

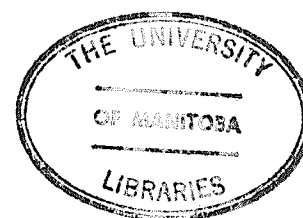
SOME ANT-APHID ASSOCIATIONS IN MANITOBA
WITH OBSERVATIONS ON INTERACTIONS BETWEEN
Formica oreas comptula WHEELER AND
APHIDS AT BIRDS HILL PARK, MANITOBA

A Thesis
Submitted to the Faculty
of
Graduate Studies
The University of Manitoba
by
Mary Catherine Anne Madder

In Partial Fulfillment of the
Requirements for the Degree

of

Master of Science
Department of Entomology
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DEDICATION

Dedicated to
Gladys and Jimmie Carter
of Corkery, Ontario
(for all the happy summers)

and to

my Mother

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I wish to express my gratitude to Dr. Grant Robinson for his patience, guidance and encouragement throughout this study; for his assistance in the collection of samples and identification of aphids, and for stimulating and informative field trips.

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ABSTRACT

Madder, Mary Catherine Anne. M.Sc., The University of Manitoba, October, 1978.

Some Ant-Aphid Associations in Manitoba with Observations on Interactions between Formica oreas comptula Wheeler and Aphids at Birds Hill Park, Manitoba. Major Professor: A.G. Robinson.

A survey of Manitoba ant-aphid associations was conducted by collecting and identifying samples of ants and aphids found together on aphid host plants. Qualitative and quantitative monitoring of the interactions of Formica oreas comptula with Symydobius americanus, Chaitophorus saliciniger and Pterocomma smithiae was carried out during 1977 at Birds Hill Park. Data were analyzed by stepwise multiple linear regression analyses.

Twenty-seven species (seven genera) of ants tending 62 species (28 genera) of aphids on 39 host plants were collected in Manitoba during 1976 and 1977. Formica species were the dominant aphid-attendants and Aphis species were the most frequently attended aphids. 9.7% of the associations contained two different ant species or genera together; usually one was the true aphid-attendant and the other a scavenger species.

F. oreas comptula workers were always present at the aphid colonies, at least until mid-June; however, the individual

aphid-attendants changed throughout the day and night. Demand for aphid honeydew diminished by mid-June, possibly due to departure of males and queens from the ant nest. Aphid excretory behavior changed when this decrease in ant attendance occurred, and other ant species were then frequently observed at or near the aphid colonies.

Marking experiments suggested that age polyethism and task fidelity exist in F. oreas comptula, and that some ants which were present at the aphid colonies in the spring may have been foragers surviving from the previous summer. Inexperienced foragers may have learned honeydew foraging routes by following experienced foragers and by retracing the route several times.

Regression analyses have indicated that the number of F. oreas comptula present at an aphid colony significantly decreased with seasonal progression and significantly increased with increasing aphid colony size, barometric pressure and number of ants leaving the aphid colony; increasing temperature, relative humidity and possibly rainfall contributed to a lesser extent to such an increase. The number of ants leaving an aphid colony increased with increasing numbers of ants present at the colony and temperature, but decreased with increasing relative humidity. The only variables which made a significant contribution to the number of ants going up to an aphid colony were the number of ants present at the aphid colony, the number of ants leaving the aphid colony, and the size of the

aphid colony.

F. oreas comptula were aggressive toward moving insects near the aphid colonies they were tending; they did not respond to syrphid larvae feeding on the aphids. Aphid parasitism and predation were not prevented by the ants' presence, and were greatest in colonies of C. saliciniger.

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INTRODUCTION

Few surveys have been conducted to determine the ant-aphid associations of North America (Nielsson et al. 1971). Reference to the ant-aphid fauna of Canada, and more particularly to that of Manitoba, is sparse and often obscured by inclusion as titbit information in ecological and taxonomic investigations of the Formicidae. Subjective observations constitute the major source of information on ant-aphid behavioral interactions. Quantitative information concerning the relationship as it relates to the collection of aphid honeydew, environmental parameters, size of aphid population, or species preferences is lacking.

This investigation was undertaken: to determine which species of ants and aphids are in association in Manitoba; to determine from such a species survey whether there are species preferences apparent between ants and aphids or whether ant-attendance is species-coincident and opportunistic; to observe population changes of several aphid species over time; to note whether such aphid population changes appear to be mediated by the presence or absence of ants; to determine if the number of ants present and tending at an aphid colony is

influenced by

1. The species of aphid being tended,
2. The number of aphids present in the colony,
3. Environmental parameters such as temperature, relative humidity, barometric pressure, precipitation and sky conditions,

4. Time of year,

5. The number of ants going to the aphid colony,

6. The number of ants leaving the aphid colony;

to determine if the number of ants going to an aphid colony is influenced by

1. Factors 1 to 4 above,

2. The number of ants present at the aphid colony,

3. The number of ants leaving the aphid colony;

to determine if the number of ants leaving an aphid colony is influenced by

1. Factors 1 to 4 above,

2. The number of ants present at the aphid colony,

3. The number of ants going to the aphid colony;

to observe the response of attendant ants to the presence of aphid predators and/or parasites in or near an aphid colony, and the response of aphids when ant-attendance diminishes and ceases.

CHAPTER I

LITERATURE REVIEW

Occasionally in nature a relationship develops between unlikely associates and the association of ants with aphids exemplifies such a relationship. The predacious-scavenger nature of ants is well known (Finnegan 1974, Carroll and Janzen 1973), and the presence of numerous colonies of soft-bodied aphids should represent to them a prime source of dietary protein. But during the course of their evolution ants have "discovered" that the ingestion of aphid metabolic wastes is of more benefit than their consumption of the whole organism. These metabolic wastes excreted via the aphid's anus are the residual solution, called honeydew, which result from the aphids' ingestion of excess quantities of phloem sap. It contains trisaccharides, organic acids, alcohols, salts and small amounts of amino acids (Auclair 1963). The gregarious and sedentary habits of aphids enhance their relationship with ants and enable the ants to conserve time and energy in not having to forage far for such a bulk of food (Wheeler 1910). Sugar-rich exudate from homopterans and extra-floral nectaries represent the only stationary and immediately renewable food harvested by many ants (Carroll and Janzen 1973).

It is not known when during their evolution a relation-

ship developed between ants and aphids. That their association together is an ancient phenomenon was shown by Oligocene Baltic Amber deposits which contained fossilized ants and aphids little changed from some species which can be found in association with one another today (Wheeler 1910, 1914, Wheeler and Wheeler 1963, Wilson 1971).

Defining the Relationship

Flanders (1951, p. 93) described the relation of ants with plant-feeding Homoptera as helotic, the extent of helotism being determined by the needs of the ant population. He defined helotism as "any symbiotic relation of organisms in which one symbiont acts as the slave of the other, as that of...the trophic service rendered to ants by coccids (facultative helotism)".

Other authorities have viewed the consociation of ants with aphids as a mutualistic relationship. Wheeler (1910) believed that the term "mutualism" was warranted because aphids are of service to ants and benefit in return from the companionship of the active, aggressive attendants. Way (1963) also approved of this term, which he defined as an association between ants and other insects which is mutually beneficial but which does not necessarily imply obligate dependence or interdependence.

In justifying the application of the term "mutualism" to the relationship, Wheeler (1910) cited a number of structural and behavioral modifications which he believed indicated the existence of adaptations by aphids and ants to their mutual association. Those modifications which are relevant to this investigation are discussed below, while references to current literature on topics not directly dealt with in the literature review are provided.

The modifications believed by Wheeler (1910) to indicate adaptations by aphids included:

1. Absence of predator avoidance behavior and siphuncular defense in the presence of ants, whose presence is accepted as a matter of course.
2. Modification of aphid excretory behavior from sudden jerk expulsion of excrement in the absence of ants to gradual extrusion of honeydew droplets when ants are present.
3. Development of a perianal circlet of stiff hairs which is used to support the honeydew droplet while it is imbibed by an ant, a structural modification which occurred in aphid species living habitually with ants (refer to Way 1963) .
4. A modification of aphid sap ingestion, in that the volume ingested is increased when aphids are ant-attended. (In addition to this observation, several other physiological modifications of ant-attended aphids have since been documented and these are also referenced: color changes (Bradley and Hinks 1968); increased volume and rate of ingestion and

excretion (Banks 1958, Banks and Nixon 1958, El-Ziady 1960, Herzig 1937, Sudd 1967); acceleration of reproductive rate (Banks 1958, Blackman 1974, El-Ziady 1960, El-Ziady and Kennedy 1956, Herzig 1937, Kennedy and Booth 1954); prolongation of wingless state (Banks 1958, von Dehn 1963, El-Ziady 1960, El-Ziady and Kennedy 1956, Johnson 1959 a, b, Kleinjan and Mittler 1975, Lees 1966, Steel 1976, Way 1963)).

5. Reduction or absence of repugnatorial glands in aphids which live habitually with ants (refer to Way 1963).

Wheeler (1910) believed the following behavioral modifications were indicative of ants having adapted to life with aphids:

1. Modification of aggressive behavior, in that encountered aphids are not seized and killed by ants, as are other sedentary insects (refer to Carroll and Janzen 1973, Paul 1974, Way 1963).
2. Inducement of honeydew excretion by stroking the aphids a certain way and knowledge of where to expect the impending droplet.
3. Active protection of aphids from predatory insects.
4. Protection behavior and sense of ownership manifested by seizing and carrying the aphids to safety when threatened, harboring the aphids within their nests, and collecting aphid eggs in autumn, storing and caring for them in the nest throughout the winter, and placing newly hatched nymphs on plants in the spring (refer to Cutwright 1925, Donisthorpe 1927, Fossel

1972, Herzig 1937, Lubbock 1882, Nixon 1951, Pontin 1960, Way 1963, Wheeler and Wheeler 1963, Wilson 1955).

5. Construction of sheds or pavilions to protect "their cattle" and themselves.

6. Construction of galleries to the soil surface which facilitated the exit from the ant nest of winged sexual aphids (refer to Way 1963).

7. Clipping off wings of alate female aphids, perhaps to allow for easier imbibition of honeydew by ants or to prevent the aphids from escaping (refer to Flanders 1951, Way 1963).

Wheeler's (1910) analysis of the relationship between ants and aphids represented a synthesis of the knowledge which existed to that time, and most of his statements have subsequently been evaluated and supported or refuted.

Behavioral Modifications of Ant-Attended Aphids

Absence of Predator-Avoidance Behavior

The gregarious sedentary habits of aphids make them especially vulnerable to attack by predators (Downes 1974, Wheeler 1910). Their normal defensive response is one of avoidance, partially brought about by the release of alarm pheromones from droplets of siphuncular exudate. The diffusion of alarm pheromones throughout an aphid colony, together with the stimulus of a struggling victim, caused aphids to disperse, walk away, jump or fall off the host

plant (Blackman 1974, Nault et al. 1976). When expelled from the siphunculi, droplets coalesced and rapidly crystallized to form a hard waxy plaque on the surface of any solid object (Edwards 1966). The droplets also sometimes effectively immobilized a predator, although its effectiveness depended on the size of the aphid and the part of its body seized by the predator (Dixon and Stewart 1975).

Nault et al. (1976) reported that aphids which were tended by ants dispersed less readily upon exposure to alarm pheromone than did non-attended aphids. Further, aphid alarm behavior was altered by the presence of ants in that the aphids' main response changed to one of non-dispersion and body wagging. Since success of the ant-aphid association depends on maintenance of an intact aphid aggregation, Nault et al. (1976) believed that alteration of aphid alarm behavior by ants contributes to the stabilization of their association.

Modification of Excretory Behavior

In the absence of ants, honeydew droplets are disposed of by ejection through the air away from the aphid (Banks 1958); the method varies with the species of aphid and its age (Broadbent 1951). Excretory behavior involves raising and swinging the abdomen high into the air and kicking the droplet off with a leg as it emerges, jerking the droplet off the cauda, or shooting it off by contracting the abdomen (Banks 1958, Broadbent 1951).

Banks (1958) confirmed that a change in aphid excretory behavior occurred when ants were in attendance. He said that aphids made no attempt to eject the honeydew droplets which they exuded in response to ant-antennal palpations nor did they make any of the flexing or swinging motions of the leg and abdomen. If an excreted droplet was not sucked up by an ant it was withdrawn and held in the rectum until the aphid was again solicited by an ant or until it could no longer refrain from excretion (Banks 1958, El-Ziady 1960).

El-Ziady (1960) observed that older adult Aphis fabae Scopoli were induced to wander from their clusters of nymphs by Lasius niger L. Prolonged inhibition of excretion, caused by L. niger collecting honeydew from the nymphs only, seemed to cause the wandering behavior.

Wheeler (1910) said that the habit of gradual drop extrusion has become fixed in some species of aphids, and solicitation and ensuing extrusion can be imitated by brushing an aphid's abdomen with a soft object such as a camel-hair bristle.

Behavioral Modifications of Attendant Ants

Absence of Aggression Toward Aphids

As proposed by Wheeler (1910), Way (1963) described the normal attitude of worker ants toward aphids as

non-aggressive, with their slow and deliberate movements resembling brood-care behavior. Herzig (in Paul 1974) proposed that only dead aphids were removed and carried away by ants, and that ants were deterred from attacking aphids by the unpalatable siphuncular wax while they were simultaneously attracted by their honeydew. But Pontin (in Paul 1974) found that secretion of siphuncular wax incited Lasius to attack the aphids they were investigating rather than repel them. Paul (1974) has observed Formica aquilona (Yarrow) attack and kill Tuberolachnus salignus (Gmelin) and he believed that ants learned that aphids were a source of honeydew before they ceased their aggression towards them.

In conflict with Wheeler's views, Carroll and Janzen (1973) stated that the more dependent an ant colony was on Homoptera, the more likely it was that the ants were harvesting them as lipid and protein sources as well.

Droplet-Inducing Behavior

Wheeler (1910) stated that aphids were induced to excrete droplets of honeydew by the stimulation derived from palpations and stroking of their abdomens by ant antennae. Jones (1929) (and almost every reference in the literature dealing with ant-aphid interactions) also stated that antennal stroking initiated emission of honeydew droplets by aphids. Nixon (1951) suggested that further information was required before these ant-antennal movements could be considered to be any different from those

observed under many other circumstances. He also suggested that the reception of the honeydew droplets in the "right place" (Wheeler 1910) was perhaps due to scent perception by the ant rather than "knowing" per se as implied by Wheeler. Kloft (1959) suggested that the posterior view of an aphid moving its legs about and offering a droplet of honeydew possibly resembles the head and antennal movements of donor ants who feed other workers in the colony by regurgitation, thus eliciting the droplet-inducing behavior in aphid-attendants.

Active Defense and Protection of Aphids

Larval and adult coccinellids, syrphid and chrysopid larvae, mirids and spiders are the major predators of aphids (Banks and Macaulay 1967, Bradley and Hinks 1968, Downes 1974, Eisner et al. 1978, Rathke et al. 1967, Way 1963). The best known of aphid parasites are members of the Aphidiidae (Hymenoptera) (Starý 1966).

Bradley and Hinks (1968) reported that colonies of Cinara on Jack Pine were not randomly distributed, but were only found on trees near large ant nests. Colonies of ant-attended aphids rarely spread to new plants outside the ants' foraging territories, because spiders (Thomisidae and Salticidae which actively hunt their prey) were present when female aphids alighted and any new aphid colonies were destroyed (Bradley and Hinks

1968). Scheurer (1971) observed that aphids were very restless when spider predators were a threat; their restlessness disappeared when the threat of spider predation was subsequently eliminated by the intensive visiting of ants. Eisner et al. (1978) described the mimic behavior of a species of Chrysopa in its attempts to "outwit" ants tending the woolly alder aphid Paraprociophilus tesselatus (Fitch). They explained that by plucking off and covering itself with waxy outgrowths of the aphids' integument, the larva was able to prey on aphids in the colony without attack from tending ants. Denuded larvae were quickly grasped in the ants' mandibles and dropped off or carried from the host plant.

The issue that ants protect aphids from their predacious and parasitic enemies (Wheeler 1910) was confused by the many different observations which have been published. Eisner et al. (1978) observed that the ants tending P. tesselatus were very aggressive toward any disturbance at the aphid colonies but ants not on guard, i.e., walking along branches, were more timid and fled when disturbed. Burns (1973) found that "pugnaciousness" of Dolichoderus taschenbergi (Mayr) workers and their attacks on marauding insects increased with distance from a honeydew source as the numbers of workers present increased. Bradley and Hinks (1968) also observed that D. taschenbergi and Formica obscuripes Forel fiercely defended their aphid colonies, and the former species immediately attacked any object moving within 38 cm of its aphids. When

ants were removed by destruction of their nests, the numbers of flies and wasps around aphid colonies increased (Bradley and Hinks 1968, Flanders 1951). Hukusima and Takeda (1969) also found that the number of aphid predators increased when ants were excluded, and that a preference for one aphid species over another may have been shown by the intensity of the ants' protectiveness, presumably due to a difference in the aphids' honeydew.

Bradley and Hinks' (1968) observations on protection of aphids from parasites agreed with those of Way (1963); they found that although ants rarely attacked parasites they sufficiently interfered with their activities so as to make the ants' presence worthwhile to the aphids. Finnegan (1977) reported that Cinara parasitism was much higher in the absence of Formica lugubris Zett. attendants.

Nixon (1951) stated that ants were inconsistent in their response to protect aphids, their attitude usually was hostile and that the reaction of any particular species of ant would depend somewhat on its innate temperament. Species of ants such as Lasius and Formica probably display a much less aggressive attitude toward aphid enemies than does Oecophylla smaragdina (F.), which is fierce in defense of its arboreal territories.

Herzig (1937) found that what appeared to be ant defense activities were initiated by swift movements around and within the aphid group. He said the ants may have been responding to

what they interpreted as threats to themselves and their own safety; the aphids were perhaps only coincidentally protected. Bradley (1961) and Herzig (1937) reported that slow-moving coccinellid larvae and adults and syrphid larvae were all but ignored by ant attendants, whereas Nault et al. (1976) stated that coccinellid adults were attacked and removed from the aphid host plant by Formica subsericea Say. Marsh (1910) observed a species of Formica killing and removing syrphid larvae, adult coccinellids, nabids and a species of Chrysopa as it protected Aphis gossypii Glover. Coccinellid larvae were not molested but syrphid larvae were the objects of special attack, with 10 to 12 larvae being carried away at one time.

Whatever nominal protection is afforded aphids by the presence of ants collecting their honeydew, it has been shown that aphids respond positively through increased populations (Banks 1962, Banks and Macaulay 1967, Bradley and Hinks 1968, Flanders 1951, Ghilarov 1937, Herzig 1937, Nixon 1951, Wilson 1971).

Construction of Shelters

Stopes and Hewitt (1909) proposed that ants collected an increased amount of honeydew when aphids fed in shelters which protected them from inclement weather because the aphids' period of sap ingestion was lengthened. Root chambers are considered to be a type of shelter provided to aphids by their ants.

Wellenstein (in Way 1963) stated that F. rufa L. and L. niger

would not collect honeydew when it was wet or windy, unless it was very early in the year when food was scarce. However, honeydew collection occurred when the aphids (from aerial parts of the plants) occupied root chambers dug out by F. rufa. Ghilarov (1937) reported that Aphis scorzonerae (Mordv.), which lived on the roots of rubber-producing plants and was tended by Lasius alienus (Forster), had deep pits carved out of the roots for it by the ants wherein the aphids fed. The degree of this aphid species' dependence on L. alienus for survival is not known, as no one knows whether A. scorzonerae can exist in the absence of the prepared feeding chambers. Jones (1929) stated that by building different structures over aphid colonies, ants protected their herds from enemies and restricted the aphid colonies' movements. Nixon (1951) described sheltering as being sealed within a micro-environment free of predators and parasites. He stated that subjective interpretation of the ants' sheltering behavior was difficult to avoid because the behavior appeared to be quite intentional, in order to protect a valuable food source. Way (1963) believed that, since ants seldom visited unsheltered Homoptera during bad weather but did visit sheltered ones, shelters were constructed primarily for the ants' own protection during bad weather.

There was no information as to what proportion of the aphid population was enclosed within such shelters, and therefore it was not possible to estimate the overall benefit

derived by an aphid population from this protective behavior.

Prevalence of Associations Between Ants and Aphids

As an example of the numbers of species which have been found in association in a given geographic area, consider Jones' (1929) findings for Colorado: 34 genera of aphids (including 149 species) were tended in different combinations by 15 genera of ants (including 92 species).

Formicidae

Gregg (1972) sampled the ant fauna of a number of zones which transected mid-continental North America. He included areas of Manitoba in the study (e.g., Birds Hill Park, The Pas, Thompson (Canadian Zone), and Churchill (Hudsonian Zone). Forty-three species and subspecies of ants were reported by him to be present in the Canadian Zone. Although not mentioned, many of these species were known aphid-attendants in other areas of North America.

The association of ants with aphids has become most highly developed in the Formicinae (e.g., Camponotus, Formica, Lasius) and the Dolichoderinae (e.g., Iridomyrmex, Dolichoderus, Tapinoma). The Myrmecinae developed more diverse food habits, although some of their genera have species which also collect honeydew (e.g., Solenopsis, Pheidole, Crematogaster, Myrmica) (Creighton 1950, Jones 1929, Nixon 1951, Wheeler 1910, Wheeler and Wheeler 1963, Wilson 1955).

Jones (1929) found that some ants were more prevalent as attendants than others. He observed that Formica spp. were the dominant ant attendants in Colorado, followed secondly by Camponotus, and then by Myrmica and Lasius equally.

Jones (1929) noted that attendant ants were present as a single species at an aphid colony, or that there were as many as three different species or genera present at the same time at the same aphid colony. About 10% of all attendant species were found to be in mixed species groups, with Formica having been the most frequent mixer (Jones 1929).

Aphidoidea

With one exception, all species of Lachnidae in the Middle East are tended by ants (Bodenheimer and Swirski 1957) and ants are associated with most Cinara species in Canada (Bradley 1961, McNeil et al. 1977). Lachnid honeydew and lachnid populations tended by ants are frequently referred to in European literature because of their importance to beekeepers (Atanassov 1974, Egger 1973, Fossel 1972, Horstmann 1972, Kloft 1959).

