphid colonies seemed to remain in a loose association with one another regardless of whether ants were present. The effect of ants on alate production and compaction of colonies needs further study. The data on compactness of *A. fabae* colonies are not complete enough to make any conclusive statement.
REFERENCES CITED


APPENDIX

Observations of Predator Ant Reactions

Numerous observations of the coccinellid predators *C. transversoguttata richardsoni* and *C. novemnotata* behavior were made and recorded during the two field seasons. The following is a summary of the behavior patterns observed. *Coccinella transversoguttata richardsoni* and *C. novemnotata* adults approached the *A. fabae* colony in a variety of ways. They either flew in directly to the plant harboring aphids or landed on nearby vegetation. The plant next to the thistle often served as a resting place and a bridge to the aphid colony on the plant. Ants tending the aphids were rarely found away from the aphid colony. As the colony grew larger the ants' ability to protect the aphids from coccinellid predation decreased. The ability of the ants to defend the aphid colony was a subjective observation that needs to be quantified.

When the colony consisted of only a few *A. fabae* individuals clustered under the thistle bud, the ants were effective in their protection. The effective protection was attributed to the aphid colony area being very small as the numbers of ants tending that colony remained fairly constant over colony size. When the colony grew larger the same ants could not cover the area as effectively and the coccinellids were able to attack the aphids without much interference. The most effective coccinellid tactic was to rest on the vegetation touching the thistle. They crawled from the vegetation to the thistle and began to feed on the *A. fabae*. When the coccinellids crawled onto...
the thistle they sat perfectly still for a few seconds and then began to feed on the aphids.

The ants responded to vibrations of the plant. They also responded to movement of an object near them or a shadow that passed over the plant. A stationary coccinellid tended not to attract the ant’s attention. The hypothesis that vibrations or visual detection of movement caused the ants to react was tested by tapping the plant or dropping a small piece of dry vegetation on the plant, a short distance from the aphid colony being tended by *F. obscuripes*. The ants reacted immediately and came to the area of disturbance. If the disturbance was the dry piece of vegetation, it was attacked and thrown from the plant. If the disturbance was tapping the plant, the ants would run around in an excited defensive posture apparently seeking the source of disturbance. A coccinellid crawling onto the plant apparently did not cause enough vibrations or movement to be detected by the ants. One coccinellid was observed to feed as long as eight minutes before it was discovered and challenged by *F. obscuripes*.

Another tactic used by the coccinellids was to land on the ground, near the base of the *A. fabae* infested thistle, then proceed to crawl up the thistle stem to the colony. The *F. obscuripes* quickly discovered those individuals as they neared the main colony. The coccinellids in most cases did not reach the main aphid colony but, would feed on those individual *A. fabae* that had strayed onto the lower leaves. When the coccinellids were discovered, *F. obscuripes* would bite at the legs and head of the coccinellids. The coccinellid’s
reactions were to run back down the stem, onto the leaves of the thistle, or onto leaves of touching vegetation. The release of a defensive secretion was not observed. After the ants had returned to the colony the coccinellids would crawl back onto the thistle and attempt to feed on the aphids again. There were a few exceptions when *F. obscuripes* immediately attacked the coccinellids that were attempting to crawl up the stem of the thistle. A few coccinellids continued to move and to feed on the aphid colony, ignoring the attacking *F. obscuripes*. The *F. obscuripes* would finally leave and the coccinellids would continue to feed on the aphids. The coccinellids had less trouble with the tending ants toward the end of the season when the ants were less aggressive.

Observations of aphid colonies revealed the presence of numerous syrphid larvae. Syrphid adults were observed flying into the area of the *A. fabae* colony tended by *F. obscuripes*, and hovering a few seconds near the aphid colony. If the ants did not challenge them they would land on the thistle buds or the leaves, curve the abdomen under, and lay an egg. The egg laying was too quick to be effectively timed on a stop watch. If the ants detected the movement of the fly hovering and challenged the predator, the fly would pull back and move to another part of the plant. One syrphid made 10 oviposition attempts and was only challenged twice. Another was observed to lay 10 eggs in less than five minutes.
Late Season Observation

Observations were made on September 1, 1986 of Site I to determine if ants were still tending the naturally established A. fabae colonies. The same type of survey was taken the second season on August 21, 1987, in Sites II and III. The numbers of colonies with ants tending was recorded from 216 plants.

The late season Site I survey indicated that more than half (136 of 216) previously tended A. fabae colonies were no longer tended by ants. The remaining 80 colonies still had ants feeding on honeydew.

Most A. fabae colonies sustained heavy predation by coccinellid beetles. Adult coccinellid species and their late stage larvae were feeding on the aphid colonies. Those A. fabae colonies that had coccinellids present would have from 1 to 20 adult coccinellids feeding on the aphids. The same area was checked again September 1. A random check of 19 A. fabae colonies found that 18 colonies had coccinellid adults and or larvae feeding on the aphids. Seven of these colonies were tended by E. obscuripes, E. podzelica or L. sitkaensis and when disturbed they did not exhibit defensive behavior but instead left the plant. This behavior was unexpected in that all of the tending ant species, except L. sitkaensis, were aggressive at the beginning of the season. Another difference between early and late season was that 100% of A. fabae colonies in the early season were tended by ants compared to 37% in the late season.