The Callipterinae of the Middle East are usually not visited by ants, although some species of Myzocallis have a few irregular visitors, as have the Chaitophorinae (e.g., Chaitophorus) and the Pterocommatinae (e.g., Pterocomma) (Bodenheimer and Swirski 1957). According to Bodenheimer and Swirski (1957), genera of Dactynotini (Aphidinae), especially

those with long siphunculi, are not visited by ants (e.g., Macrosiphoniella, Macrosiphum, Dactynotus, and Myzus), but Anuraphidini (e.g., Nearctaphis) and Aphidina (e.g., Aphis) are usually tended. They also stated that ants did not tend Pemphigus, Prociphilus and Thecabius (Pemphigidae), but Bradley and Hinks (1968) reported that a species of Prociphilus was tended in Manitoba by Acanthomyops latipes (Walsh), and P. tessellatus was tended by three species of ants in New York State (Eisner et al. 1978).

In his study of Colorado ants and aphids Jones (1929) found that the most frequently tended aphids were those of the genus Aphis (50 species), followed by those of the genus Cinara (23 species). Macrosiphoniella sanborni Gill. and a number of species of Macrosiphum and Myzus were reported by Jones (1929) to have been tended as were species of Prociphilus, Pemphigus, Thecabius, Pterocomma and Chaitophorus. Cutwright (1925) reported that some species of the abovementioned Pemphigidae were visited by ants in Ohio, and that Prociphilus erigeronensis (Thomas) was taken from the nests of Lasius umbratus (Nylander).

Intimacy and Dependence on the Relationship

The association of ants with aphids has ranged from casual (of little benefit to the aphid other than some honeydew removal and incidental protection from enemies) to intimate

(obligate myrmecophily) where an aphid species was constantly provided sustenance, shelter and protection (Herzig 1937, Muir 1959, Nixon 1951, Way 1963, Wheeler 1910).

Way (1963, p. 307) defined myrmecophilous aphids as "those which benefit from ants and are more or less adapted to live with them in a relationship which need not be either obligatory or mutually beneficial". But a myrmecophilous aphid species in the absolute sense is difficult to define. Schumacher (in Nixon 1951) suggested that mobility of the aphid be used as the defining criterion, on the basis that the greater the aphid's mobility the less dependent it is on ants.

One of the factors limiting the degree of intimacy between ants and aphids is the aphid's life cycle (Way 1963). Holocyclic heteroecious species (e.g., A. fabae), which have alternating sexual and parthenogenetic generations on two different host plants, are never intimately associated with ants, but monoecious species (e.g., Aphis maidiradicis Forbes) are able to associate year round with ants (Way 1963). Zwölfer (in Way 1963) found that a more intimate association exists between ants and species of underground aphids, which are anholocyclic (continuously parthenogenetic), than those which are holocyclic. Rainwater (1935) cited an example of an anholocyclic obligate myrmecophile (Smynthuroides betae Westwood, almost constantly tended by Lasius neoniger Emery and Pheidole bicarinate vinelandica Forel) which was so inactive toward the adult stage that, if turned onto its back, would die unless assisted in righting itself.

The association of ants with aphids has also ranged from casual to constant attendance, depending on the species of ant and its nutritional requirements. Some subterranean species of ants have developed an absolute dependence on aphid honeydew and, for some, the substance may have become their only source of nutriment (Creighton 1950, Nixon 1951, Wheeler and Wheeler 1963, Wilson 1971). Honeydew excreted by Cinara spp. appeared to be the major food source for Camponotus herculeanus L., C. noveboracensis (Fitch), and C. pennsylvanicus (DeGeer) in Northwestern Ontario (Sanders 1970, 1972). Bradley and Hinks (1968) noted that F. obscuripes and D. taschenbergi probably require honeydew to complete their full development, and that one nest consequently serviced aphids on up to 50 trees within a radius of 23 m. Some ants, e.g., Leptothorax, have been shown to benefit from aphid honeydew excretions without the obligation of tending the aphids, simply by having licked up fallen honeydew on leaves (Sudd 1967, Wheeler 1910).

The availability of foods other than honeydew probably governs the degree of an ant species' dependence on aphids, and aboveground foragers have a greater range of food sources than do subterranean species (Way 1963). F. rufa group were found to prey heavily on insects in the late spring and early summer, but fed mostly on honeydew in late summer (Carroll and Janzen 1973, Holt 1955, Sudd 1967). Rosengren (1971) reported that honeydew (from underground Cinara spp. on spruce

roots) was the most important food source in late autumn for F. rufa. He monitored the number of ants over five minutes going toward an ant mound, at 15 minute intervals from 1000 to 1700 hrs. A total of 5260 ants carried an estimated 18.3 g of honeydew (fresh weight) or 3.3 g of sugar (dry weight). Although Rosengren did not mention the volume of honeydew per F. rufa crop, Flanders (1951) said that one replete Formica exsectoides Forel carried 3 mg.

Holt (1955) calculated that on a typical day (14 hr period) 60 to 70 thousand F. rufa workers (weighing approximately 700 g) collected approximately 820 g of food during a total of 300,000 foraging trips. Forty-four percent of the food was honeydew. According to Horstmann (1974), during one year, workers of a medium-sized Formica polycтена (Foerster) nest (characterized by 0.27 ha of territory and a nest exit rate of 10 workers per second at 15°C) collected approximately 6.1 million prey pieces (volume of 28 l) and 155 l of honeydew. He estimated the annual input from nest territory to have been 58 kcal/m² from honeydew and 23 kcal/m² from prey. Honeydew comprised 50% of the food of Formica subnitens Creighton by midsummer (Ayre, in Bradley 1961). Fossel (1972) pointed out that honeydew from aphids on dwarf-pine (Pinus mugo Turra) above the tree-line represented the sole source of carbohydrate for indigenous ants. The ants were therefore mostly found in the shelter of the dwarf-pine bushes close to their milk-cows (Fossel 1972). Another example was the

field ant (Dorymyrmex pyramicus (Roger)) which ranges from North Dakota to Argentina (Wheeler and Wheeler 1963) and was known predominantly as a predator-scavenger species. As a predator-scavenger species, this ant's great abundance was hard to explain in terms of the total energy available to it. De la Cruz and Wiegert (1967) showed that the energy balance of D. pyramicus was to a very large extent compensated by the ingestion of aphid exudate. Using ^{32}P -labelled horseweed and camphorweed (the dominant producer species in the ant's habitat) de la Cruz and Wiegert (1967) found that an herbivorous mechanism existed in D. pyramicus. The ant apparently ingested honeydew directly or indirectly from aphids feeding on horseweed and heavily grazed camphorweed upon which there were no aphids. They also found that the isotope uptake curves for ants feeding on aphid honeydew were typical and high in activity (because the aphids fed on phloem sap which initially contained a very high concentration of the isotope). It may therefore be possible to use isotope uptake curves to discriminate between ants tending aphids and those simply grazing on plants and the plants' primary consumers (de la Cruz and Wiegert 1967); the ants' degree of dependence on honeydew might also be determined.

Polyethism, Route and Task Fidelity

Polyethism was defined by Carroll and Janzen (1973) and Wilson (1963) as a division of labor within an ant colony. According to King and Walters (in Horstmann 1972) the smaller workers of F. obscuripes (= rufa melanotica Emery) foraged for honeydew and larger ones tended the nest and collected honeydew from the smaller ants by regurgitation in the field. Herbers (1977) reported that majors and medias of F. obscuripes foraged, thatched and tended aphids, while minors remained in the nest. Horstmann (1972) found that larger workers of F. polyctena foraged a greater distance from the nest than did smaller workers; the latter remained in closer proximity to the nest, climbed trees more often, and therefore gathered relatively more honeydew.

Bradley (1961) observed that attendant ants of Cinara hottesi Gillette and Palmer transferred crop honeydew to carrier ants; he said that the latter ascended the trees for this purpose. Carrier ants were characterized by their abdominal distention and rapid departure from the aphid colony in a straight line down the tree (Bradley 1961). Horstmann (1972) stated that 19% of ascending F. polyctena workers did not run down again, but fell off the trees instead.

Workers of Lasius fuliginosus Latr. imbibed and trans-

ported aphid honeydew without intermediate carrier ants, although they frequently regurgitated to workers encountered during descent and on the trails (Dobrzanska 1966). Their departure from the aphid colony and movement down the tree was erratic, with frequent stopping, turning around, ascending and descending; this behavior sometimes lasted 40 to 60 mins. Dobrzanska (1966) noted that the replete workers often spent up to several hours additional time in a "station" at the bottom of the tree, and often regurgitated to fellow workers. She intimated that, as a last resort, the full workers headed in the general direction of the nest to rid themselves of the honeydew. Workers of this species have also been observed to descend "aphid trees" with empty crops (Dobrzanska 1966).

Dobrzanska (1966) stated that two functional worker groups existed in Formica species investigated by her, concerned with tending aphids. One group was composed of workers filled with honeydew, which headed straight for the ant nest by the shortest route possible; they sometimes stopped to regurgitate a drop to a "starved fellow ant". These workers returned to the aphid colony at a considerable speed with empty crops. The other functional group was composed of workers which stayed on the aphid-infested trees, but descended erratically with empty crops. According to Dobrzanska (1966) the empty workers did not visit aphids, but probably used the tree trunk as their feeding ground.

Age polyethism has been shown to exist in F. polychetena.

Following emergence from their pupal cocoons, workers spent 45 to 75 days tending eggs and larvae within the nest, and the length of time for transition to outside worker category depended on the time required for resorption of their well-developed oöcytes (Otto, in Rosengren 1971). Lange (1967) further showed that honey solution was not equally distributed to workers in the nest, that more equal amounts were distributed to workers leaving the ant nest, and that the pattern of distribution was not influenced by worker size. He also noted that workers with degenerated oöcytes received honey solution sooner and in greater amounts than did workers with well-developed oöcytes (nurses), and they also donated the solution more often. An age-determined sequence of tasks (nurse → domestic → forager) was shown in Myrmica rubra L. (Weir 1958), and Rosengren (1977a) reported that several forager categories existed in F. polychtena which were related to age-determined differences in basic behavior.

Herbers (1977) reported that workers of F. obscuripes repeated the same task daily with a high degree of fidelity. Rosengren (1971) demonstrated that a high degree of both route and task fidelity existed in F. rufa (possibly = polychtena; see Rosengren 1977a), whose foragers continued the same task for nearly four months in one season. He also demonstrated that route fidelity was preserved over winter, and that early spring traffic on foraging routes consisted of experienced (previous year's) foragers who were later joined by novice (first-year)

foragers (Rosengren 1971, 1977a). The experienced foragers actively guided the novices along the old routes (Rosengren 1971), re-establishing the previous route system before commencement of aphid activity (Rosengren 1977a). This might explain what Stager and Chauvin (in Rosengren 1971) referred to as "topographical constancy of wood ant routes" which was viewed by Rosengren (1977a) as "an adaptation to a relatively stable coniferous habitat".

Species Preferences

Bradley and Hinks (1968) observed that Cinara banksiana Pepper and Tissot was not as attractive to F. obscuripes and D. taschenbergi as were other Cinara species. Fossel (1972) referred to the preference of Formica and Lasius species for C. piceicola (sensu Pasek) (the most abundant and widespread lachnid in the Austrian Alps) and mentioned that due to their intensive tending, very little aphid honeydew was left for foraging honey bees. On the other hand, C. pilicornis (Hartig) and C. pectinatae (Nordl.) were seldom tended by ants and these therefore yielded up to 80 kg of aphid honeydew per hive of bees (Fossel 1972). Jones (1929) stated that some species of Aphis were much more attractive to ants than were other species. However, Ayre (in Bradley 1961) concluded that ants were indiscriminate in their choice of aphid species, and Bradley (1961) said that their association was governed by chance moderated only by the necessity of both species being present in the same area.

Factors Affecting Foraging Activities

Temperature and Relative Humidity

Foraging activity of D. taschenbergi was found to be governed by temperature; trails were empty during the night and early morning when temperatures were low, or when the ground temperature was high during the day (Bradley and Hinks 1968). During moderate temperature periods the attendant ants constantly changed but movement ceased during incompatible periods, although a large number of ants always remained with the aphids (Bradley and Hinks 1968). Activity in ant species studied by Pickles (in Holt 1955) was highest during hot sultry weather and lowest when cold and windy. Finnegan (1973) found that Formica sublucida Wheeler, F. sanguinea subnuda Emery and F. fossiceps Buren increased their foraging in response to an increase in soil temperature under laboratory conditions, and foraging activity-peaks occurred in late morning and mid-afternoon; the barometric pressure and relative humidity had no apparent effect. Horstmann, and De Bruyn and Kruk-De Bruin (in Rosengren 1977b) found that under field conditions the optimum temperature for F. polyc-tena foraging activities was 22.5°C. Rosengren (1977b) suggested that the optimum temperature for foraging activity may have been a function of relative humidity, since he found that an increase in relative humidity at 25-26°C removed the inhibitory effect of high temperature on F. polyc-tena foraging

activities under laboratory conditions. Sneli (in Rosengren 1977b) could not correlate a very intense activity peak of natural wood ant colonies with morning temperatures. This activity peak was found by Rosengren (1977a) to be more sharply defined in spring and early summer. He stated that in early spring the daily emergence of F. polyctena workers from their mound started at a well-defined time, presumably when the ambient temperature rose above a certain threshold. Often thereafter the numbers of ants travelling on a given route appeared to increase exponentially, reaching their maximum within an hour and, provided the temperature did not drop, traffic was almost exclusively composed of outgoing workers for about half an hour. A stream of returning foragers developed slowly; it sometimes took several hours before a steady state was reached (i.e., when outgoing equalled incoming foragers). Later in the season Rosengren (1977a) found that the stream of incoming ants was already large early in the morning, since nocturnal foraging became more prevalent when the weather was warm. He said that even in cold weather these wood ants often spent the night in the aphid colonies, returning to their nest in the morning when traffic started up from the mound. Sanders (1972) observed that C. herculeanus, C. noveboracensis and C. pennsylvanicus shifted from a diurnal activity pattern, which correlated closely with litter temperature early in the season, to a more crepuscular one later in the season; C. pennsylvanicus shifted to a nocturnal

pattern. Their peak activity occurred in June and early July and corresponded to the period of rapid larval growth; it thereafter dropped independent of temperature and ceased in early October.

Light-Dark Cycle

Rosengren (1977b) found that in a laboratory colony of F. polyctena an activity rhythm in the population as a whole could be induced or maintained by a light-dark cycle or a temperature cycle (under constant light conditions). At the end of the scotophase (12:12 LD) the activity rose, often reaching its maximum prior to the onset of light, while in a thermal 12:12 cycle, activity reached its maximum in the middle of the warm period. Rosengren (1977b) pointed out that a light-dark cycle was generally coupled to a temperature cycle and entrainment by the light cycle probably functioned to synchronize the foraging population's activity more exactly than was possible by temperature alone.

Attendance Time

Bradley and Hinks (1968) reported that F. obscuripes and D. taschenbergi remained with their aphids day and night from May (when the aphids hatched) until late September or October (when aphid oviposition occurred). Scheurer (1971) observed that Cinara pini L. were tended by Formica pratensis Retzius almost immediately from the time the aphid stem mothers emerged from their eggs. Bradley (1961) found that the

same marked ants stayed with their aphids day and night as long as the aphid colony remained on the tree, in one case up to six weeks. Contrary to this Finnegan, (1977) observed that F. lugubris aphid attendants constantly changed, with marked individuals being observed from time to time. Banks and Nixon (1958) observed that the number and size of the aphid group determined the attendance time of an ant, which averaged 20 mins., and nearly all the ants were observed tending until their crops were filled.

Herzig (1937) suggested that an unfilled crop was the only stimulus which kept an ant tending aphids over any extended period of time, especially in spring when the size of the aphid and therefore the amount excreted was small.

Number of Attendants

According to Burns (1973), the amount of honeydew being excreted determined the number of attendant ants at a particular source. When the source consisted of clustered aphids, which provided a lot of honeydew in a small area, a surplus of D. taschenbergi honeydew foragers were present. Burns (1973) concluded that this tending behavior prevented honeydew loss to the nest, since the abundance of attendants optimized stimulation of honeydew production and honeydew collection. Scheurer (1971) found that the number of ants visiting aphid colonies decreased when honeydew production decreased, as a

result of the production of alatae. Rosengren (1971) noted a temporary rise in number of ants on a route baited with syrup. This rise corresponded with Zoebelen's (in Rosengren 1971) observation that variations in the amount of aphid honeydew produced may cause traffic intensity on ant foraging routes to change accordingly (Rosengren 1971).

Honeydew Foraging Trails

F. obscuripes honeydew foragers were found to use well-defined trails which extended 15 to 23 m from the nest and usually terminated in smaller branching trails leading to individual trees (Bradley and Hinks 1968). A trail varied from broad and shallow to narrow and about 2.5 cm deep, depending on the immediate terrain (Bradley and Hinks 1968). Dobrzanska (1966) noted that L. fuliginosus sometimes used tunnels. Most of the activity of C. herculeanus, C. noveboracensis and C. pennsylvanicus was found to be confined to tunnels, apparently an adaptation resulting from tending root-aphids (Sanders 1970). There was a marked absence of Camponotus tunnels crossing a bush trail, as tunneling was inhibited by soil compaction or sparseness of litter. C. herculeanus were seen by Sanders (1970) to have emerged from a tunnel on one side of a bush road, crossed on the surface, and entered a tunnel on the other side. F. rufa trails were shown to seldom terminate at a particular "aphid tree" (Rosengren 1971); workers departed from

the main trails to tend aphids on trees which were along the main routes, or to reach other foraging areas. Underground aphid galleries excavated around pine and spruce roots were also found close to or below the main trails of F. rufa (Rosengren 1971).

Interspecific Competition

The presence of different Cinara species together had no observable effect on the relationship between them and their attendant ants (Bradley and Hinks 1968). But ant competition affected the distribution of associated aphid colonies. Nests of D. taschenbergi and D. obscuripes were usually located a minimum of 15 m apart within the same area, with 40 or more aphid colonies usually located around each nest (Bradley and Hinks 1968). Those species which required honeydew as a major component of their diet (e.g., Camponotus, Formica subaenescens Emery, F. fossiceps and F. sanguinea subnuda) located their nests at the limits of or completely removed from the foraging territory of D. taschenbergi and F. obscuripes with a maximum of six, usually one or two, aphid colonies nearby (Bradley and Hinks 1968). Nests of ants which were casual aphid attendants (e.g., Lasius, Formica lasioides Emery, Myrmica) were located both inside and outside the foraging territory of the former two species, and had no influence on aphid colony distribution (Bradley and Hinks 1968).

Burns (1973) observed that when D. taschenbergi stopped tending a honeydew source other ant species (e.g., F. subaenescens) began to collect the honeydew. Aphid colonies tended by F. pratensis were immediately captured and tended when D. taschenbergi raided one of the former's nests (Dobrzanska 1966).

Reproductive Behavior of Ants

Brood-Rearing Period

Formica ants suspended brood-rearing for the winter, whereas Camponotus and Myrmica ants maintained live larvae throughout the winter (Hölldobler 1971). Queen larvae (and presumably male larvae) of F. rufa and F. polyctena were reared by workers in the spring (Delage-Darchen 1976).

Queen and Male Ants

Male C. herculeanus eclosed in mid-August and for the first few months before winter remained in the "social phase" of their nine to ten month existence (Hölldobler, in Wilson 1971). During this phase they received and passed on liquid food, having consumed almost no solids. During winter they entered their "sexual phase", and the exchange of food declined sharply so that they must have relied on reserves built up during their social phase. Their nuptial flight and ensuing death occurred the following summer. F. polyctena followed a similar

behavior pattern except that the adult male life span was contained in one summer season. Wilson (1971) reported that the social behavior of virgin queens prior to their nuptial flight was similar to that of the males, i.e., mutual grooming and food exchange.

Biology and Ecology of the Experimental Species

Formica oreas comptula Wheeler

Wheeler and Wheeler (1963) reported that this ant ranges from North Dakota and Saskatchewan to Utah, Idaho and Washington. Wheeler and Wheeler (1963, App. VI) found that larvae were present in North Dakota nests between 19 June and 22 August and pupae between 19 June and 30 August; winged females were found from 30 June to 7 July, and males were reported for 26 June only. Cole (1934) found three nests on a sagebrush-covered hillslope in Idaho, beneath flat rocks. Sixty-two nests of various construction and habitat were found in North Dakota; most of them were located in wooded areas or at the edge of woods while one-quarter were in grassland areas (Wheeler and Wheeler 1963). Some of the North Dakota nests were below stones, sometimes banked with detritus; some were in or under wood, in stumps or logs banked with detritus, or in soil without any material around the entrance. Twenty-three exposed nests had mounds

of fine plant debris (Wheeler and Wheeler 1963).

This ant was reported by Jones (1929) to have tended 12 aphid species in Colorado. Wheeler and Wheeler (1963) found it tended aphids on oak and poplar in North Dakota.

Chaitophorus saliciniger (Knowlton)

Richards (1972) reported that this aphid species is monoecious (e.g., Salix spp.) and "apparently holocyclic". Colonies were mostly found on developing leaves and terminal new growth of the host plant.

Pterocomma smithiae (Monell)

P. smithiae is widespread and feeds on Populus and Salix spp. It is reported as a large aphid, monoecious and holocyclic, feeding on the branches, stems and roots of the host plants (Richards 1967).

Symydobius americanus Baker

This aphid species is also probably monoecious and holocyclic (A.G. Robinson, pers. comm.), feeding on leaves and stems of birch.

CHAPTER II

MATERIALS AND METHODS

Collection and Identification of Ant-Aphid Associations

During the summers of 1976 and 1977 samples of aphids being tended by ants were collected from plants throughout the Province of Manitoba.

The choice of a collecting area depended upon accessibility, physiography, plant composition, and knowledge that aphids had been collected within the area in previous seasons. Selection of individual sampling sites was random following arrival at a general location.

Aerial portions of plants were visually scanned for aphid colonies being tended by ants; when found, data were recorded as outlined in the field data sheet illustrated in Appendix A.

A sample of an ant-aphid association was collected using a pair of pruning shears to snip off portions of the plant upon which the ants and aphids were located. An open 20.5 by 25.5 cm polyethylene bag, containing a numbered paper, was held directly below the portion of the plant being pruned; after receiving the sample the bag was twist-tied closed. The field data sheet and corresponding sample were designated with an identical number.

The bags of samples were returned to the laboratory and stored in a freezer. After storage for at least several hours the ants and aphids were transferred to numbered glass vials containing 70% ethyl alcohol where they remained until processed for identification.

The samples of aphids were processed for identification using a modified version of methods outlined by Richards (1964). Aphid scientific names are in accordance with Eastop and Hille Ris Lambers (1976).

Ants were identified using Creighton (1950), Francoeur (1973), Wheeler and Wheeler (1963) and Wilson (1955). Francoeur (pers. comm.) has examined European forms allied to Formica fusca L. and he can now demonstrate that none of the Nearctic material should be designated as F. fusca. He said that F. subaenescens will be revived; therefore, all ant material identified in this investigation as F. fusca has been designated as F. subaenescens.

Experimental Observations of Ant-Aphid Interactions

Qualitative and quantitative observations of the interactions between one species of ant and three species of aphids were carried out during the summer of 1977.

Site Selection

Permission was granted by the Director of Parks for

the Province of Manitoba to select an area within Birds Hill Provincial Park for the purpose of conducting a study of the interactions between ants and aphids.

A site was chosen in the park which was accessible but not regularly visited by the public (to minimize the possibility of vandalism), had a large colony of ants present, and a variety of host plants in the immediate vicinity of the ant nest. This latter factor increased the possibility of a number of different aphid species colonizing the plants in the area, from which the experimental species could be selected.

Preparation of the Site

Three sides of the study area were naturally defined and thus determined the width of the grid, i.e., the south and east boundaries were limited by thick bush, and the west boundary by a hiking trail. The north boundary was chosen to include the maximum area which could be studied.

A string grid consisting of 56, 2 by 2 m quadrats was constructed. The quadrats were labelled A to F along the north-south borders and 1 to 9 along the east-west borders of the study area (Figs. 1 and 2).

Plant composition and distribution were recorded for each quadrat (Fig. 1).

Every aphid colony found within a quadrat prior to the beginning of the experimental observation period was tagged

Figure 1. Composition and Distribution of Ant Nests
and Plants within Each Quadrat of the Experimental
Site at Birds Hill Park, 30 May, 1977.

Symbols Code:

Nest of <u>Formica</u> <u>oreas</u> <u>comptula</u>	2
Nest of <u>Formica</u> <u>hewitti</u> or <u>F. podzolica</u>	10
<u>Lithospermum</u> <u>canescens</u>	1
<u>Populus</u> <u>balsamifera</u>	4
<u>Populus</u> <u>tremuloides</u>	5
<u>Salix</u> <u>bebbiana</u>	6
<u>Salix</u> sp.	7
<u>Rosa</u> <u>acicularis</u>	8
<u>Apocynum</u> <u>cannabinum</u>	9
<u>Betula</u> <u>glandulosa</u> var. <u>glandulifera</u>	11
<u>Crataegus</u> sp.	12
Fern	13
<u>Amelanchier</u> <u>alnifolia</u>	14
<u>Rubus</u> <u>strigosus</u>	15
Dead Tree	16
<u>Prunus</u> <u>virginiana</u>	17
<u>Acer</u> sp.	18
<u>Cornus</u> <u>stolonifera</u>	19
<u>Viburnum</u> <u>rafinesquianum</u>	20
<u>Corylus</u> <u>cornuta</u>	21
<u>Viburnum</u> <u>lentago</u>	22
<u>Quercus</u> <u>macrocarpa</u>	23
<u>Picea</u> sp.	24
Stevenson screen	☒

and numerically coded in sequence of its discovery within the quadrat. A tag was tied to the plant stem or branch which led to the respective aphid colony. By the time the experimental observation period commenced ants were passing over the stem markers without response to them.

The complete numerical code for each aphid colony consisted of the quadrat number, the quadrat letter, and the aphid colony's number. For example, colony 5-D-9 was the ninth colony found and labelled in quadrat 5-D. One colony in 5-D consisted of a combination of three tagged colonies with the colony number as 5-D-347.

All colonies tagged were sampled for species identification. Depending on the number of aphids in the colony, from one to several adult aphids were aspirated into a glass vial containing 70% ethyl alcohol (Fig. 4). The vial was labelled with the colony code, returned to the laboratory and processed for identification as previously described.

A Stevenson screen was located in quadrat 1-C (Fig. 3). This contained a recording device which monitored daily ambient temperature, relative humidity and barometric pressure.

Marking Experiments

Prior to constructing the grid, an attempt was made to determine the nest origin of the ants observed tending aphid colonies in the study area. Since it was impossible to mark each group of ants at each of the aphid colonies with a

Figure 2. West Boundary of Study Area Illustrating String Grid, and Hiking Trail to the Right of the Wooden Stakes.

Figure 3. Stevenson Screen Containing Device to Monitor Daily Ambient Temperature, Relative Humidity and Barometric Pressure.

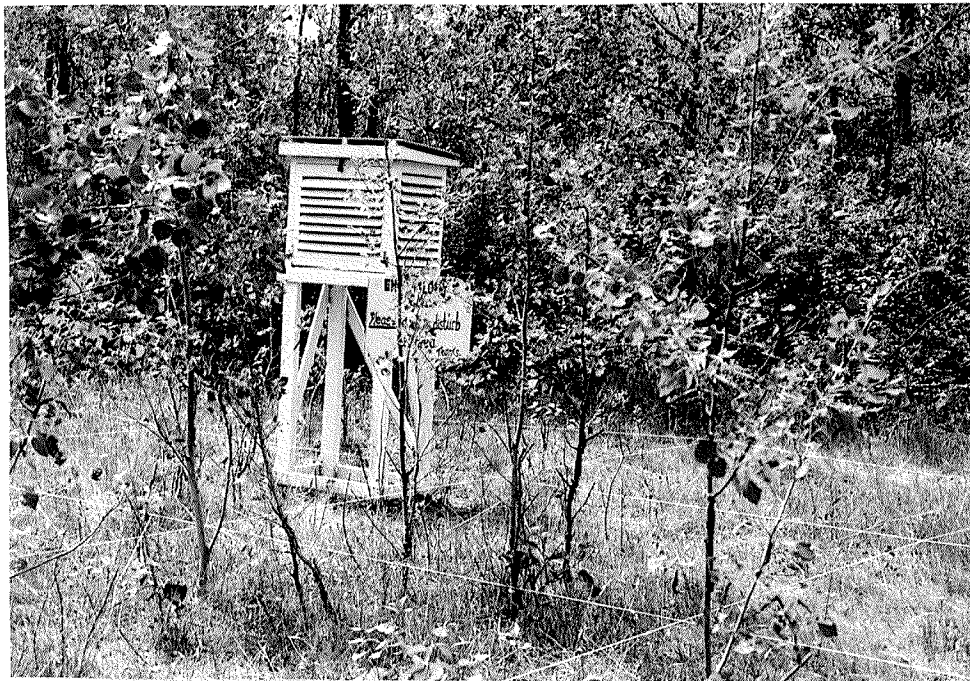




Figure 4. Aspiration of Aphids from a Colony Being Tended by Formica oreas comptula on Salix bebbiana into a Glass Vial Containing 70% ETOH.

different marker, ants originating at the ant nests were marked and watched for at the surrounding aphid colonies.

A method of marking honey bees developed by Mr. Lloyd Harris (in prep.), Entomology, University of Manitoba, was used to mark the ants. A laboratory ant culture of F. obscuripes was tested using the method to ensure that the substance applied was not toxic and that it did not interfere in any obvious way with their normal activities.

Three weeks prior to commencement of the experimental observation period approximately 2000 ants from a nest in quadrat 1-A (Fig. 5) and approximately 1000 ants from a nest in quadrat 6-B (Fig. 6), were marked with orange and pink coloured paint respectively.

Ants were removed from the nest, placed inside a polyethylene bag and lightly anaesthetized with gaseous carbon dioxide. The anaesthetized ants were emptied from the bag and quickly marked on their abdominal dorsum with a dot of paint applied from a 1 cc disposable syringe. The anaesthetic lasted one to two minutes and the ants were returned to the nest surface usually as they were reviving. Although the majority of anaesthetized ants recovered almost immediately and quickly returned to their surface or inner-nest activities, some ants remained on the nest surface with a minimum amount of activity for up to 10 minutes following recovery from the anaesthetic.

On 19 May about 10 out of approximately 20 ants, tend-



Figure 5. Nest of Formica oreas comptula Located in
Quadrat 1-C of Study Area at Birds Hill Park, Manitoba
on 8 June, 1977.

Figure 6. Nest of Formica oreas comptula Located in
Quadrat 6-B of Study Area at Birds Hill Park,
Manitoba (a) on 8 June, 1977 and (b) on 15 July,
1977.



a



b

ing Aphis viburniphila Patch on Viburnum rafinesquianum Schultes on a trail located about 400 m from the experimental site, were marked with paint. These ants were not anaesthetized and, because of their quick defensive movements when approached with the syringe, were crudely marked on the gaster, leg or head. These marks made it possible to recognize individual ants from day to day, both by the shape of the mark and its location.

Choice of Experimental Aphid Species

A maximum of 18 aphid colonies could be monitored by two observers over a two hour period during any sampling day. Therefore, options for the choice of number of aphid species to be studied included 18 colonies of one aphid species, nine colonies of two aphid species, and six colonies of three aphid species. The choice of an aphid species was therefore governed by the number of its colonies present in the study area, with the following exception.

The dominant plant within the study area was Populus tremuloides Michx. and the dominant aphid species were those which lived on this host plant. However, the several different aphid species, which may have been present on P. tremuloides at the same time, could not be distinguished with certainty without microscopic examination. Because of the time which would have been required to complete such an examination to differentiate these species, and the possibility that more than one aphid

species may have been present in an aphid colony unknown to the observer throughout the experimental observation period, the colonies of aphids located on P. tremuloides were not chosen, in spite of their great colony numbers.

Aphid colonies on Betula glandulosa var. glandulifera (Regel) Gl. (Dwarf Birch) were numerous and in all but one case were identified as S. americanus (Fig. 7). There was also a number of colonies of C. saliciniger (Fig. 8) on Salix bebbiana Sarg. (Willow) and P. smithiae (Fig. 9) on Populus balsamifera L. (Balsam Poplar); the latter was not as abundant as the former two species. All colonies of these aphids were at this time being tended by ants.

Because it was felt that there was a greater possibility that six colonies of each of these three species of aphids would be present throughout the experimental observation period than 18 colonies of one species, the latter mentioned three aphid species were chosen as the experimental species. These species may sometimes be referred to herein as the "birch aphid", the "willow aphid" and the "balsam poplar aphid" respectively.

Experimental Observation Period and Monitoring Procedure

Experimental observations on the 18 aphid colonies began 8 June and terminated 27 July, 1977.

The same 18 aphid colonies were monitored every Monday, Wednesday and Friday once every two hours. Each sample day

Figure 7. Collection of Honeydew by Formica oreas
comptula from Symydobius americanus: (a) Aphid
Feeding Site Located along the Branch of Betula
glandulosa var. glandulifera and (b) Aphid
Feeding Site Located on the Terminal Growth of
B. glandulosa var. glandulifera.



a



b

Figure 8. Collection of Honeydew by Formica oreas
comptula from Chaitophorus saliciniger Feeding
on Salix bebbiana.

Figure 9. Collection of Honeydew by Formica oreas
comptula from Pterocomma smithiae Feeding on
Populus balsamifera.



began at approximately 0630 hrs (time period 1). During this time the number of aphids in each of the 18 aphid colonies to be monitored that day was counted and recorded (Appendix B). Later in the season it was during this time period that a new aphid colony was chosen as a replacement colony whenever needed to maintain a total of six colonies per aphid species. Time periods 2 to 8 were bi-hourly periods beginning at 0820, 1020, 1220, 1420, 1620, 1820 and 2020 hrs respectively.

During the seven latter time periods two observers each monitored the same nine aphid colonies, in the same sequence, throughout the experimental observation period. Time periods 7 and 8 were monitored only to and including 27 June, 1977.

At the beginning of each of time periods 2 to 8 the observers went to their respective first colony of aphids and monitored activities at the colony in the following sequence, with information being recorded on the data sheet illustrated in Appendix C.

The number of ants present in or near the aphid colony was counted and recorded. A thermometer ($^{\circ}\text{C}$) with a picture hanger wired onto its end was hung as close to the aphid colony as possible (shaded from or exposed to the sun to correspond with the exposure of the aphid colony). Environmental data such as precipitation and sky conditions were recorded. Ant stem activity to and from the aphid colony was monitored using a stopwatch and click-counters for three successive two-minute

periods. A random point for monitoring ant stem activity on the branch leading to each of the 18 colonies had been chosen during site preparation. Each point remained constant during the study and usually consisted of the string tag used to identify the colony. During each two-minute period the numbers of ants passing up and down over the stem marker were recorded. The mean total stem activity, mean total stem activity up to the aphid colony, and mean total stem activity from the aphid colony were calculated and recorded. Colony temperature was recorded from the suspended thermometer.

The remaining eight colonies were monitored in the same way by each observer, with 10 to 12 minutes observation and recording time required for each aphid colony monitored.

Qualitative notes were also made during these time periods. The presence of predators, adult parasites and aphid mummies¹ within or near the aphid colonies was noted during initial tagging and sampling activities, as well as routinely during the experimental observation period.

Emergence and mating activities of males and females from the nest in quadrat 6-B were observed and recorded on 6 and 7 June, 1977.

¹Aphids which are parasitized by Aphidiidae are mummified; the resultant "mummy" is characteristically a brittle, round to oval pearly-brown shell from which the adult parasite eventually emerges (Starý 1966).

Statistical Analysis

Data¹ were transcribed by keypunch onto standard computer cards. During this process the variables 'precipitation' and 'sky' were coded 0 to 3 (no rain, light, moderate and heavy rain) and 1 to 5 (clear, intermittent cloud, hazy, lightly and heavily overcast) respectively.

The variables referred to herein as 'stem activity up' and 'stem activity down' refer to the mean total number of ants which crossed the stem marker in two minutes going up to the aphid colony or leaving the aphid colony respectively.

Departures from assumptions which underlie any analysis of variance necessitate the transformation of non-normal variables to a new scale so that they will conform prior to the statistical analysis (Sokal and Rohlf 1969). For this reason the following variables were transformed. 'Number of ants present at the aphid colony', 'stem activity up', 'stem activity down' and 'number of aphids in the aphid colony' were logarithmically transformed, in order to decorrelate the means from the variances. Arcsine transformation of 'per cent relative humidity' was carried out as $\arcsin \sqrt{p}$, where p is a proportion. 'Day of season' was logged based on the observation that peak aphid-tending activities had apparently already occurred when the observations were begun on 8 June.

Data were grouped and analyzed according to time period

¹Due to its bulk the raw data could not be included herein; a computer print-out is available upon request from the author.

for each of the three aphid species. For example, data collected during the experimental observation period at all birch aphid colonies during time period 4 were grouped together and then statistically analyzed as follows:

A Hewlett-Packard 9830-A programmable calculator with card-reader was used to carry out a Hewlett-Packard program for Stepwise Multiple Linear Regression Analysis of data from each time period per species.

Stem activity up, stem activity down, precipitation and sky were not monitored during time period 1. The regression analysis of data for each aphid species from time period 1 therefore included fewer independent variables than did the analyses for the remaining time periods.

Due to the absence of precipitation at birch and willow aphid colonies during time periods 7 and 8, this variable could not be included in the respective regressions.

Mean and standard deviation of each variable and a matrix of bivariate correlations were computed for each time period for each of the three aphid species. Gross mean of each of the variables monitored during time periods 2 to 6 was calculated as follows:

$$\text{Gross Mean of Variable}_x = \frac{\left(\bar{X}_{\text{var.x}} \right)_{\text{Time 2}} (N_{\text{Time 2}}) + \dots + \left(\bar{X}_{\text{var.x}} \right)_{\text{Time 6}} (N_{\text{Time 6}})}{(N_{\text{Time 2 to Time 6}})} \quad (\text{Equation 1})$$

The adjusted group mean of each dependent variable (for each of time periods 2 to 8 for each aphid species) (i.e., for

dependent variable X at time period Y, aphid species Z) was calculated as follows:

$$\begin{aligned} \text{Adjusted Group Mean} = & \\ & \left(\text{SRC}_{\text{var. x}} \right) \left(\text{GM}_{\text{var. x}} \right) + \left(\text{SRC}_{\text{var. y}} \right) \left(\text{GM}_{\text{var. x}} \right) + \dots \\ & + \left(\text{SRC}_{\text{var. z}} \right) \left(\text{GM}_{\text{var. x}} \right) + \text{Constant} \end{aligned} \quad (\text{Equation 2})$$

where SRC was the respective significant regression coefficient and GM was the gross mean of the respective variable.

The results of the multiple linear regression analyses were tested (Equation 3) to ensure that the regression equations provided values which were predictive of observed values:

$$\hat{Y} = b + a_1x_1 + \dots + a_ix_i \quad (\text{Equation 3})$$

where \hat{Y} represented the predicted value of the respective dependent variable; b was the constant (intercept) and a_i were the significant regression coefficients (slope), both of which were obtained from the respective Table of Significant Regression Coefficients found in the Results and Discussion section herein; x_i represented the observations (appropriately transformed) of each of the independent variables shown to be significant by the regression analysis.

CHAPTER III

RESULTS AND DISCUSSION

Collection and Identification of Ant-Aphid Associations

Three hundred and sixty-four samples of ant-aphid associations were collected in Manitoba during 1976. Eighteen associations were collected in 1977, in addition to the 149 samples taken from quadrats at the experimental site in Birds Hill Park.

Identification of these samples indicated that there were at least 27 species in seven genera of ants collecting honeydew from at least 62 species in 28 genera of aphids on 39 host plants within the province of Manitoba. The species of aphids tended by each ant species on the various host plants are listed in Table 1. Table 2 lists the species of attendant ants for each aphid species, host plants, number of records and collection sites for each association. The sites wherein each ant species was collected are set out in Appendix D.

Formicidae

Similar to Jones' (1929) findings in Colorado, Formica ants were the dominant and least species-specific aphid attendants in Manitoba. Fourteen species of Formica were collected with 55 aphid species. The second most prevalent attendants were ants of the genus Lasius, with four species found tending

TABLE 1. Ant-Aphid Associations Collected in the Province of Manitoba during 1976-77 and the Respective Host Plants, Listed by Species of Attendant Ant.

[illegible]

TABLE 2. Attendant Ants of Each Aphid Species, Host Plant(s), Site(s) and Number of Records of Each Ant-Aphid Association Collected in Manitoba during 1976-77.

			Number of Records	
			1977	1976
<u>Aphis</u> sp.	Host Plant(s): Spiraea alba ¹ ; Artemisia sp. ²			
¹ Dolichoderus taschenbergi	Sandilands Provl. Forest			1
² Lasius neoniger	" " "			1
<u>Aphis armoraciae</u> Cowen	Rudbeckia hirta ¹ ; Picea glauca ²			
² Formica obscuripes	Sandilands Provl. Forest			1
¹ Formica oreas comptula	Carberry			1
<u>Aphis asclepiadis</u> Fitch	Apocynum cannabinum			
Myrmica brevispinosa	Birds Hill Provl. Pk.			1
Formica podzolica	Sandilands Provl. Forest			1
<u>Aphis citricola</u> vander Goot	Spiraea sp.			
Lasius pallitarsis	City of Winnipeg			1
<u>Aphis fabae</u> Scopoli	Viburnum opulus nanum ¹ ; Philadelphus coronarius ² ; Xanthium strumarium ³			
³ Myrmica brevispinosa	Morden			1
^{1,2} Lasius pallitarsis	U Manitoba; City of Winnipeg			3
* ^{2,3} Formica podzolica	City of Winnipeg; Morden			2
<u>Aphis farinosa</u> Gmelin	Populus balsamifera ¹ ; Salix sp. ² ; Salix planifolia ³			
² Lasius pallitarsis	Spruce Woods Provl. Forest			1
¹ Formica podzolica	Sandilands Provl. Forest			1
³ Formica neorufibarbis	Churchill			2
<u>Aphis gossypii</u> Glover	Galium boreale ¹ ; Oenothera biennis ² ; Diervilla lonicera ³			
^{1,3} Myrmica emeryana	Whiteshell Provl. Pk. (Hanson Ck.)			3
³ Dolichoderus plagiatus	Pinawa (Atomic Energy FIG Area)			2
³ Tapinoma sessile	Agassiz Provl. Forest			1
³ Camponotus noveboracensis	" " "			1
² Lasius alienus	Pinawa (Atomic Energy FIG Area)			1
² Formica lasioides	" " "			1
³ Formica sanguinea subnuda	" " "			1
² Formica obscuripes	Sandilands Provl. Forest			1

TABLE 2 cont'd.

68
Number of
Records
1977 1976

A. gossypii

¹ Formica (rufa) species?	Sandilands Provl. Forest	2
¹ Formica subsericea	Whitemouth L.	1
³ Formica subaenescens	Pinawa (Atomic Energy FIG Area)	1

Aphis helianthi Monell Cornus stolonifera

Camponotus nearcticus	Sandilands Provl. Forest	1
Lasius pallitarsis	U Manitoba	1
Formica podzolica	Birds Hill Provl. Pk.	1
Formica subaenescens	" " " "	1

Aphis knowltoni Hottes and Frison Taraxacum officinale

Myrmica brevispinosa	Beaconia	1
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Aphis maculatae Oestlund Populus tremuloides¹; P. balsamifera²;
Populus sp.³

¹ Myrmica emeryana	Sandilands Provl. Forest; Whiteshell Provl. Pk. (Hanson Ck.)	2
³ Tapinoma sessile	Whiteshell Provl. Pk. (Lone Is. L.)	1
¹ Camponotus herculeanus	Northwest Angle Provl. Pk.	1
^{1,2,3} Camponotus noveboracensis	Camp Morton; Rennie; City of Winnipeg; Sandilands Provl. Forest; LaBarriere Pk; Whiteshell Provl. Pk. (Lone Is. L.)	7
² Lasius pallitarsis	Sandilands Provl. Forest	1
¹ Formica lasioides	" " "	1
¹ Formica sanguinea subnuda	Whiteshell Provl. Pk. (Lone Is. L.)	1
¹ Formica (rufa) species?	Sandilands Provl. Forest	1
¹ Formica subsericea	Whitemouth L.	1
^{1,3} Formica subaenescens	Northwest Angle Provl. Pk; Whiteshell Provl. Pk. (Lone Is. L.); Sandilands Provl. Forest	10

Aphis neogillettei Palmer Cornus stolonifera

Myrmica emeryana	Spruce Woods Provl. Forest	1
Dolichoderus plagiatus	Birds Hill Provl. Pk.	1
Tapinoma sessile	Richer; Sandilands Provl. Forest	2
Camponotus herculeanus	Rennie	1
Camponotus noveboracensis	Birds Hill Provl. Pk; Sandilands Provl. Forest; Hnausa Pk.	3
Lasius alienus	Rennie; Birds Hill	2
Lasius pallitarsis	U Manitoba; Spruce Woods Provl. Forest; Stoney Mountain; Whiteshell Provl. Pk. (Hanson Ck.)	4
Lasius subumbratus	Spruce Woods Provl. Forest	1
Formica lasioides	Rennie	1
Formica sanguinea subnuda	Richer; Hecla Island	2
Formica obscuripes	Morden; Stoney Mountain	2
Formica oreas comptula	Spruce Woods Provl. Forest; Birds Hill Provl. Pk; Birds Hill; Aweme	1 4

TABLE 2 cont'd.

Number of Records	
1977	1976

A. neogillettei

Formica podzolica	Birds Hill ; Richer; Stoney Mountain;		
	Birds Hill Provl. Pk.; U Manitoba	5	
Formica subaenescens	Aweme	1	

Aphis oenotherae Oestlund Epilobium angustifolium

Formica podzolica	Thompson	2	
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Aphis oestlundi Gillette Oenothera biennis

Formica obscuripes	Sandilands Provl. Forest	1	
Formica subsericea	" " "	1	

Aphis rubicola Oestlund Rosa acicularis¹; Rubus strigosus²

² Myrmica emeryana	Birds Hill Provl. Pk.	1	
^{2,1} Camponotus noveboracensis	Sandilands Provl. Forest; Birds Hill Pk.	3	
² Formica podzolica	" " "	1	

Aphis spiraephila Patch Spiraea alba

Myrmica emeryana	Whiteshell Provl. Pk.(Hanson Ck.)	1	
Lasius alienus	" " "	1	
Lasius pallitarsis	" " "	1	
Formica podzolica	" " ; Sandilands Provl. For.	3	

Aphis varians Patch Epilobium angustifolium

Myrmica emeryana	Whiteshell Provl. Pk.(Hanson Ck.)	1	
Camponotus noveboracensis	Pinawa (Atomic Energy FIG Area); Northwest Angle Provl. Pk; Whitemouth L.	5	
Formica lasioides	Whitemouth L.	1	
Formica obscuripes	Sandilands Provl. Forest	1	
Formica oreas comptula	Agassiz Provl. Forest	1	
Formica podzolica	Pinawa (Atomic Energy FIG Area); Whiteshell Provl. Pk.(Hanson Ck.)	4	
Formica subsericea	Whitemouth L.	2	
Formica subaenescens	Northwest Angle Provl. Pk.	3	
Formica neorufibarbis	Churchill	1	

Aphis viburniphila Patch Viburnum rafinesquianum¹; V. trilobum²

¹ Formica obscuripes	Morden	2	
¹ Formica oreas comptula	Morden; Birds Hill Provl. Pk.	1	1
² Formica montana	U Manitoba	1	

Aphis whiteshellensis Rojanavongse and Robinson Amelanchier alnifolia

Myrmica emeryana	Whiteshell Provl. Pk.(Hanson Ck.)	2	
Formica subaenescens	" " "	1	

TABLE 2 cont'd.

Aphthargelia symphoricarpi (Thomas) *Symphoricarpos occidentalis*

<i>Camponotus noveboracensis</i>	Stoney Mountain	1
<i>Lasius alienus</i>	Morden	4
<i>Lasius pallitarsis</i>	Spruce Woods Provl. Forest	2
<i>Formica lasioides</i>	Sandilands Provl. Forest	1
<i>Formica obscuripes</i>	" " "	1
<i>Formica ulkei</i>	Cook's Creek	1
<i>Formica podzolica</i>	Stoney Mountain	1

Asiphonaphis pruni Wilson and Davis *Prunus virginiana*¹;
*P. pensylvanica*²; *Populus* sp.³

¹ <i>Lasius alienus</i>	Carberry	1
^{1,2,3} <i>Formica obscuripes</i>	Sandilands Provl. Forest; Morden	5
¹ <i>Formica oreas comptula</i>	" " "	1
¹ <i>Formica (rufa) species?</i>	" " "	1

Asiphum tremulae (L.) *Populus tremuloides*

<i>Dolichoderus taschenbergi</i>	Sandilands Provl. Forest	1
<i>Formica sanguinea subnuda</i>	" " "	1
<i>Formica oreas comptula</i>	" " "	1
<i>Formica podzolica</i>	" " " ; Thompson	3
<i>Formica subaenescens</i>	" " "	1

Ceruraphis viburnicola (Gillette) *Viburnum opulus nanum*

<i>Formica podzolica</i>	U Manitoba	1
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Chaitophorus sp. (pustulatus grp.) *Salix* sp.

<i>Formica oreas comptula</i>	Aweme	1
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Chaitophorus macrostachyae (Essig) *Salix* sp.

<i>Formica obscuriventris</i>	Morden	2
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Chaitophorus neglectus Hottes and Frison *Populus tremuloides*

<i>Formica sanguinea subnuda</i>	Sandilands Provincial Forest	1
<i>Formica subaenescens</i>	" " "	1

Chaitophorus nigrae Oestlund *Salix* sp.¹; *Salix bebbiana*²

¹ <i>Myrmica brevispinosa</i>	Birds Hill Provl. Pk.	2
¹ <i>Dolichoderus plagiatus</i>	" " " "	1
¹ <i>Camponotus noveboracensis</i>	Hecla Island	1
¹ <i>Lasius alienus</i>	Whiteshell Provl. Pk. (Hanson Ck.)	1
¹ <i>Lasius pallitarsis</i>	Spruce Woods Provl. Forest	1
¹ <i>Formica sanguinea subnuda</i>	" " " "	1
¹ <i>Formica obscuripes</i>	Lewis	3
² <i>Formica oreas comptula</i>	Birds Hill Provl. Pk.	12

TABLE 2 cont'd.

Number of
Records
1977 1976

C. nigrae

¹ Formica (rufa) species ?	Sandilands Provl. Forest	1
¹ Formica hewitti	Northwest Angle Provl. Pk.	1
¹ Formica podzolica	Thompson; Birds Hill Provl. Pk; Sandilands Provl. Forest; Birds Hill	4
¹ Formica subaenescens	Richer	1

Chaitophorus nigricentrus Richards *Salix* sp.¹; *Salix bebbiana*²

¹ Formica sanguinea subnuda	Birds Hill Provl. Pk.	1
¹ Formica obscuripes	Sandilands Provl. Forest	1
² Formica oreas comptula	Birds Hill Provl. Pk.; Birds Hill	10
¹ Formica podzolica	Birds Hill	1
¹ Formica subaenescens	Birds Hill Provl. Pk.	1

Chaitophorus nudus Richards *Populus tremuloides*

<i>Lasius alienus</i>	Carberry	1
<i>Formica oreas comptula</i>	Sandilands Provl. Forest; Agassiz Provl. Forest; Carberry; Aweme; Birds Hill Provl. Pk.	24 7
<i>Formica</i> (rufa) species ?	Carberry; Sandilands Provl. Forest	2

Chaitophorus populicola Thomas *Populus tremuloides*¹; *P. balsamifera*²;
Populus sp.³; *Salix bebbiana*⁴

^{2,3} <i>Myrmica brevispinosa</i>	Portage La Prairie	5
¹ <i>Myrmica emeryana</i>	Sandilands Provl. Forest; Whiteshell Provl. Pk. (Hanson Ck.); Birds Hill Provl. Pk.	5
¹ <i>Leptothorax muscorum</i>	Whiteshell Provl. Pk. (Hanson Ck.)	1
² <i>Dolichoderus taschenbergi</i>	Aweme	1
^{1,2} <i>Tapinoma sessile</i>	Agassiz Provl. Forest; Sandilands Provl. Forest	2
¹ <i>Camponotus herculeanus</i>	Northwest Angle Provl. Pk.	1
^{1,2,3} <i>Camponotus noveboracensis</i>	Agassiz Provl. Forest; Aweme; Camp Morton; Carberry; Fortier; LaBarriere Pk; Lewis; City of Winnipeg; Pinawa (Atomic Energy FIG Area); Portage La Prairie; Rennie; Sandilands Provl. Forest; Stoney Mountain; Whitemouth L; Whiteshell Provl. Pk. (Hanson Ck.); Lone Is. L.)	25
^{1,2} <i>Lasius alienus</i>	Pinawa (Atomic Energy FIG Area); Portage La Prairie; Sandilands Provl. Forest; Whiteshell Provl. Pk. (Hanson Ck.)	6
^{1,2} <i>Formica lasioides</i>	Sandilands Provl. Forest; Rathwell	3
^{1,2} <i>Formica sanguinea subnuda</i>	Fortier; Hecla Island; Sandilands Provl. Forest; Northwest Angle Provl. Pk; White- shell Provl. Pk. (Hanson Ck.); Birds Hill Provl. Pk.	9

TABLE 2 cont'd.

Number of Records	
1977	1976

C. populicola

2, ¹ Formica obscuripes	Sandilands Provl. Forest; Portage La Prairie; Stoney Mountain; Lewis	8	
³ Formica obscuriventris	Morden	1	
2, ¹ , ⁴ Formica oreas comptula	Carberry; Aweme; Birds Hill		
¹ Formica (rufa) species ?	Provl. Pk.; Birds Hill	24	6
¹ Formica hewitti	Sandilands Provl. Forest		2
1, ² , ⁴ Formica podzolica	Hecla Island		1
¹ , ² Formica subsericea	Birds Hill; Sandilands Provl. Forest; Northwest Angle Provl. Pk;		5
	Whitemouth L.; Lewis		4
¹ , ³ Formica subaenescens	Whiteshell Provl. Pk. (Lone Is. L.)		
	Sandilands Provl. Forest; Northwest Angle Provl. Pk.		11

Chaitophorus populifolii (Essig) Populus tremuloides¹;
P. balsamifera²; Salix bebbiana³

¹ Myrmica emeryana	Sandilands Provl. Forest; Whiteshell Provl. Pk. (Hanson Ck.)		2
¹ Camponotus noveboracensis	LaBarriere Pk; Stoney Mountain; Dakotah		3
¹ Lasius alienus	Sandilands Provl. Forest		1
¹ Formica obscuripes	Stoney Mountain		1
1, ² , ³ Formica oreas comptula	Birds Hill Provl. Pk.	4	
¹ Formica podzolica	Northwest Angle Provl. Pk.		1

Chaitophorus saliciniger (Knowlton) Cornus stolonifera¹;
Salix sp.²; Salix bebbiana³

³ Formica oreas comptula	Birds Hill Provl. Pk.	20	
2, ¹ Formica podzolica	Sandilands Provl. Forest; Thompson;		
	Birds Hill Provl. Pk.	1	5
³ Formica hewitti	" " " "	1	

Cinara sp. Pinus banksiana; Picea glauca

Formica oreas comptula	Sandilands Provl. Forest; Birds Hill Provl. Pk.	1	1
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Cinara banksiana Pepper and Tissot Pinus banksiana

Dolichoderus taschenbergi	Sandilands Provl. Forest		1
Lasius alienus	" " "		1
Formica obscuripes	" " "		5
Formica podzolica	" " "		1

Cinara braggi (Gillette) Picea glauca

Formica podzolica	Carberry		1
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TABLE 2 cont'd.

Number of	
Records	
1977	1976

<u>Cinara canatra</u> Hottes and Bradley <i>Pinus banksiana</i>		
Formica obscuripes	Sandilands Provl. Forest	2
Formica oreas comptula	" " " ; Agassiz Provl. Forest	2
<u>Cinara coloradensis</u> (Gillette) <i>Picea glauca</i>		
Dolichoderus taschenbergi	Carberry	1
<u>Cinara fornacula</u> Hottes <i>Picea glauca</i>		
Formica lasioides	Sandilands Provl. Forest	1
Formica obscuripes	" " "	1
Formica podzolica	Whiteshell Provl. Pk. (Hanson Ck.); Northwest Angle Provl. Pk.; Sandilands Provl. Forest	5
Formica subaenescens	Northwest Angle Provl. Pk.	1
<u>Cinara laricifex</u> (Fitch) <i>Larix laricina</i>		
Camponotus herculeanus	Churchill	2 3
Formica sanguinea subnuda	Sandilands Provl. Forest	1
Formica podzolica	" " "	4
Formica densiventris	" " "	1
Formica hewitti	" " "	1
Formica neorufibarbis	Churchill	1 2
<u>Cinara obscura</u> Bradley <i>Picea glauca</i>		
Formica obscuripes	Lewis	1
Formica neorufibarbis	Churchill	1
<u>Cinara pergandei</u> (Wilson) <i>Pinus banksiana</i>		
Camponotus noveboracensis	Lewis; Sandilands Provl. Forest	4
Formica sanguinea subnuda	Pinawa (Atomic Energy FIG Area)	1
Formica obscuripes	Sandilands Provl. Forest	1
Formica obscuriventris	Agassiz Provl. Forest	1
Formica oreas comptula	" " " ; Whitemouth L.	2
Formica podzolica	Pinawa (Atomic Energy FIG Area)	1
<u>Cinara petersoni</u> Bradley <i>Juniperus horizontalis</i>		
Formica sanguinea subnuda	Carberry	1
Formica spatulata	Rathwell	1
<u>Cinara spiculosa</u> Bradley <i>Larix laricina</i>		
Camponotus herculeanus	Churchill	1
Formica neorufibarbis	"	1

TABLE 2 cont'd.

Number of
Records
1977 1976

<u>Hamamelistes spinosus</u> Shimer	Betula glandulosa var. glandulifera		
Formica oreas comptula	Birds Hill Provl. Pk.	1	
<u>Hoplochaitophorus quercicola</u> (Monell)	Quercus macrocarpa		
Myrmica brevispinosa	Morden		1
Camponotus noveboracensis	" ; Spruce Woods Provl. Forest		2
Lasius alienus	"		2
Formica obscuripes	Carberry		2
Formica oreas comptula	Whitemouth L.; Birds Hill Provl. Pk.; Aweme	1	4
Formica podzolica	Morden		1
Formica subsericea	Whitemouth L.		2
<u>Hysteroneura setariae</u> (Thomas)	Prunus ¹ ; Prunus pumila ²		
² Tapinoma sessile	Sandilands Provl. Forest		1
¹ Lasius pallitarsis	City of Winnipeg	1	
² Formica podzolica	Sandilands Provl. Forest		1
<u>Lachnus allegheniensis</u> McCook	Quercus macrocarpa		
Formica sanguinea subnuda	Birds Hill		1
Formica podzolica	" "		1
<u>Macrosiphoniella</u> sp.	Artemisia frigida		
Formica subsericea	Whitemouth L.		1
<u>Macrosiphoniella absinthii</u> (L.)	Artemisia sp.		
Formica lasioides	Stoney Mountain		1
<u>Maculolachnus sijpkensi</u> Hille Ris Lambers	Rosa acicularis		
Formica obscuripes	Sandilands Provl. Forest		4
Formica oreas comptula	Birds Hill Provl. Pk.; Birds Hill	1	2
<u>Mastopoda pteridis</u> Oestlund	Pteridium aquilinum		
Myrmica emeryana	Birds Hill Provl. Pk.		1
<u>Meliarhizophagus fraxinifolii</u> (Riley)	Fraxinus sp.		
Camponotus noveboracensis	Morden		1
<u>Myzocallis punctatus</u> (Monell)	Quercus macrocarpa		
Formica oreas comptula	Sandilands Provl. Forest		1
Formica subsericea	Whitemouth L.		1

TABLE 2 cont'd.

75
Number of
Records

1977 1976

Myzus cerasi (Fabricius) Prunus pensylvanica

<u>Dolichoderus taschenbergi</u>	Carberry	1
<u>Dolichoderus plagiatus</u>	Rathwell	1
<u>Tapinoma sessile</u>	Sandilands Provl. Forest	1
<u>Camponotus herculeanus</u>	Pinawa (Atomic Energy FIG Area)	2
<u>Camponotus noveboracensis</u>	Sandilands Provl. Forest	1
<u>Lasius alienus</u>	Whiteshell Provl. Pk. (Hanson Ck.); Birds Hill	2
<u>Formica lasioides</u>	Sandilands Provl. Forest	1
<u>Formica sanguinea subnuda</u>	Rennie; Northwest Angle Provl. Pk.	2
<u>Formica obscuripes</u>	Sandilands Provl. Forest	2
<u>Formica oreas comptula</u>	Whitemouth L.	2
<u>Formica podzolica</u>	Sandilands Provl. Forest; Pinawa (Atomic Energy FIG Area); Rennie; Carberry	6
<u>Formica subaenescens</u>	Agassiz Provl. Forest	1
<u>Formica subsericea</u>	Whitemouth L.	1

Nearctaphis sp. Crataegus sp.

<u>Formica oreas comptula</u>	Birds Hill Provl. Pk.	1
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Nearctaphis clydesmithi Hille Ris Lambers Crataegus sp.

<u>Formica obscuripes</u>	Stoney Mountain	1
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Nearctaphis crataegifoliae (Fitch) Crataegus sp.

<u>Formica obscuripes</u>	Sandilands Provl. Forest	3
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Nearctaphis sensoriata (Gillette and Bragg) Amelanchier alnifolia

<u>Lasius alienus</u>	Agassiz Provl. Forest	1
<u>Formica oreas comptula</u>	Sandilands Provl. Forest	1

Neosymydobius mimicus Hottes Quercus macrocarpa

<u>Dolichoderus taschenbergi</u>	Carberry	1
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Paraprociophilus tessellatus (Fitch) Alnus rugosa

<u>Formica podzolica</u>	Sandilands Provl. Forest	1
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Pemphigus sp. Populus tremuloides

<u>Dolichoderus taschenbergi</u>	Sandilands Provl. Forest	1
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Periphyllus negundinis (Thomas) Acer negundo

<u>Formica sanguinea subnuda</u>	Fortier	1
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Prociphilus sp. Moss

<u>Myrmica emeryana</u>	Sandilands Provl. Forest	1
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Prociphilus erigeronensis (Thomas) ?Grass roots permeating ant nest

<u>Lasius pallitarsis</u>	Fortier	1
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TABLE 2 concluded.

Number of
Records

			1977	1976
<u>Pseudopteroomma canadensis</u>	Richards	Populus tremuloides		
Dolichoderus taschenbergi	Sandilands Provl. Forest			1
<u>Pterocomma bicolor</u>	(Oestlund)	Populus balsamifera ¹ ; Salix sp. ² ; Populus sp. ³		
³ Myrmica brevispinosa	Portage La Prairie			1
¹ Camponotus noveboracensis	Sandilands Provl. Forest; Birds Hill Provl. Pk; Whiteshell Provl. Pk. (Hanson Ck.)			6
² Lasius subumbratus	Spruce Woods Provl. Forest			1
¹ Formica sanguinea subnuda	Sandilands Provl. Forest			1
¹ Formica oreas comptula	Birds Hill Provl. Pk.		2	
¹ Formica subaenescens	" " " "			2
<u>Pterocomma smithiae</u>	(Monell)	Populus balsamifera ¹ ; Salix sp. ² ; Salix planifolia ³		
² Lasius pallitarsis	Spruce Woods Provl. Forest			1
¹ Formica oreas comptula	Birds Hill Provl. Pk.		29	
³ Formica neorufibarbis	Churchill		1	
<u>Rhopalosiphum</u> sp.	Crataegus sp.			
Formica oreas comptula	Birds Hill Provl. Pk.			1
<u>Rhopalosiphum cerasifoliae</u>	(Fitch)	Prunus virginiana		
Myrmica emeryana	Cook's Creek			1
Formica sanguinea subnuda	Sandilands Provl. Forest			1
Formica oreas comptula	" " "			1
<u>Symydobius americanus</u>	Baker	Betula glandulosa var. glandulifera ¹ ; B. papyrifera ²		
¹ Myrmica emeryana	Birds Hill Provl. Pk.		1	
¹ Tapinoma sessile	" " " "		1	
² Formica obscuripes	Lewis			2
¹ Formica oreas comptula	Birds Hill Provl. Pk.		21	
Formica hewitti and/or E. podzolica	" " " "		**	
<u>Thecabius affinis</u>	(Kaltenbach)	Populus tremuloides		
Formica podzolica	Thompson			1

* Host plants are noted in order of diminishing frequency.

** Several visual sightings recorded but no sample taken.

22 aphid species, followed by three species of Camponotus which were collected with 17 aphid species. Two species each of Myrmica and Dolichoderus were found with 19 and 11 species of aphids respectively.

Some Formica species were found to be more prevalent as aphid attendants than other Formica species. This also appeared to be true for some other genera such as Lasius and Camponotus (Table 1). Formica podzolica Francoeur, F. oreas comptula and F. obscuripes tended 30, 25 and 23 aphid species respectively, and F. sanguinea subnuda and F. subaenescens were found tending 16 and 14 species of aphids; F. obscuriventris Mayr, F. hewitti Wheeler and F. subsericea respectively tended only three, four and five aphid species. The difference in prevalence of some ant species as aphid attendants may have been due to several factors. For example, it may have been a function of a limitation in the natural distribution of the ant as a result of habitat preferences; or, the particular ant species may not have needed honeydew in its diet and thus had no reason to tend aphids; the plant spectrum within the ant's range may not have been particularly suited to the establishment of ant-attended aphid species in the area; or, the difference in prevalence may have been due to inefficient surveying of certain areas wherein these ants were found. For example, F. obscuriventris was collected only at two sites in the province which were rather atypical and surveyed only once during the study. One site was near the edge of Lake

Minnewasta, in an area characterized by reed-like grasses, willow and poplar shrubs; the other collection site was in a dry, sandy-gravel area of Agassiz Provincial Forest characterized by mature stands of Pinus banksiana Lamb. Another area sampled only once yielded the sample of Formica ulkei Emery which was found tending aphids on a hedgerow herb located between two large plowed fields. Another area sampled once, led to the discovery of Formica spatulata Buren; Juniperus horizontalis Moench. was pulled from the ground and ants streamed off the roots where they had been tending Cinara petersoni Bradley. Juniper mats were widely distributed over the rather dry, grey sandy soil which characterized this area, and no ant nests were observed anywhere in the area above the juniper. The only other ants found in this area were Dolichoderus plagiatus (Mayr) and F. lasioides which were collected from Prunus pensylvanica L. and P. tremuloides respectively. Creighton (1950) stated that the host of F. spatulata was F. fusca (= subaenescens), but no ants of the fusca group were found in this area at the time of sampling. In contrast to the abovementioned single records, the single collection of Camponotus nearcticus Emery was made in an area which was often surveyed throughout the study and therefore it is possible that this ant species is not abundantly distributed in the province.

In very close agreement with Jones' (1929) estimate was the finding that 9.7% of the ants collected tending aphids

in Manitoba during 1976 were in mixed species groups (Table 3). But the collection of an association containing mixed ant species does not necessarily imply that the individual ant species were interacting with each other. In a number of cases it appeared that one ant species acted as the aphid-attendant while the other species was a scavenger, foraging in the attendant species' territory but avoiding direct contact with it. Observations of F. oreas comptula and F. podzolica and/or F. hewitti at Birds Hill Park and of Lasius pallitarsis (Provancher) and F. podzolica in the City of Winnipeg on the same respective host plant tend to support this view.

F. podzolica and/or F. hewitti were often observed to quickly move over the leaf surfaces, sometimes stopping very briefly to imbibe some honeydew from aphids at the edge of a colony. They never interacted with the respective attendant species and took direct evasive action to avoid contact with the latter, sometimes jumping from the plant at the very instant of antennal contact between the two. When samples containing Tapinoma sessile (Say)/C. noveboracensis and F. podzolica/D. taschenbergi were collected the latter species of each mixed group were observed tending aphids and the former species were only discovered when the samples were later processed in the laboratory. This implied that T. sessile and F. podzolica were present on the same respective host plant but were not tending the aphids at the same time as C. noveboracensis and D. taschenbergi. The ratio of the number of individuals of

TABLE 3. Ant Species Collected in Mixed Species Groups while Tending Aphids on One Host Plant.

Mixed Ant Species	No. of Mixed Collec.	Collec. Date
<i>Lasius pallitarsus</i> + <i>Formica podzolica</i>	1	6-06
<i>L. alienus</i> + <i>F. lasioides</i>	1	22-06
+ <i>F. obscuripes</i>	1	2-06
<i>Camponotus noveboracensis</i> + <i>Tapinoma sessile</i>	3	18, 22-06
+ <i>F. podzolica</i>	1	13-08
+ <i>F. neorufibarbis</i>	1	3-08
+ <i>F. subaenescens</i>	3	4-06; 17, 27-07
<i>C. herculeanus</i> + <i>F. podzolica</i>	1	22-06
+ <i>F. neorufibarbis</i>	1	3-08
+ <i>F. lasioides</i>	1	29-06
+ <i>F. subaenescens</i>	1	29-07
<i>F. sanguinea subnuda</i> + <i>F. podzolica</i>	4	22, 29-06; 10, 27-07
+ <i>Myrmica emeryana</i>	1	29-06
+ <i>F. hewitti</i>	2	20-07; 3-09
+ <i>F. subaenescens</i>	3	9, 13-06; 27-07
<i>F. oreas comptula</i> + <i>F. podzolica</i>	2	18-06; 10-07
+ <i>F. subsericea</i>	3	9-06; 29-07
<i>M. brevispinosa</i> + <i>F. podzolica</i>	2	16-07; 13-08
<i>M. emeryana</i> + <i>T. sessile</i> *	1	27-07
+ <i>Leptothorax muscorum</i>	1	1-09
<i>Dolichoderus taschenbergi</i> + <i>F. podzolica</i>	1	11-08
<i>F. sanguinea subnuda</i> + <i>F. subaenescens</i> + <i>D. plagiatus</i> **	1	22-06

*The two species did not interact;

**Several cuttings from different plants were gathered together.

each species collected in a mixed sample might be considered a fair indicator of whether or not there were interactions occurring between the two different species. For example, ratios of 19:1, 35:3 and 53:2 of F. sanguinea subnuda or F. oreas comptula to F. podzolica would indicate that the latter species was scavenging at the time that the sample was collected. But a ratio of 10:18 of F. sanguinea subnuda to F. subaenescens in one sample would indicate that these species were truly interacting in some way in the collection of aphid honeydew. It is possible that Camponotus are tolerant of the presence of other ant species. In one sample six F. podzolica were collected with 15 C. herculeanus unnoticed at the time of collection. Some aggression would have certainly manifested itself in some way, either during the initial observation and collection or during transportation of the bagged sample to the laboratory, if there was not some tolerance or interaction occurring between the two species. However, no aggressive behavior between any ants was observed while they were contained in polyethylene bags, and most of the ants usually continued to tend the aphids until the samples were put into the freezer. However, with the exception of several of the samples which contained F. oreas comptula with F. subsericea and F. sanguinea subnuda with F. subaenescens, it is doubtful that the species groups listed in Table 3 were truly mixed and sharing the aphid colonies at which they were collected.

Aphidoidea

During 1976-77 the most frequently attended aphids were those of the genus Aphis (17 species), Cinara (10 species) and Chaitophorus (8 species) (Table 2). Chaitophorus populicola Thomas was tended by the greatest number of different ant species (17 species), followed by Aphis neogillettei Palmer which had 14 species of attendant ants, and Myzus cerasi (Fabricius) and Chaitophorus nigrae Oestlund with 12 and 11 different species of attendants respectively. P. tremuloides, P. balsamifera and Cornus stolonifera Michx. were well-distributed throughout the central and southern areas of Manitoba; the greater numbers of attendant ant species with aphids associated with these host plants were probably a result of the plants' extensive distribution in that, since the plants had such an extensive geographic range, they probably occurred in a greater number of ant species' territories. Aphid species feeding on these host plants were numerous and likewise well-distributed during 1976, but the occurrence of almost all aphid species during 1977 was dramatically decreased. Paralleling C. populicola's extensive distribution was one of its attendants, C. noveboracensis, which had the greatest geographic range of any of the ant species found tending aphids. Contrary to the findings of Bodenheimer and Swirski (1957), one species each of Macrosiphoniella and of Myzus was visited by ants in Manitoba. Ants were also found visiting Paraprociophilus tessellatus, Thecabius affinis (Kalt.) and a species of

Pemphigus; Prociphilus erigeronensis was found in the nest of L. pallitarsis 6 May, 1976.

There appears to have been a preference for aphids hosted by Populus and Salix spp. (Table 1) but, as previously mentioned, this was probably a function of host plant distribution. Based on the survey reported herein and observations at Birds Hill Park of interacting ant and aphid species, I concur with Ayre (in Bradley 1961) and Bradley (1961) that ant species collecting aphid honeydew were opportunistic and did not appear to discriminate between aphid species, except for the basic discrimination between species which preferred to be tended and those which preferred not to be (e.g., Dactynotus).

Survey of Associations at Birds Hill Park Experimental Site

The species of aphids tended by F. oreas comptula within each quadrat of the experimental site on 30 May, 1977 are listed in Table 4. As can be seen from Fig. 1 P. tremuloides and P. balsamifera were the dominant host plants within the area; as a result the dominant aphid species were those colonizing these host plants.

F. podzolica and F. hewitti were also found to be present in the area and individuals of these species were occasionally observed to visit aphid colonies from 24 June. T. sessile, Myrmica emeryana Forel and D. plagiatus were also observed in the area from time to time from 29 June, the former two species occasionally tending S. americanus colonies located on a dwarf birch branch about 15 cm above the ground.

TABLE 4. Aphid Species Tended by Formica oreas comptula, Their Distribution and Number of Samples Collected Per Species within Each Quadrat at Birds Hill Park, Manitoba, on 30 May, 1977.

Aphis neogillettei Palmer on Cornus stolonifera

Quadrat	6-D
No. of Samples	(1)

A. viburniphila Patch on Viburnum rafinesquianum

Quadrat	7-D
No. of Samples	(1)

Chaitophorus sp. (immatures) on Populus tremuloides
P. balsamifera and Salix bebbiana

Quadrat	2-A 2-C 5-D 6-B 7-A 7-F 9-C
No. of Samples	(1) (1) (2) (1) (2) (1) (2)

C. nigrae Oestlund on S. bebbiana

Quadrat	3-E 4-D 6-B 6-C 7-F
No. of Samples	(1) (3) (1) (1) (6)

C. nudus Richards on P. tremuloides

Quadrat	1-C 2-B 2-C 2-E 3-A 3-B 4-A 4-B 5-A 7-A 7-D 8-A
No. of Samples	(2) (2) (3) (1) (1) (1) (1) (1) (4) (1) (1) (1)
	8-B 9-A 9-B 9-C
	(1) (2) (1) (1)

C. populicola Thomas on P. tremuloides, P. balsamifera and S. bebbiana

Quadrat	2-A 3-A 3-D 4-C 5-B 5-E 6-A 6-B 6-C 7-A 8-A 8-B
No. of Samples	(1) (1) (1) (1) (3) (1) (2) (2) (1) (5) (1) (1)
	9-A 9-C 9-D
	(1) (1) (1)

C. populifolii (Essig) on P. tremuloides, P. balsamifera and S. bebbiana

Quadrat	2-B 5-D 8-B
No. of Samples	(1) (2) (1)

TABLE 4 concluded.

C. saliciniger (Knowlton) on S. bebbiana

Quadrat	5-D 5-F 7-F
No. of Samples	(14) (3) (3)

Hamamelistes spinosus Shimer on Betula glandulosa var. glandulifera

Quadrat	3-E
No. of Samples	(1)

Maculolachnus sijpkensi HRL on Rosa acicularis

Quadrat	5-E
No. of Samples	(1)

Pterocomma bicolor (Oestlund) on P. balsamifera

Quadrat	7-A 9-C
No. of Samples	(1) (1)

Pterocomma smithiae (Monell) on P. balsamifera

Quadrat	5-B 5-D 5-E 6-C 7-A 7-B 7-C 7-D 8-B 9-C 9-D
No. of Samples	(2) (3) (2) (1) (2) (4) (2) (2) (2) (5) (4)

Symydobius americanus Baker on B. glandulosa var. glandulifera

Quadrat	3-E 4-E
No. of Samples	(13) (8)

Experimental Observations of Ant-Aphid Interactions

Attendance Time

The experimental area at Birds Hill Park was first visited 11 May, 1977. Vegetation was just beginning to leaf out, but already there were well-established aphid colonies on V. rafinesquianum, P. tremuloides and P. balsamifera being tended by F. oreas comptula. By 20 May the ants present at the aphid colonies on P. tremuloides were sometimes so numerous that it was difficult to see the aphids. Periodic observations of aphid colonies were made throughout some nights in May and early June; these revealed that F. oreas comptula remained with their aphid colonies all night, and that honeydew foragers continued to go to and from the aphid colonies, although sometimes very slowly due to low nighttime temperatures. It was not established whether these activities were continued by F. oreas comptula later in the season.

Marking Experiments

One day following marking of ants at the nest in quadrat 6-B several marked ants were observed participating in thatching activities on the nest surface. Two days following marking of ants at the nest in quadrat 1-A one marked ant was observed walking over the nest surface. No marked ants were subsequently observed at either nest, on any of the surrounding vegetation, or at any of the aphid colonies nearby during the remainder of the experimental period.

The same ants which were marked on 19 May while tending A. viburniphila were still present and tending the aphid colony together with a number of unmarked ants at 2300 hrs and early the following morning. By 3 June only three marked ants remained with a number of unmarked ants tending the colony. Two marked ants (designated "A" and "B") were observed periodically at the aphid colony throughout 10 June, but they were absent from the colony at midnight, although many other ants were present. On 11 June four marked ants (including "A" and "B") were present periodically during the day until 2000 hrs. One of these ants ("A") was observed tending the aphid colony on 22 June; this was the final sighting of marked ants at the aphid colony, although the aphids were still thriving and being tended by F. oreas comptula when the area was last visited in early August.

The results of these marking experiments suggest that age polyethism and task fidelity exist in F. oreas comptula. The fact that the ants marked from the nests were seldom seen on its surface and never observed away from it suggests that the marked ants were of the inside worker category referred to by Otto (in Rosengren 1971). The presence of marked ants tending A. viburniphila for over one month at the same aphid colony demonstrated that the same ants consistently tended the same aphid colony, although periodically, over an extended period of time. The slow disappearance of these variously marked ants suggests that they may have been foragers from the previous year which were dying off and being replaced by younger

honeydew foragers.

Erratic Forager Behavior

Occasionally early in the experimental observation period, an ant was observed to run up a branch leading to an aphid colony, following another sometimes larger ant; the former often turned, ran down the branch, and then came back up again. Sometimes the follower ant repeated the route several times, but it seldom went to the aphid colony. This behavior gave the impression that the follower ant was in the process of learning a foraging route and that the leader ant already knew the route.

Analysis of Data

The daily number of aphids and daily mean number of ants present in each aphid colony monitored from 8 June are presented in Table 5. Examples of these data are illustrated in Figs. 10, 11 and 12. Mean and standard deviation of the grouped data from each time period for each variable are set out in Appendix E for each of the three aphid species. Bivariate correlations between day, temperature, relative humidity, barometric pressure, number of ants present at the aphid colony and number of aphids in the colony for each of the three aphid species during time period 1 are presented in Appendix F. In addition to the variables mentioned in Appendix F, Appendix G contains bivariate correlations between these and rain, sky, and ant stem activity to and from the aphid colony for each aphid species during each of time periods 2 to 8.

Variables contributing to the relationships determining

TABLE 5. Daily Mean Number of Ants and Daily Number of Aphids in Each Aphid Colony Per Aphid Species Monitored from 8 June, 1977 at Birds Hill Park.

Birch:												
	Colony 3-E-2		Colony 3-E-3a		Colony 3-E-3b		Colony 4-E-5		Colony 4-E-6		Colony 4-E-9	
Date	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids
0806			14.67	53							2.33	11
10	81.40	380	11.83	78	22.67	185	18.17	68	44	315	3	19
13	87	424	8.50	60	32.63	202	12.38	78	51.63	425	7.63	51
15	70.25	531	12.33	58	33.75	303	11.38	120	34.44	420	7.38	101
17	46.20	372	6.83	75	29.83	375	11.17	126	24.33	500	5.67	80
20	47.88	802	7	105	33.86	388	19.88	214	25.25	283	11.63	156
22	30.50	566	8.30	126	23.88	351	15.75	250	12.50	378	9.38	269
24	8.25	571	1.63	41	9	572	3.38	500	1.75	310	2.88	210
27	9.17	400	0.67	9	5.17	390	1.33	300	0.67	200	1.33	52
29	7.88	380	0.50	14	3.38	140	0.25	44	0.38	190	1.50	21
0107	9.38	470	0.88	18	4	166	1.25	60	0.25	130	1.75	31
04	5.83	340	0.50	28	2	200	0.67	83	0.33	170	1	100
06	—	—	—	—	—	—	—	—	—	—	—	—
08	5.33	140	0	0	1.17	15	1	84	0	32	0.83	66
11	2.50	120	—	—	0.33	18	0	8	0.17	50	0.83	150
13	4	200	—	—	0	16	0.33	8	0	32	0.33	1
15	16.33	170	—	—	0.67	13	0	0	8	0	0	0
18	7.50	140	—	—	0	0	—	—	15	—	—	—
20	9.33	154	—	—	—	—	—	—	0	—	—	—
22	8.67	170	—	—	—	—	—	—	—	—	—	—
25	6.80	190	—	—	—	—	—	—	—	—	—	—
27	6.83	142	—	—	—	—	—	—	—	—	—	—

Willow:												
	Colony 5-D-5		Colony 5-D-9		Colony 5-D-13		Colony 5-D-14		Colony 5-D-347		Colony 5-D-25	
Date	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids
0806	6.67	65	7.67	125	7.67	48						
10	20	155	25.50	318	11.83	95	34.33	295	48.60	584	5.60	52
13	12.88	269	30.13	645	10.13	105	31.75	352	41.50	523	5	59
15	14.89	162	27.75	833	8	113	30.50	324	43.44	816	4.89	53
17	10.83	301	26.33	1074	9.17	125	19.17	410	32	1107	3.33	50
20	12.38	400	28.50	1110	9.63	127	18	289	35.14	816	3.63	108
22	8.50	412	16.38	1512	4.88	161	12	406	20.63	801	3	110
24	4.38	522	8.25	1010	2.38	172	5.75	415	12.25	525	1.88	200
27	2.50	606	4.50	1583	1.17	115	2	449	5.17	480	0.50	170
29	1.75	413	3.38	1323	0.25	92	1.63	612	3.25	485	0.25	128
0107	2.25	355	5.25	978	0.50	60	2.38	608	3	648	0	50
04	1	331	0.71	936	0.17	50	0.33	461	1.33	392	0.33	80
06	—	—	—	—	—	—	—	—	—	—	—	—
08	0.33	120	0.50	226	0.80	100	0.50	88	0.33	122	0	0
11	0.17	32	0.17	184	0.50	100	0	6	0	44	—	—
13	0	0	0.33	118	0	128	0	30	0.33	18	—	—
15	—	—	1.40	122	0.83	145	0.17	51	0	16	—	—
18	—	—	0.67	42	0.17	100	0	94	0.17	31	—	—
20	—	—	0.50	21	1.17	120	0.67	169	0	20	—	—
22	—	—	—	23	1.33	213	0.50	184	0	10	—	—
24	—	—	0	0	0.50	210	1	220	0	0	—	—
27	—	—	—	—	1.17	62	0.50	110	—	—	—	—

Balsam Poplar:												
	Colony 5-E-2		Colony 5-E-5		Colony 9-D-5		Colony 9-C-14		Colony 9-C-18		Colony 5-D-18	
Date	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids	Mean No. of Ants	No. of Aphids
0806			23	53	12.67	13	12.67	36	7.67	20	28.67	45
10	23.50	20	22.33	30	10.17	11	16.50	28	9	8	35.60	44
13	19.63	37	22.88	60	8.38	8	19.50	54	4.50	15	30.50	70
15	17.25	25	25.13	89	8.75	9	20.13	89	4.75	9	29.63	93
17	19.33	61	27.83	140	8.50	10	16.33	143	3	9	27.50	95
20	16.38	81	23.29	160	6.13	16	11.88	176	4	12	23.86	125
22	8.88	80	16.38	150	3.25	10	6.50	108	2.50	13	20.88	240
24	6	54	6.50	142	2	11	4.25	123	2.38	16	11.75	200
27	3.17	30	2.33	50	0.33	4	3.33	95	2.50	25	6.83	228
29	1.25	31	2	33	0	0	2.88	65	2	30	10.63	228
0107	1.88	18	2.14	27	—	—	2.86	76	2.25	42	8.50	138
04	0.17	10	1.67	12	—	—	1.83	62	0.50	44	8.67	234
06	—	—	—	—	—	—	—	—	—	—	—	—
08	0	0	0	0	—	—	2.50	100	0	0	8	175
11	—	—	—	—	—	—	1.67	150	—	—	8.20	173
13	—	—	—	—	—	—	0.67	103	—	—	7.67	155
15	—	—	—	—	—	—	3.33	109	—	—	11.83	117
18	—	—	—	—	—	—	2.17	104	—	—	6.67	135
20	—	—	—	—	—	—	2.33	19	—	—	6.17	72**
22	—	—	—	—	—	—	0	0	—	—	—	—

*No Data.

**Monitoring was discontinued due to interference from another aphid species.

Figure 10. Daily Mean Number of Ants and Number of
Aphids in Birch Aphid Colonies (a) 3-E-2 and
3-E-3B from 8 June, 1977 at Birds Hill Park.

Ants -----
Aphids ————

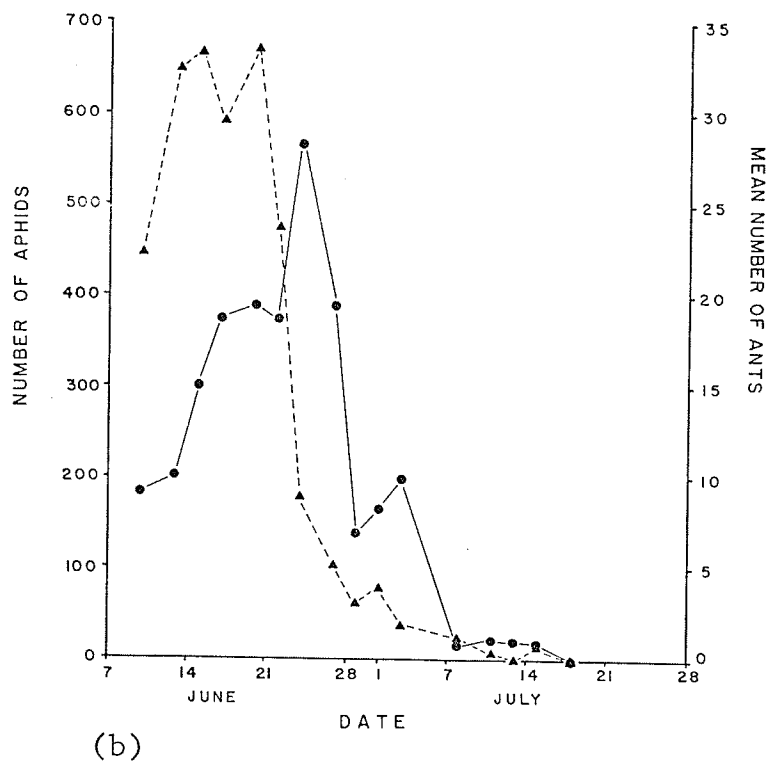
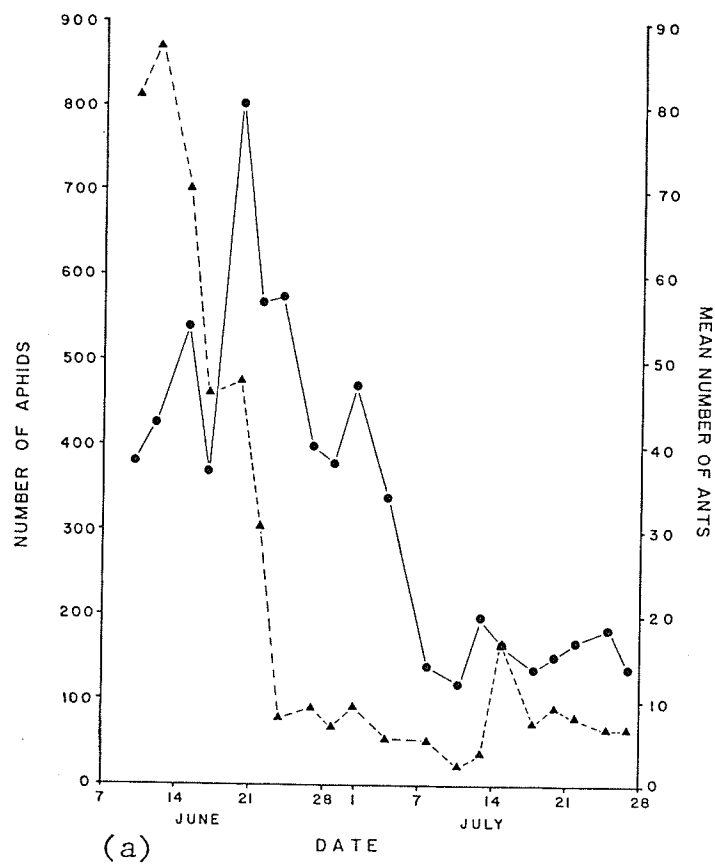


Figure 11. Daily Mean Number of Ants and Number of
Aphids in Willow Aphid Colonies (a) 5-D-9 and
(b) 5-D-347 from 8 June, 1977 at Birds Hill Park.

Ants - - - - -
Aphids ————

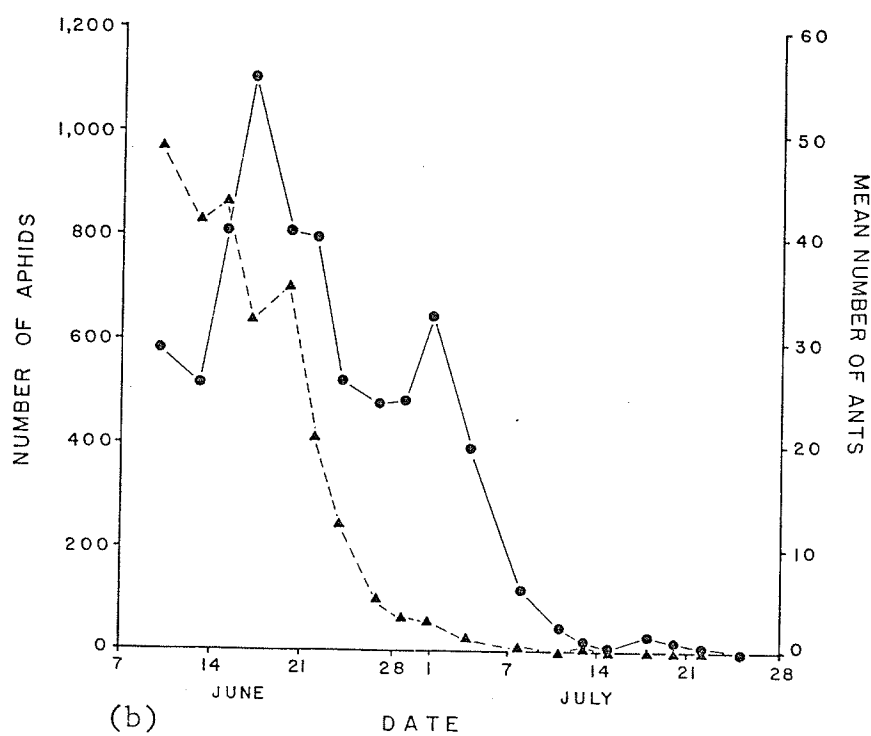
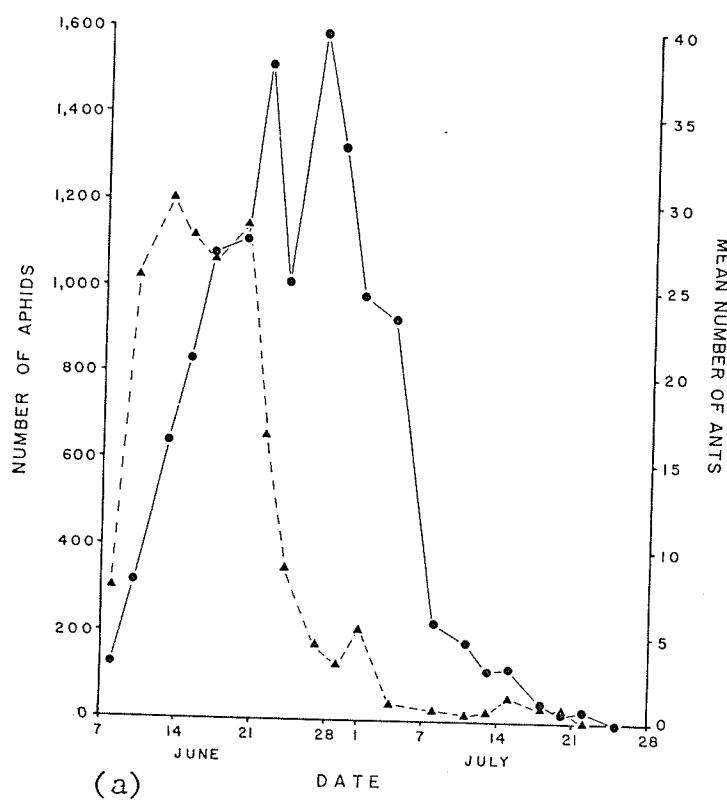
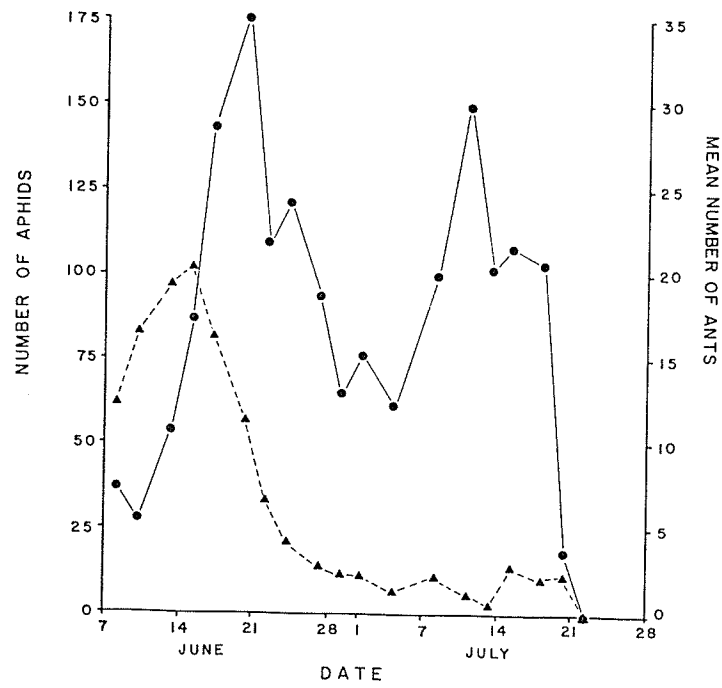
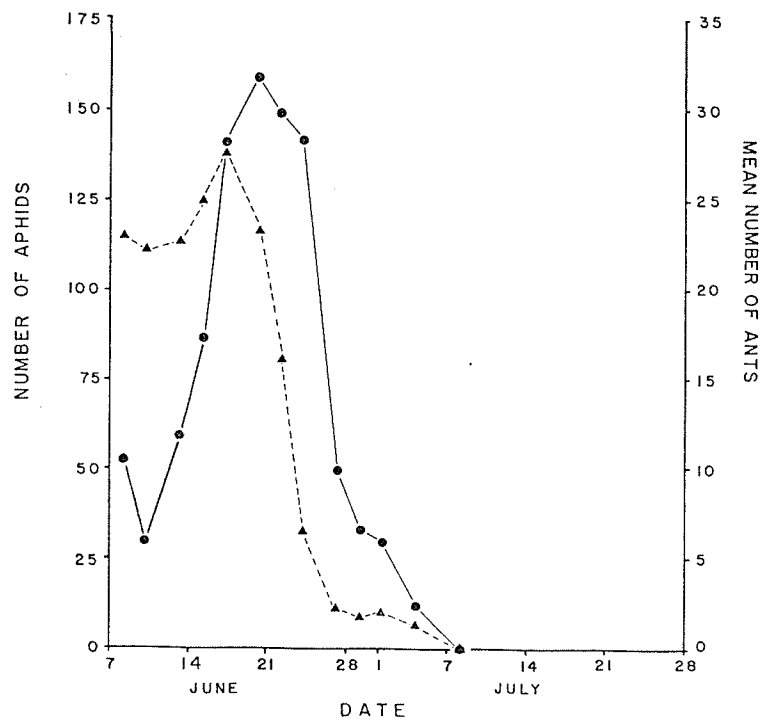


Figure 12. Daily Mean Number of Ants and Number of Aphids in Balsam Poplar Aphid Colonies (a) 9-C-14 and (b) 5-E-5 from 8 June, 1977 at Birds Hill Park.

Ants -----
Aphids —————



(a)



(b)

the dependent variables 'number of ants present at the aphid colony', 'stem activity up' and 'stem activity down', and the variables' significance as determined by stepwise multiple linear regression analyses are illustrated in Tables 6, 7 and 8 respectively. The amount of variation about each dependent variable which has been accounted for (R^2) by inclusion of the significant variables in each of the regression analyses is also shown in these tables.

Equations 1 and 2 were used to calculate the adjusted group means (Tables 9 and 10) of the three interdependent variables. This was done in order to minimize the amount of variance between each mean, so that comparisons could be made between the aphid species and between time periods. However, a statistical comparison between the adjusted group means was not possible since the Gaussian matrix for error estimates was not obtained and therefore error estimates could not be calculated. The data in Table 10 are therefore included only to determine whether there are any apparent trends and are not meant to represent a complete statistical comparison.

Bivariate Correlations Between Environmental Parameters

Referring to bivariate correlation matrices shown in Appendices F and G, we see that in most cases ambient temperature and relative humidity have high negative values, the relative humidity having decreased as the ambient temperature increased. Ambient temperature and day of season were

TABLE 6.

Significant Regression Coefficients from Stepwise Multiple Linear Regression Analyses of Number of Ants Present at Aphid Colony on Day of Season, Per Cent Relative Humidity, Barometric Pressure, Precipitation, Sky, Stem Activity Up, Stem Activity Down, Ambient Temperature, and Number of Aphids in Aphid Colony.

Aphid Species Time Period (N)	Constant	Day (log)	% Relative Humidity (arcsin \bar{p})	Barometric Pressure (mmHg)	Rain (Coded 0 to 3)	Sky (Coded 1 to 5)	Stem Activity Up (log ₁₀ (N+1))	Stem Activity Down (log ₁₀ (N+1))	Temperature (°C)	No. of Aphids (log ₁₀ (N+1))	Coeff. of Multiple Determin. R ²
A 2 90	0.829	-0.776 (3)	—	—	—	—	—	0.639 (3)	—	0.529 (3)	0.659
3 92	-17.4	-0.604 (3)	—	0.0233 (2)	0.409 (1)	—	—	0.619 (3)	—	0.608 (3)	0.739
4 93	-29.7	-0.495 (2)	0.0135 (3)	0.0376 (3)	—	—	—	0.773 (3)	0.0390 (1)	0.509 (3)	0.763
5 105	-11.6	-0.775 (3)	—	0.0165 (1)	—	—	—	0.881 (3)	—	0.415 (3)	0.733
6 97	-36.9	-0.785 (3)	0.00939 (2)	0.0471 (3)	—	—	—	0.581 (3)	0.0516 (3)	0.618 (3)	0.828
B 2 99	2.03	-2.26 (3)	—	—	-0.606 (3)	—	—	0.510 (3)	0.0339 (1)	0.390 (3)	0.837
3 101	0.511	-1.10 (3)	—	—	0.500 (2)	—	—	0.582 (3)	—	0.594 (3)	0.762
4 99	-10.8	-0.978 (3)	—	0.0151 (1)	—	—	—	0.456 (3)	-0.0227 (1)	0.705 (3)	0.778
5 111	0.839	-1.30 (3)	—	—	—	—	—	0.546 (3)	—	0.532 (3)	0.724
6 104	1.85	-1.57 (3)	-0.00905 (2)	—	—	0.0640 (1)	—	0.612 (3)	—	0.413 (3)	0.786
C 2 82	1.96	-1.42 (3)	—	—	—	-0.0450 (1)	—	0.250 (2)	—	0.444 (3)	0.621
3 84	-16.1	-0.798 (3)	—	0.0222 (1)	—	—	—	0.220 (1)	—	0.521 (3)	0.530
4 87	-23.9	-0.541 (3)	—	0.0327 (3)	0.156 (2)	—	—	0.427 (3)	—	0.333 (3)	0.631
5 94	-20.8	-0.687 (3)	—	0.0283 (3)	—	0.0496 (1)	—	0.340 (3)	—	0.472 (3)	0.618
6 88	1.30	-1.04 (3)	—	—	—	—	0.322 (1)	0.248 (1)	—	0.483 (3)	0.616
A 7 48	-21.5	-0.923 (3)	0.00698 (1)	0.0286 (1)	—	—	—	0.519 (3)	—	0.656 (3)	0.836
8 48	-15.9	-1.50 (3)	—	0.0232 (1)	—	—	—	0.852 (3)	—	0.440 (2)	0.793
B 7 47	-48.2	-1.85 (3)	—	0.0615 (3)	—	0.0760 (1)	—	—	0.0774 (3)	1.02 (3)	0.826
8 48	-54.4	-1.46 (3)	0.00565 (1)	0.0695 (3)	—	—	—	—	0.0840 (3)	0.974 (3)	0.868
C 7 48	-19.6	-1.23 (3)	—	0.0274 (2)	—	—	—	—	—	0.603 (3)	0.767
8 48	-23.6	-1.26 (3)	0.00631 (1)	0.0311 (2)	—	—	—	—	0.0459 (2)	0.684 (3)	0.837
A 1 94	-47.2	-1.04 (3)	—	0.0606 (3)	—	—	—	—	0.0956 (2)	0.743 (3)	0.494
B 1 105	-32.1	-2.60 (3)	—	0.0433 (3)	—	—	—	—	0.0921 (3)	0.578 (3)	0.776
C 1 81	-18.4	-1.04 (3)	0.00772 (1)	0.0241 (1)	—	—	—	—	0.0340 (1)	0.555 (3)	0.604

Aphid Species A = Symydobius americanus; B = Chaitophorus saliciniger; C = Pterocomma smithiae.

— = $p > 0.10$; (1) = $0.10 \geq p > 0.01$; (2) = $0.01 \geq p > 0.001$; (3) = $0.001 \geq p$; Blank = No data, thus not tested.

TABLE 7. Significant Regression Coefficients from Stepwise Multiple Linear Regression Analyses of Stem Activity Up on Day of Season, Per Cent Relative Humidity, Barometric Pressure, Precipitation, Sky, Number of Ants Present in Aphid Colony, Stem Activity Down, Ambient Temperature, and Number of Aphids in Aphid Colony.

Aphid Species	Time Period	(N)	Constant	Day (log)	% Relative Humidity (arcsin \bar{p})	Barometric Pressure (mmHg)	Rain (Coded 0 to 3)	Sky (Coded 1 to 5)	No. of Ants (log ₁₀ (N+1))	Stem Activity Down (log ₁₀ (N+1))	Temperature (°C)	No. of Aphids (log ₁₀ (N+1))	Coeff. of Multiple Determin. R ²
A	2 90	-	0.559	-	-	-	-	-	-	0.662 (3)	-	0.200 (1)	0.514
	3 92	-	0.162	-	-	-	-	-	0.119 (1)	0.611 (3)	-	-	0.586
	4 93	-	0.599	-	-	-	-	-	-	0.628 (3)	-	0.240 (2)	0.589
	5 105	-	12.3	-	-	0.0157 (2)	-	-	-	0.719 (3)	-	0.150 (1)	0.712
	6 97	-	0.245	-	-	-	-	-	0.183 (1)	0.606 (3)	-	-	0.567
B	2 99	-	0.765	-	-	-	-	-	0.142 (1)	0.489 (3)	0.0209 (1)	-	0.460
	3 101	-	0.307	-0.291 (2)	-	-	-	0.0350 (1)	-	0.555 (3)	-	0.191 (2)	0.560
	4 99	-	0.636	-0.189 (1)	-	-	-	-	-	0.433 (3)	-	0.275 (3)	0.462
	5 111	-	0.0495	-0.291 (2)	-	-	-	-	-	0.663 (3)	-	0.103 (1)	0.643
	6 104	-	0.287	-0.196 (1)	-	-	-	-	-	0.635 (3)	-	0.180 (1)	0.616
C	2 82	-	11.9	-	-	0.0155 (1)	-	-	-	0.550 (3)	-	-	0.393
	3 84	-	0.656	-	-	-	-	-	-	0.527 (3)	-	0.252 (2)	0.390
	4 87	-	0.209	-0.231 (1)	-	-	-	-	-	0.584 (3)	-	0.197 (1)	0.487
	5 94	-	0.0167	-	-	-	-	-	-	0.593 (3)	-	-	0.470
	6 88	-	0.385	-	-	-	-	-	0.280 (3)	0.305 (3)	-	-	0.428
A	7 48	-	0.108	-	-	-	-	-	-	0.690 (3)	-	-	0.685
	8 48	-	0.940	-	-	-	-	-	-	0.649 (3)	-	0.369 (2)	0.576
B	7 47	-	0.569	-0.406 (1)	-	-	-	-	-	0.384 (3)	-	0.389 (2)	0.551
	8 48	-	1.16	-	-	-	-	-	0.251 (1)	0.423 (2)	0.0462 (1)	-	0.522
C	7 48	-	0.458	-	-	-	-	-0.113 (3)	0.532 (3)	-	-	-	0.390
	8 48	-	0.549	-	-	-	-0.821 (1)	-	0.301 (2)	0.471 (3)	-	-	0.472

Aphid Species A = Symydobius americanus; B = Chaitophorus saliciniger; C = Pterocomma smithiae.

- = $p > 0.10$; (1) = $0.10 \geq p > 0.01$; (2) = $0.01 \geq p > 0.001$; (3) = $0.001 \geq p$; Blank = No data, thus not tested.

TABLE 8.

Significant Regression Coefficients from Stepwise Multiple Linear Regression Analyses of Stem Activity, Down on Day of Season, Per Cent Relative Humidity, Barometric Pressure, Precipitation, Sky, Number of Ants Present in Aphid Colony, Stem Activity Up, Ambient Temperature, and Number of Aphids in Aphid Colony.

Aphid Species Time Period	(N)	Constant	Day (log)	% Relative Humidity (arcsin \sqrt{p})	Barometric Pressure (mmHg)	Rain (Coded 0 to 3)	Sky (Coded 1 to 5)	No. of Ants (log ₁₀ (N+1))	Stem Activity Up (log ₁₀ (N+1))	Temperature (°C)	No. of Aphids (log ₁₀ (N+1))	Coeff. of Multiple Determ'n. R ²
A 2 90		-4.94	—	—	0.00503 (1)	—	—	0.284 (3)	0.405 (3)	0.0373 (1)	—	0.626
3 92		-0.122	—	—	—	—	-0.0628 (2)	0.217 (3)	0.559 (3)	—	—	0.664
4 93		-0.0714	—	-0.00677 (3)	—	—	—	0.326 (3)	0.391 (3)	—	—	0.706
5 105		-0.307	0.164 (1)	-0.00343 (1)	—	—	—	0.280 (3)	0.508 (3)	—	—	0.775
6 97		-0.196	—	-0.00308 (1)	—	—	—	0.333 (3)	0.357 (3)	—	—	0.690
B 2 99		-0.473	—	—	—	—	—	0.236 (3)	0.323 (3)	—	—	0.592
3 101		-0.813	—	—	—	—	—	0.163 (3)	0.433 (3)	0.0200 (2)	—	0.528
4 99		0.287	—	-0.00668 (3)	—	—	—	0.290 (3)	0.431 (3)	—	-0.182 (1)	0.508
5 111		-0.576	—	—	—	—	—	0.130 (3)	0.557 (3)	—	—	0.635
6 104		-0.526	—	—	—	—	—	0.206 (3)	0.507 (3)	0.00913 (1)	—	0.657
C 2 82		-0.573	—	—	—	—	—	—	0.596 (3)	—	0.206 (1)	0.399
3 84		-0.153	—	—	—	—	—	—	0.579 (3)	—	—	0.330
4 87		-1.10	—	—	—	—	—	0.309 (3)	0.521 (3)	0.0321 (3)	—	0.569
5 94		-0.164	—	-0.00443 (2)	—	—	—	0.289 (3)	0.572 (3)	—	—	0.566
6 88		10.2	—	—	-0.0149 (1)	—	—	0.303 (3)	0.423 (3)	0.0268 (2)	—	0.462
A 7 48		-0.775	—	—	—	—	—	0.188 (1)	0.616 (3)	—	0.213 (1)	0.764
8 48		-1.09	0.567 (2)	—	—	—	—	0.360 (3)	0.349 (3)	—	—	0.668
B 7 47		-1.23	—	—	—	—	—	0.183 (1)	0.547 (3)	0.0420 (1)	—	0.524
8 48		-0.444	—	—	—	—	—	0.209 (1)	0.473 (3)	—	—	0.475
C 7 48		-0.0793	—	-0.0110 (3)	—	—	—	0.364 (2)	—	—	—	0.332
8 48		-0.224	—	—	—	0.724 (1)	—	—	0.619 (3)	—	—	0.368

Aphid Species A = Symydobius americanus; B = Chaitophorus saliciniger; C = Pterocomma smithiae.

— = $p > 0.10$; (1) = $0.10 \geq p > 0.01$; (2) = $0.01 \geq p > 0.001$; (3) = $0.001 \geq p$; Blank = No data, thus not tested.

TABLE 9. Gross Mean of Each Variable (Derived from Time Periods 2 to 6 Only; Data Transformed as in Table 6).

Day (log)	Tempera- ture (°C)	(%) Relative Humidity ($\arcsin \sqrt{p}$)	Barometric Pressure (mmHg)	Rain	Sky
1.27	21.98	52.05	757.37	0.16	2.77
No. of Ants at Colony ($\log_{10}(N+.1)$)	No. of Aphids ($\log_{10}(N+.1)$)	Stem Activity Up ($\log_{10}(N+.1)$)	Stem Activity Down ($\log_{10}(N+.1)$)		
0.41	2.01	-0.41	-0.44		

TABLE 10. Adjusted Group Means for Number of Ants Present at Aphid Colony, Stem Activity Up, and Stem Activity Down (All Data $\log_{10}(N+.1)$).

TIME PERIOD	APHID SPECIES A*		APHID SPECIES B		APHID SPECIES C	
	No. of Ants Present (Log)	(Antilog)**	No. of Ants Present (Log)	(Antilog)	No. of Ants Present (Log)	(Antilog)
2	0.61477	4.02	0.36554	2.22	0.81735	6.47
3	0.45497	2.75	0.13174	1.25	0.72005	5.15
4	0.41057	2.47	0.09506	1.14	1.02488	10.49
5	0.33500	2.06	0.01665	0.94	0.99704	9.83
6	0.40133	2.42	0.12647	1.23	0.92596	8.33
7	0.39018	2.36	0.04621	1.01	0.82549	6.59
8	0.27932	1.80	0.46883	2.84	1.02776	10.56
Stem Activity Up			Stem Activity Up		Stem Activity Up	
2	-0.44909	0.26	-0.46288	0.24	-0.38377	0.31
3	-0.38201	0.31	-0.43165	0.27	-0.38148	0.32
4	-0.39425	0.30	-0.51287	0.21	-0.36371	0.33
5	-0.41156	0.29	-0.40523	0.29	-0.24731	0.47
6	-0.43700	0.27	-0.45401	0.25	-0.40513	0.29
7	-0.19513	0.54	-0.47302	0.24	-0.55371	0.18
8	-0.48496	0.23	-0.22723	0.49	-0.76828	0.07
Stem Activity Down			Stem Activity Down		Stem Activity Down	
2	-0.35554	0.34	-0.50867	0.21	-0.40216	0.30
3	-0.43632	0.27	-0.48226	0.23	-0.38911	0.31
4	-0.45007	0.25	-0.48260	0.23	-0.47771	0.23
5	-0.37135	0.33	-0.44998	0.25	-0.51017	0.21
6	-0.36651	0.33	-0.44845	0.26	-0.53193	0.19
7	-0.52248	0.20	-0.49662	0.22	-0.50369	0.21
8	-0.36610	0.33	-0.55190	0.18	-0.35712	0.34

* A = *S. americanus*; B = *C. salicinigier*; C = *P. smithiae*.

** (N - .1)

positively correlated, the temperature having increased as the season progressed. Thus the negative correlation between relative humidity and day of season was actually due to the ambient temperature.

Bivariate correlations of temperature and barometric pressure indicate, especially during time periods 1 and 8 when the greatest differences occurred, that as one variable increased the other decreased. This appears to be true for correlations between relative humidity and barometric pressure, but significance is almost restricted to time periods 1 and 8, and the correlation values are much lower (Appendices F and G).

Bivariate negative correlations occurred between ambient temperature, rain, sky and day of season, indicating that as the season progressed and the temperature increased, the sky was less cloudy and less rain fell. The bivariate positive correlations between relative humidity, rain and sky indicate that as relative humidity increased, so did cloud cover and rainfall.

Most of these correlations were expected natural phenomena but some variables, such as barometric pressure, were complexly interrelated with other variables.

Factors Influencing the Number of Aphids in the Colony

Day of Season. As can be seen from Appendices F and G, birch and willow aphid populations have a high negative correlation with the day of season. However, as the season

progressed, the balsam poplar aphid colonies increased somewhat in numbers, as indicated by the significant positive correlations (Appendices F and G).

Ambient Temperature. There appears to have been no correlation between temperature and balsam poplar aphid populations (Appendices F and G). However, there may have been an effect on the populations of the other two aphid species; the birch aphid populations have significant positive correlations with temperature in several instances, and there are a couple of significant negative correlations between willow aphid populations and temperature.

Number of Ants Present at the Aphid Colony. The number of ants present at the aphid colony and the number of aphids in the colony have, especially for birch and willow aphid populations, very high positive correlations. The values of the positive correlations between balsam poplar aphid numbers and numbers of ants present are much less than those for birch and willow, and the value even becomes non-significant during time period 4 (Appendix G).

It can be seen from Table 5 and Figs. 10, 11 and 12 that at the commencement of monitoring activities the number of aphids per colony was increasing. The birch, willow and balsam poplar aphid populations monitored from 8 June peaked between 20-24 June, 24-29 June and 20-22 June respectively, thereafter decreasing. Balsam poplar aphid populations appeared to be more stable, their numbers fluctuating less

than those of birch and willow aphid populations. Balsam poplar aphid colonies were even observed to increase slightly in number of individuals and colonies as the season progressed, whereas the birch and willow aphid populations steadily declined. It is also apparent from an examination of these data that the number of attendant ants at each aphid colony began to decrease after 20 June, and this decrease became pronounced by 24 June; a slight increase in ants present at the aphid colonies again occurred on 15 July. The fact that the numbers of ants decreased at all aphid colonies at about the same time that the birch and willow aphids decreased caused the very significant correlations shown in Appendices F and G. But, because some of the balsam poplar aphid colonies did not decline when the numbers of ants present did, the correlations occurring between the two variables were lower.

In each of Figs. 10, 11 and 12 it can be seen that the aphid populations appear to have declined shortly after ant attendance diminished (Table 5). The question arises as to whether the number of aphids declined as a result of the decrease in ant attendance, or whether they were already in the process of declining. However, it was not possible to determine if the declination of the aphid populations was precipitated by the reduction in ant attendance.

Factors Influencing the Number of Ants Present at the Aphid Colony, Stem Activity Up and Stem Activity Down

Day of Season. The very significant negative correla-

tions between this variable and number of ants present at all aphid colonies are apparent from Appendices F and G. There is a particularly high negative correlation during time period 1 for willow aphid colonies, with the number of ants present during time period 1 having decreased as the season progressed. The multiple linear regression analyses (Table 6) also show that the day of the season was extremely significant ($0.001 \geq p$) in contributing to the number of ants present at all the aphid colonies.

There is a high negative correlation between ant stem activity up and down and day of season for willow aphid colonies during each time period (Appendix G), with stem activity decreasing as the days passed. The bivariate correlations for birch and balsam poplar aphid colonies are not as consistent, with birch stem activity up and down showing correlation with day only during time periods 2, 6 and 7. Stem activity up to balsam poplar aphid colonies correlates with day of season only during time periods 5, 6 and 8 (Appendix G). Only six of the 21 regressions are significant ($0.10 \geq p > 0.01$) or highly significant ($0.01 \geq p > 0.001$) in the analyses of stem activity up (Table 7); day of season actually contributed nothing to the relationship involving numbers of ants going up to the birch aphid colonies. Five of the values (Table 7) are for the willow aphid species and, as the correlations (Appendix G) similarly inferred, the slopes of the regressions are negative, indicating that stem activity up to the willow

aphid colonies decreased during time periods 3 to 7 as the season progressed. Only two cases in 21 of stem activity down regressed on day of season (Table 8) respectively show a significant and highly significant contribution to the relationship; these were possibly due to random chance indicating that, contrary to inferences from the bivariate correlations in Appendix G, day of season made no significant contribution to the number of ants leaving the aphid colonies.

A further question thus arises, as to whether ant attendance diminished due to a decline in the state or quality of the aphid populations and/or their produce, or because the demands of the ant colony were decreasing. The source of the change in attendance behavior may have originated with the occupants of the ant nest and its foraging community. The numerous reproductives waiting inside the nest until their nuptial flight took place (6 June, with sporadic appearances thereafter until 27 June) probably consumed a great amount of the honeydew brought to the nest by the honeydew foragers. It is possible that the demand for honeydew lasted until about 26 June, slowly decreasing as the male ant population decreased and the queens underwent transition to a proteinaceous diet in preparation for oöcyte development.

Ambient Temperature. There are no significant correlations between number of ants present at birch aphid colonies and ambient temperature (Appendices F and G). Significant negative correlations are apparent during time periods 1 to 6

and 2 to 5 at willow and balsam poplar aphid colonies respectively, with the highest correlation values occurring in both cases during time period 4. The negative bivariate correlations indicate that the number of ants present at willow and balsam poplar aphid colonies decreased as the temperature increased. However, the stepwise multiple linear regression analyses (Table 6) indicate that ambient temperature did, in fact, contribute significantly to the relationship for the birch aphid, and the influence of this variable on the balsam poplar aphid was not as great as the correlations inferred. In 10 out of 24 regressions temperature was significant (at varying levels) in contributing to the number of ants present at the aphid colonies (Table 6). Contrary to the relationship implied by the correlations (Appendices F and G), and with the exception of the willow aphid datum at time period 4 (Table 6), the slopes of the regressions are all positive. In other words, the number of ants present at the aphid colonies increased with increasing ambient temperature.

The contribution of temperature to the number of ants present at all aphid colonies was largely restricted in significance to time periods 1, 7 and 8 (Table 6). It is during these morning and evening time periods that the greatest amount of variation in temperature is expected to occur, since daytime temperatures fluctuate much less. Therefore, the variable would be expected to exhibit some significant influence during the mentioned time periods.

During time period 4, a significant contribution was made by temperature to the numbers of ants present at birch aphid colonies (Table 6), and the positive slope indicates that the number of ants at the aphid colonies increased with increasing temperature. This significance is also apparent at willow aphid colonies during time period 4; however, the slope of this regression is negative, thereby indicating that the increasing temperature contributed significantly to a decrease in the numbers of ants present at willow aphid colonies during time period 4. However, both relationships are relatively poorly defined, in contrast with those of time periods 1, 6, 7 and 8 where significance levels are high or extreme, and all slopes are positive. Temperature did not significantly contribute to the numbers of ants present at balsam poplar aphid colonies during any but time periods 1 and 8.

Bivariate correlations of ambient temperature and stem activity up are positive, but not very significant, for birch aphid data during several time periods, and negative in three out of four almost non-significant correlations for willow aphid data. Temperature apparently contributed nothing to the relationship involving ant stem activity up to balsam poplar aphid colonies, since the one not very significant correlation may have been due to chance. Referring to Table 7 it can be seen that in fact no significant contribution to ant stem activity up was made by ambient temperature; the two cases of

significance were likely due to random chance. The bivariate correlations of ambient temperature with stem activity down are all positive but, similar to the results generated for stem activity up, the correlation levels are very low (Appendix G). In this case, there was no contribution made by temperature to stem activity down from willow aphid colonies. Again, the regression analyses clarifies the contribution made by the various variables to the relationship. We see from Table 8 that temperature contributed at varying levels of significance to the numbers of ants leaving the aphid colonies in six out of 21 cases. The slopes of the regressions are all positive, indicating that the stem activity down increased as the temperature increased.

Relative Humidity. There are no significant bivariate correlations between the number of ants present at the birch aphid colonies and per cent relative humidity; the variables are positively correlated, at low levels, for willow and balsam poplar aphid data in a number of cases (Appendices F and G). However, in seven out of 21 regressions of number of ants present on relative humidity (Table 6) the latter variable is shown (at varying significance levels) to have made a contribution to the overall relationship. Three of the significant cases occurred in the first and the last time periods, similarly to temperature; it is during these time periods that relative humidity is expected to change dramatically, compared with the moderate changes which occur during the day, and thus

become significant. With one exception, the slopes of the regressions of ants present on relative humidity (Table 6) are positive and, except for birch time period 4, very shallow. These indicate that the numbers of ants present at the aphid colonies increased as the relative humidity increased. Willow, time period 6, is the one exception with a negative, shallow slope, indicating that the numbers of ants present at willow aphid colonies decreased with increasing humidity during time period 6.

From Appendix G it is apparent that there are no significant correlations between ant stem activity up and relative humidity. The results shown in Table 7 also indicate that relative humidity made no contribution whatsoever to the relationship governing the number of ants going up to any of the aphid colonies. Relative humidity and stem activity down are negatively correlated during several mid-day and evening time periods for birch and balsam poplar aphid data; there are no significant correlations in the willow aphid data. From the regression analyses (Table 8) we can see that the six significant cases out of 21 indicate that relative humidity made a significant contribution to the number of ants leaving the aphid colonies. The negative slopes indicate that increasing relative humidity contributed to a decrease in the number of ants leaving an aphid colony. These data correspond with the results discussed above, in that the ants were remaining at the aphid colonies as the humidity increased.

Barometric Pressure. In almost all cases, barometric pressure and number of ants present at the aphid colony are positively correlated, and their levels of correlation increase during mid-day time periods (Appendices F and G). In 17 out of 21 cases (Table 6) barometric pressure contributed significantly, with 11 of the 17 cases being highly or extremely significant. The slopes of the regressions are positive, the numbers of ants present at the aphid colonies having increased with increasing barometric pressure.

There is only one case of significant correlation between barometric pressure and ant stem activity up, and one with ant stem activity down, at balsam poplar aphid colonies; however, birch and willow aphid data are positively correlated in a number of cases (Appendix G). The regression analyses of stem activity up (Table 7) and stem activity down (Table 8) on barometric pressure indicate that in each instance the two cases of significance were probably due to randomness.

The results of the regression analyses indicate that as barometric pressure increased the number of ants remaining with the aphid colonies also increased (Table 6), but that no significant influence was made by barometric pressure on ant stem activity (Tables 7 and 8). Intuitively one would expect that an increase in numbers present would be accompanied by a concomitant change in numbers going to and from the aphid colonies; the reason for these anomalous results is not known.

Rain. During time periods 3 and 4 there are significant

positive correlations between rain and number of ants present at the aphid colonies (Appendix G). Three of the four significant regression coefficients (Table 6) have positive slopes and occurred during time periods 3 and 4. In two of these cases, increased intensity of rainfall was highly significant in contributing to an increase in the number of ants present at willow and balsam poplar aphid colonies. However, during time period 2 the slope of the regression for willow aphid colonies is negative and is extremely significant (Table 6), indicating that fewer ants were present at the willow aphid colonies as rainfall intensity increased. It should be noted that during this time period, for this latter group, temperature also made a significant contribution to the relationship determining the number of ants present at willow aphid colonies. Therefore increased temperature and increased intensity of rainfall both contributed to a reduction in the number of ants present at willow aphid colonies.

Perhaps during a heavy downpour of rain at lower temperatures ants could not leave the aphid colonies as readily as they could during rainfall at higher temperatures. Field observations during rainfalls of various intensities at lower temperatures revealed that ants continued their activities, but that their movements were slower. Ants were also observed to sometimes lose their footing on wet branches of willow; and were sometimes knocked to the ground by very large rain drops. The thicker branch and leaf arrangement of dwarf birch appeared

to give better protection to the ants from heavier rainfall.

In several instances rain is positively correlated with stem activity up (Appendix G). The only significant correlations of rain with stem activity down occurred in time periods 3 and 4 for the balsam poplar aphid. The regression analyses indicate that rain had no significant effect on ant stem activity other than that which might be attributed to random chance (Tables 7 and 8).

Sky. There are no significant correlations between sky conditions and the numbers of ants present at birch or balsam poplar aphid colonies (Appendix G). However, there are significant positive correlations in four instances in the willow aphid data (Appendix G), the number of ants present at the willow aphid colonies having increased with increasing cloud cover. This variable is similarly significant in four out of 21 regressions (Table 6); three of the four slopes are positive, confirming that sky conditions contributed somewhat to the relationship determining the number of ants present at the aphid colonies.

It appears from Appendix G that increasing cloudiness is negatively correlated with ant stem activity to and from birch aphid colonies during time periods 2 to 5. The several other significant correlations in willow and balsam poplar aphid data indicate that, during the latter two time periods, stem activity either increased or decreased at dusk. However, as can be seen in Tables 7 and 8, sky conditions probably did

not contribute to the relationship determining ant stem activity. Since the method for assessing the variable 'sky' was crude, it is possible that the data do not disclose the real contribution which cloud cover or light intensity made to the relationships discussed herein.

Number of Aphids in the Aphid Colony. The significant correlations between aphid and ant numbers were discussed earlier, within the section entitled Factors Influencing the Number of Aphids in the Colony, under the subheading Number of Ants Present at the Aphid Colony.

The contribution made by the independent variable 'number of aphids' to the relationship governing the number of ants present at the aphid colonies is apparent in the regression analyses (Table 6). The slopes of the regressions are all positive and, with one exception, are all extremely significant. Variance due to the interaction of the independent variables was removed by the regression analysis so that the significance of aphid numbers to ants present at balsam poplar aphid colonies became apparent (Table 6). In all cases, at least until ant attendance diminished, it is obvious that the bigger the aphid colony the greater the number of ants which was present at the aphid colony.

There are high significant positive correlations between stem activity up and stem activity down with the number of aphids in birch and in willow aphid colonies (Appendix G). There are fewer correlations with balsam poplar aphid

numbers, as four cases are not significant and three of these are for stem activity down; the correlation values are also lower. There appears to be greater correlation between stem activity up and aphid numbers. In 11 out of 21 cases (Table 7) and three out of 21 cases (Table 8) the number of aphids in the colony made an important contribution (at varying levels of significance) to the relationship governing ant stem activity up and down respectively. The slopes of the regressions in Table 7 are positive, indicating that stem activity up increased with increasing aphid colony size. The three significant cases out of 21 (Table 8) may have been the result of randomness, with down activity not in actual fact having been influenced by the size of the aphid colony.

The ant colony's demand for honeydew was probably the predominant factor governing both the number of ants present and collecting honeydew at the aphid colony and the stem activity to and from the aphid colony. But, aside from this obvious fact, the yield of aphid honeydew being given up to the ants at any particular time and overall, and the duration of tending by an ant in order to fill its crop with honeydew (if this was in fact a prerequisite to the ant's departure from the aphid colony) will have been of primary importance. Differences in the size of the aphids and in their populations probably resulted in variation of honeydew volume excreted by the three aphid species. This might explain why the balsam poplar aphid data do not correlate as frequently or as highly

with other variables, as do the birch and willow aphid data. The balsam poplar aphids were fewer in number per colony (and therefore fewer droplets would have been excreted compared with birch and willow), although greater in size (therefore the droplet volume per aphid was probably greater than that for birch and willow aphids). Thus, fewer balsam poplar aphid honeydew droplets, each perhaps of greater volume than birch and willow, were probably excreted, and fewer ants would therefore have been required to be present at any given time to collect the honeydew droplets. More ants would have been required to collect the smaller, more numerous birch and willow aphid honeydew droplets, so that the aphids were never left unattended long enough to excrete the honeydew on their own.

Stem Activity To and From the Aphid Colony. Stem activity up and down have very significant positive correlations with the number of ants present at the aphid colonies (Appendix G). In most cases, the values are more positive for ant stem activity down, indicating that the number of ants present at the aphid colony had a greater correlation with the number of ants leaving the colony than with the number coming up to it. However, during time periods 6, 7 and 8 at balsam poplar aphid colonies, ant stem activity up to the aphid colonies becomes the more positive correlate. The regressions of number of ants present on stem activity up and stem activity down (Table 6) indicate that the number of ants going

up to the aphid colony contributed nothing to the relationship governing the number of ants present at the aphid colony. However, the number of ants leaving the aphid colony made a significant to extremely significant contribution in 17 out of 21 cases (Table 6), and the slopes of the regressions are all positive.

Stem activity up and stem activity down have extremely high positive correlations with each other, although the values are slightly less for the balsam poplar aphid data (Appendix G). In 20 out of 21 cases for up (Table 7) and for down (Table 8) stem activity an important contribution is made by one to the relationship of the other, and the slopes of the regressions are positive. The range in variation of the significant regression coefficients (Tables 7 and 8) is small (0.32 to 0.62 and 0.31 to 0.72 respectively), indicating that these two variables are greatly interrelated.

Number of Ants Present at the Aphid Colony. The correlations of this variable with stem activity up and down have been discussed.

In seven out of 21 cases the number of ants present at the aphid colony made a significant to extremely significant contribution to stem activity up (Table 7), the latter having increased as the number of ants present increased; however, the number of ants present is poorly related to stem activity up when compared to its relation with stem activity down (Table 8). It is apparent from Table 8 that the number of ants

present at the aphid colony and stem activity down were very important to each other; in 18 out of 21 cases a contribution of varying significance was made by the former variable. The positive slopes of the regressions indicate that as stem activity down increased the number of ants present at the aphid colony also increased. This may have been indicative of a recruitment feedback mechanism whereby ants had to leave the aphid colony in order to induce stem activity up to the aphid colony, thereby indirectly increasing the number of ants present at the aphid colony. If, as was inferred earlier herein, there were periodic fluctuations in the volume of honeydew produced by the aphids being tended, such a recruitment process would have resulted in the most efficient method of honeydew collection by foraging ants.

Coefficient of Multiple Determination (R^2)

A great deal of the variation about the dependent variable 'number of ants present at the aphid colony' is accounted for by the variables examined in the regression analyses (Table 6). However, less variability in the dependent variables 'stem activity up' and 'stem activity down' is explained on the basis of the same independent variables, as illustrated by the smaller R^2 values (Tables 7 and 8). Stem activity down is better explained by the variables included in the regression than is stem activity up, as shown by the somewhat greater R^2 values in Table 8.

Adjusted Group Means

As stated earlier, these were calculated in order to determine whether any ant-attendance trends were apparent between the three aphid species and between time periods. Except for time periods 1 and 8, the stem activity data show no consistent trends between time periods, and the range of the stem activity up and down between the three aphid species appears to be not too different. In some cases the data show an increase in ant numbers at the colonies during time periods 1 and 8.

If it was necessary to rank the three aphid species on the basis of these data, it would appear that the balsam poplar aphid was accorded greater attention by foraging ants than were the other two aphid species. This was reflected both in terms of the greater numbers of ants at the colonies and the slightly higher overall rates of stem activity. The birch aphid would rank second and the willow aphid third, indicating that the latter species was the least-preferred of the three aphid species by honeydew foraging ants.

Behavioral Modifications of Aphids

Absence of Predator-Avoidance Behavior

Aphids which were being tended by ants were never observed to cease feeding and move away from their colony when a predator or other disturbance happened in or near the aphid colony.

Modification of Aphid Excretory Behavior

No aphid excretory products were visible when ants were present tending the aphid colonies until 24 June. At 0650 hrs on 24 June at Colony 4-E-5 large drops of honeydew were observed hanging off the ani of 10 birch aphids (in a cluster of about 500 aphids). The aphid colony appeared to be comprised mostly of adults. At 0920 hrs minute glistening silvery droplets of honeydew were observed shooting through the air, away from the colony; the adult aphids were much more mobile than had ever previously been observed; many balsam poplar aphids at 9-C-14 were observed moving back and forth on the host plant during the day. By 1700 hrs the four ants which were present could not cope with the volume of honeydew being excreted by the aphids in Colony 4-E-5. At 0640 hrs on 27 June, large and small drops of honeydew were hanging from the aphids' ani at Colony 4-E-5; about 300 aphids had moved to the base of the branch upon which their colony was located and only one ant was present. On 29 June, at 0650 hrs about 44 aphids remained in the colony, loosely scattered over the branch, and aphids were observed to

be moving up from the base of the stem.

The birch aphid ejected more honeydew than did the other two species. The independent excretion of honeydew droplets by the aphids on 24 to 27 June was not again observed during the investigation. This change in excretory behavior coincided with the decrease in attendant ants (Table 5) on or before 24 June and appears to have been a direct result of the decreased number of ants present to collect the aphid honeydew.

Change in Aphid Colony Appearance

Speculation as to why F. oreas comptula workers ceased to tend their aphids, as fastidiously as they had, on or about 24 June might also include the fact that composition of the aphid colonies had changed somewhat. Increased numbers of adult aphids were present; by 27 June, especially in birch aphid colonies, the aphids were in looser aggregates as opposed to tight clusters which had been apparent previously. It is therefore possible that the ants had a preference for tightly-clustered colonies of nymphal aphids. However, the change in colony composition may have coincided with a change in plant sap constituents upon which the aphids were feeding; during spring and early summer there was probably a greater concentration of nitrogenous and proteinaceous elements in the new growth than later in the season in the mature plant tissues. Thus the ants may have been responding to a concomitant change in the aphid exudate.

Behavioral Modifications of Attendant Ants

Absence of Aggression Toward Aphids

F. oreas comptula workers were never observed to act aggressively toward the aphids which they were tending. On a couple of occasions, an aphid walking down the plant stem, away from the colony, was encountered by an ant coming up to the aphid colony. The ant became noticeably agitated, darting at the aphid and quickly palpating it with its antennae; sometimes the ant opened its mandibles as if threatening the aphid. The aphid merely stopped each time the ant rushed at it, waited until the ant backed off a bit, and then started down the plant stem again. An ant belonging to the fusca group was observed on 24 June at 1505 hrs to run down a birch stem with a feebly-struggling birch aphid in its mandibles; another birch aphid was hanging on, or was stuck to the captive. One F. oreas comptula worker was observed chasing after the fusca ant, and the latter subsequently jumped off the plant with the aphids.

Active Defense and Protection of Aphids by Ants

Predators and Parasites

Several observations were recorded of ants acting aggressively toward intruders near the aphid colonies which they were tending.

In one instance, on 17 June, a forest-tent caterpillar (Malacosoma disstria Hbn.) crawled onto a stem from a leaf

and attempted to go down past the aphid colony. F. oreas comptula workers, which were tending the aphids nearby, dashed at the caterpillar grabbing at its hairs with their mandibles; other worker ants, further down the stem, came up and participated. The ants backed the caterpillar onto a leaf stem and it subsequently fell to the ground.

On 15 June, small flies were occasionally observed to "dash" at individual willow aphids (presumably parasites attempting to oviposit in the aphids); this caused the ants present to open their mandibles and rear up on their meso- and metathoracic legs.

Sarcophagids, which were also present near the willow aphid colonies on 15 June, were chased by attendant ants; however the former did not appear to be very threatened by the ants' actions, as they did not move away very quickly or very far whenever chased by the ants.

The various predators observed near or in aphid colonies included syrphid larvae (observed from 31 May)(Fig. 13) and adult and larval coccinellids (observed from 8 July). Syrphid larvae were the predominant aphid predators at Birds Hill Park during 1977. Ants were never observed to act aggressively toward these predators, although at times the ants manifested a searching behavior when adult coccinellids were near the aphid colonies. One day during the study, a syrphid larvae was observed feeding on an aphid in a balsam poplar aphid colony; an ant approached the syrphid and palpated it, together

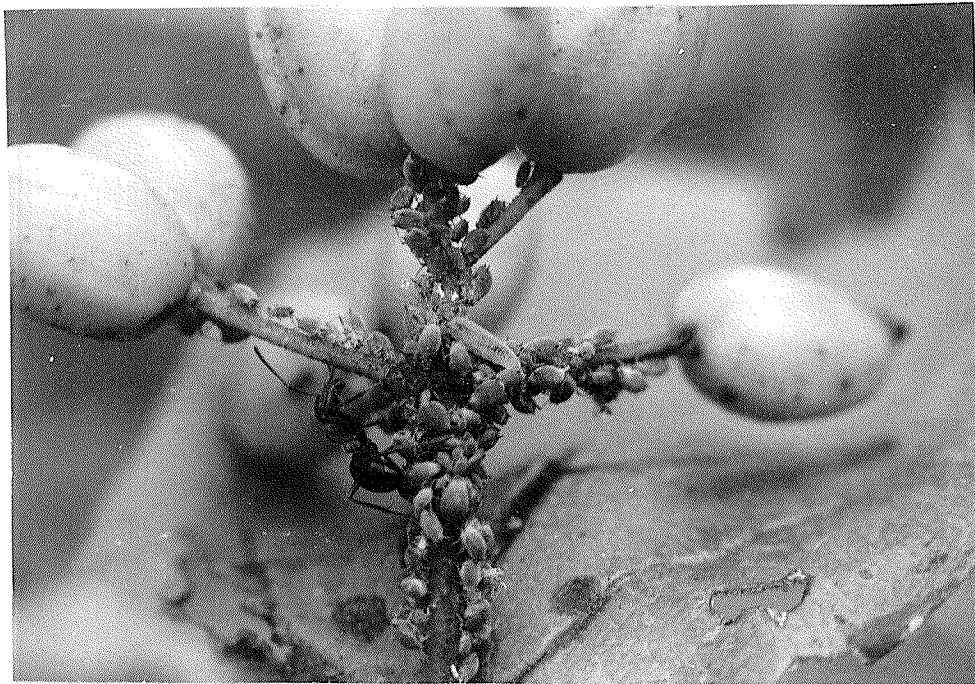


Figure 13. Syrphid Larva Preying on Aphis viburniphila
on Viburnum rafinesquianum while Formica oreas comptula
Worker Collects Honeydew from the Aphid Colony.

with the aphid which was being sucked dry. No distinction was observed to be made by the attendant ant between the aphids and the syrphid larva.

A very small winged insect was once observed to oviposit in an aphid while F. oreas comptula workers were not present. As one ant returned toward the willow aphid colony, the parasite walked around to the back of the stem thereby avoiding the ant as it passed; the ant passed by on the opposite side of the stem, unaware of the parasite's presence.

Hymenopteran parasites of aphids were present at the Birds Hill Park site, as evidenced by the presence of numerous willow aphid mummies.

Honeydew scavengers became noticeably abundant at the aphid colonies commencing 27 June. The accumulation of honeydew on the leaves from 27 June acted as an attractant to many other insects. These included hairstreak butterflies, wasps, sarcophagids, honey bees and calliphorids; F. oreas comptula aphid-attendants occasionally displayed aggression toward them. For instance, a wasp which attempted to obtain honeydew that had fallen near a birch aphid colony (or perhaps its real intention was to grab an aphid) was literally chased-pushed away from the aphids by an ant.

There appeared to be a gradation of predator/parasite susceptibility per aphid species. The willow aphid was greatly parasitized from the beginning of the season, despite the almost constant presence of F. oreas comptula workers; the

greatest total number of syrphid larvae recorded throughout the observation period were observed in these colonies. The second most preyed upon species was the balsam poplar aphid, but predation was minimal compared to that of the willow aphid. Only one aphid mummy was found in one balsam poplar aphid colony throughout the experimental observation period. The birch aphid was never observed to be parasitized. Almost no observations of birch aphid predation were made; on two occasions a larva and an adult coccinellid were respectively observed near birch aphid colonies.

From these observations it appeared that in spite of F. oreas comptula's naturally aggressive nature, the ants did not effectively prevent parasitism of the willow aphid (although the rate of parasitism was probably reduced); nor did they afford any protection from predacious syrphid larvae. It was interesting that the aphid species which often had the highest numbers of individuals per colony should have been the species most highly parasitized.

The fact that the ants did not react to the syrphid larvae implied that they were not able to detect the larvae, or perhaps that the larvae's presence was of no consequence to the ants. It was also possible that, because they moved about very little within the aphid colony, the larvae were not noticed by the ants. One would have expected some chemosensory perception of a syrphid larva by an ant which was palpating the larva with its antennae. Perhaps the syrphid larvae were able to somehow mask

themselves from such chemosensory perception by using the aphids they were preying on in some way to make themselves imperceptible to the ants.

Shelters

Fig. 14 illustrates the chamber-like openings which were observed at the base of every poplar tree in the experimental site. The chambers were not noticeable until dry grass surrounding the poplar trunk was pulled away. Ants were observed to descend the trunks of the aphid host plants and disappear below the dry grass. When the grass was cleared away ants could be seen walking on the walls of the chamber and sometimes they came up, travelling along the trunk, back to the aphid colonies.

These chambers may have represented feeding sites for root aphids, or structures similar to Dobrzanska's (1966) "stations". It is even possible that they led back to the ant nest via underground tunnels.

Honeydew Foraging Trails

Major foraging trails of F. oreas comptula were about 5 mm in depth by 10 mm in width, usually uncovered and had soil walls and floor (Fig. 15). Ants were sometimes observed crossing open areas where no trails were apparent. In one area of the experimental site, where the observers frequently walked and were probably interfering with the ant foraging



Figure 14. Root Chamber at the Base of a Poplar Sapling wherein Many Formica oreas comptula Workers Were Observed.



Figure 15. A Typical Trail Used by Formica oreas comptula to Reach Plants upon Which Aphid Colonies Were Located.

traffic, the ants travelled in tunnels covered over by dry compacted grass and debris below the observers. It appeared that honeydew foragers reached the aphid host plants by using the major trails which passed very near or led to the plants. However, most of the trails used by the ants were impossible to locate and follow, due to the thick grass and litter covering the area.

Interspecific Competition

Until 24 June no ant species other than F. oreas comptula were observed in the area. On 24 June and frequently thereafter, ants of the F. fusca group were observed on the birch and willow host plants of the experimental aphid species.

On 29 June four different ant species (Myrmica emeryana, Tapinoma sessile, F. oreas comptula and F. podzolica and/or F. hewitti) were recorded tending the same aphid colony at different times on dwarf birch.

The fusca ants characteristically had quick darting movements, and never stopped to tend the aphid colony in the same manner as F. oreas comptula workers. F. fusca scavengers actively avoided interaction with F. oreas comptula workers, falling or dropping from the host plant at the instant they made any sort of contact (e.g., antennal) with the latter species. The fusca group ants were observed to be still present when the study was terminated, roaming around, or tending colonies of aphids which had previously been fastidiously tended by F. oreas

comptula. F. oreas comptula workers were irregularly present throughout each day, in very low numbers, at every aphid colony within the experimental site when the study was terminated.

CONCLUSIONS

As a result of the study described herein, the following conclusions are made concerning ant-aphid associations in the Province of Manitoba.

1. There are a great many species of ants and aphids associating on the aphids' host plants in the Province of Manitoba. Many more associations no doubt remain to be discovered, especially those involving the interactions of root aphids with subterranean ant species and aboveground foragers.
2. Ants of the genus Formica are the dominant aphid attendants in Manitoba, followed by the genus Lasius.
3. Mixed species groups of ants occur on the same host plant whereupon aphid colonies are located. These are usually comprised of the aphid-attendant ant species and the scavenger species of ant.
4. Mixed ant species on the same aphid host plant do not indicate that the ant species are interacting.
5. Aphids of the genus Aphis are the species most frequently attended by ants in Manitoba, followed by species of the genera Cinara and Chaitophorus respectively.
6. Chaitophorus populicola has the greatest number of different attendant ant species in the Province of Manitoba.

7. There appears to be no discrimination on the part of ant species in their choice of aphid species to attend in order to collect honeydew.

8. Formica oreas comptula is one of the dominant ant species found in Birds Hill Park, Manitoba. This ant species was the dominant aphid-attendant within the area of the experimental site during 1977.

9. Tending of aphid colonies by F. oreas comptula workers starts early in the spring, as soon as there are aphids present, even prior to the plants leafing out.

10. F. oreas comptula workers remain with their aphid colonies day and night from early spring, but it is not known whether this continues during the latter part of the summer.

11. F. oreas comptula honeydew foragers continue their trips to and from the aphid colonies during the night as well as during the day; it is not known whether these foragers continue this activity during the latter part of summer.

12. The same F. oreas comptula workers will tend the same aphid colony over an extended portion of the season.

13. The F. oreas comptula workers which tend an aphid colony are not in constant attendance throughout the day, but leave the aphid colony periodically.

14. An age polyethism may exist in F. oreas comptula, in that workers may be required to spend a certain period of time in the nest following their eclosion, possibly as nurse ants, before they become honeydew foragers outside the nest.

15. Ants marked early in the spring while tending aphid colonies, which later in the spring are no longer present at the aphid colonies, may be older ants from the previous year. Their absence after a certain period of tending aphids in the spring may be due to their having died.

16. The declination of ant-attendance and of aphid populations very nearly coincide.

17. The nuptial flights of F. oreas comptula reproductives occur during the first week of June, with very sporadic appearances of reproductives for a couple of weeks thereafter.

18. Aphid honeydew is probably required by F. oreas comptula reproductives to provide stored metabolic energy for their nuptial flights and stored energy for the queens during establishment of new nests.

19. The reduction in numbers of F. oreas comptula workers at aphid colonies and in stem activity to and from the aphid colonies may be due to a decreased demand by the ant colony for aphid honeydew following the death of males and departure of many of the queens from the nest.

20. The number of F. oreas comptula workers at an aphid colony decreases with seasonal progression and increases with increasing number of aphids, barometric pressure, number of ants leaving the aphid colony, temperature and relative humidity respectively.

21. An increase in F. oreas comptula workers going to an aphid colony appears to be most significantly contributed to during spring and early summer by an increase in the number of ants leaving the aphid colony, by larger aphid colonies, and to a lesser extent by an increase in the number of ants present at the aphid colony.

22. During spring and early summer an increase in the number of F. oreas comptula workers going to an aphid colony, an increase in the number of ants present at a colony and increasing temperature appear to encourage an increase in the number of ants leaving the aphid colony.

23. Increasing relative humidity and decreasing temperature appear to inhibit the number of F. oreas comptula workers leaving an aphid colony and thus the number of ants present at the aphid colony increases.

24. Aphids do not exhibit predator-avoidance behavior when they are being tended by F. oreas comptula.

25. A change in the excretory behavior of Symydobius americanus, Chaitophorus saliciniger and Pterocomma smithiae occurs when the number of F. oreas comptula workers at the respective aphid colonies decreases following a long period of intensive ant-attendance.

26. F. oreas comptula workers may have a preference for honeydew from colonies of aphids which are most composed of nymphs, tightly clustered together.

27. F. oreas comptula workers do not display aggressive

behavior toward the aphids they tend, unless an aphid starts to wander on the host plant away from its colony.

28. F. oreas comptula workers display aggressive behavior toward moving insects which approach the aphid colonies being tended.

29. Syrphid larvae, feeding in aphid colonies tended by F. oreas comptula workers, are not recognized by the ants as aphid predators, and the ants do not respond to the larvae's presence.

30. The presence of F. oreas comptula workers within colonies of C. saliciniger does not prevent, but may reduce, parasitism of the aphids by Hymenoptera.

31. C. saliciniger is more susceptible to predation and parasitism than are P. smithiae and S. americanus.

32. S. americanus appears to be free of parasitism and is not often preyed upon by other insects.

33. Wasps and hairstreak butterflies are the dominant scavengers of aphid honeydew droppings at Birds Hill Park, Manitoba.

34. F. oreas comptula workers occupy root chambers at the base of aphid host plants and aphids feeding on host plant roots may be located therein.

35. When F. oreas comptula workers reduce or cease to tend their aphid colonies, other ant species will sporadically collect the aphid honeydew.

Recommendations for Further Study

As a result of the investigation reported herein it is recommended that:

1. The species of ants and root aphids associating in Manitoba be determined by survey.
2. A study be conducted to determine whether ant-attended aphid populations decline following a period of intensive tending by F. oreas comptula workers as a result of a decrease in the number of honeydew foragers visiting the aphid colonies.
3. A comprehensive investigation of the biology and population dynamics of F. oreas comptula be completed.
4. The effect of rain and cloud cover on ant-attendance be further investigated, using more refined measures to assess these variables.
5. Twenty-four hour monitoring periods be conducted to determine hourly and seasonal patterns of aphid-tending activities by F. oreas comptula.
6. The influence of barometric pressure on number of ants present and tending aphids and on stem activity to and from the aphid colonies be clarified.
7. The possible preference of F. oreas comptula for nymphal aphid honeydew be examined.
8. An investigation be completed to determine why syrphid larvae are free from ant attack and removal from the aphid colonies they are preying on.

9. A study be conducted to determine whether the volume of aphid honeydew excreted changes significantly between the spring and summer periods of ant attendance.

10. If a seasonal change in aphid excretory volume does occur, a study should be carried out to determine the effect such a change has on the behavior of attendant ants.

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*Original article not seen.

APPENDIX A. Data Sheet for Collection of Ant-
Aphid Associations.

SAMPLE NO. _____ DATE _____ TIME _____

COLL. BY _____

LOCATION _____

T/R/S _____ TEMPERATURE _____ °C

SOIL _____

HOST PLANT _____ CANOPY _____

APHIDS _____ Forms _____
Approx. No. _____

ANTS _____
Number _____

NOTES _____

Aphid Species: _____ Det. _____

Ant Species: _____ Det. _____

APPENDIX B. Data Sheet for Observations Made
during Time Period 1 at Birds
Hill Park.

COLONY NO.			
------------	--	--	--

Day

Month

: a.m.
TimeRecorder
Temp. °C.

% RH

Bar. Press.

NO. APTERAE

NO. ALATAE

TOTAL NO. OF APHIDS

APPENDIX C. Data Sheet for Monitoring Aphid Colonies during Time Periods 2 to 8 at Birds Hill Park

(Set thermometer now for No. 10)

(2) ⁽¹⁾
 Day _____ Month _____ Time _____ am. pm. COLONY NO.
 Recorder Data: Temp °C % RH Bar. Pressure mmHg

WIND CONDS:

(3) Calm ☐ Gentle Breeze ☒ Moderate Breeze ☐ Moderate Gusts ☒ Strong Gusts ☐
 Strong Wind ☐

(4) PRECIPIT'N: Light ☐ Moderate ☐ Heavy ☐

SKY:
 (5) Clear ☐ Inter-mitt't Cloud ☐ Hazy ☐ Lightly Overcast. ☒ Heavily Overcast. ☐

(6) NO. of ANTS with aphids (7) NO. of PREDATORS in

(8) TYPE(S) OF PREDATOR _____ Near ☐
 _____ Over ☐ aphid colony
 Larval ☐ Adult ☐

NOTES RE PREDATOR-ANT INTERACTION _____

(9) STEM COUNTS:

No. ants/2 mins.
 UP DOWN
 Total

Mean No. ants/2 mins. passing UP to colony

Mean No. ants/2 mins. passing DOWN from colony.

(10) TEMP. °C at colony

No. ants/2 mins.
 UP DOWN

Mean No. ants/2 mins. passing point x (both UP & DOWN)

APPENDIX D. Collection Sites of Each Ant Species Found during 1976-77 in the Province of Manitoba.

Myrmica brevispinosa Emery

Beaconsia; Birds Hill Provincial Park; Lake Minnewasta;
Portage LaPrairie.

Myrmica emeryana Forel

Birds Hill Provincial Park; Birds Hill; Sandilands Provincial
Forest; Cook's Creek; Spruce Woods Provincial Forest (Oxbow
Lake Nature Trail); Whiteshell Provincial Park (Hanson Ck./
Caddy Lake Area).

Leptothorax muscorum Provancher

Whiteshell Provincial Park (Hanson Ck. Area).

Dolichoderus plagiatus (Mayr)

Birds Hill Provincial Park; Atomic Energy Canada Limited Pinawa
(FIG area); Rathwell.

Dolichoderus taschenbergi (Mayr)

Aweme; Carberry; Sandilands Provincial Forest.

Tapinoma sessile (Say)

Agassiz Provincial Forest; Richer; Sandilands Provincial
Forest; Whiteshell Provincial Park (Lone Island Lake area).

Camponotus herculeanus (L.)

Churchill; Atomic Energy Canada Limited Pinawa (FIG area);
Rennie Bird Sanctuary.

Camponotus nearcticus Emery

Sandilands Provincial Forest.

Camponotus noveboracensis (Fitch)

Agassiz Provincial Forest; Birds Hill Provincial Park; Camp
Morton; Carberry; Dakotah; Fortier; Hecla Island; Hnaua Park;
La Barriere Park; Lewis; Little Mountain Park; Lake Minnewasta;
Northwest Angle Provincial Park (Moose Lake); Atomic Energy
Canada Limited Pinawa (FIG area); Rennie Bird Sanctuary;
Sandilands Provincial Forest; Spruce Woods Provincial Forest
(Oxbow Lake Nature Trail); Stoney Mountain; Whitemouth Lake;
Whiteshell Provincial Park (Hanson Ck./Caddy Lake and Lone
Island Lake areas).

Lasius alienus Förster

Agassiz Provincial Forest; Birds Hill; Carberry;
Lake Minnewasta; Atomic Energy Canada Limited Pinawa (FIG area);
Portage LaPrairie; Rennie Bird Sanctuary; Sandilands Provincial
Forest; Whiteshell Provincial Park (Hanson Ck./Caddy Lake area).

Lasius pallitarsis (Provancher)

Fortier; Sandilands Provincial Forest; Spruce Woods Provincial
Forest (Oxbow Lake Nature Trail); Stoney Mountain; UM Campus;
Whiteshell Provincial Park (Hanson Ck./Caddy Lake area); City
of Winnipeg.

Lasius neoniger Emery

Sandilands Provincial Forest.

Lasius subumbratus Viereck

Spruce Woods Provincial Forest (Oxbow Lake Nature Trail).

Formica lasioides Emery

Atomic Energy Canada Limited Pinawa (FIG area); Rathwell; Rennie
Bird Sanctuary; Sandilands Provincial Forest; Stoney Mountain;
Whitemouth Lake.

Formica sanguinea subnuda Emery

Birds Hill; Birds Hill Provincial Park; Carberry; Fortier; Hecla
Island; Northwest Angle Provincial Park (Moose Lake); Atomic
Energy Canada Limited Pinawa (FIG area); Rennie Birds Sanctuary;
Richer; Sandilands Provincial Forest; Spruce Woods Provincial
Forest (Oxbow Lake Nature Trail); Whiteshell Provincial Park
(Hanson Ck./Caddy Lake and Lone Island Lake areas).

Formica (rufa) species?

Carberry; Sandilands Provincial Forest.

Formica obscuripes Forel

Birds Hill Provincial Park; Carberry; Lewis; Lake Minnewasta;
Portage LaPrairie; Sandilands Provincial Forest; Stoney Mountain.

Formica obscuriventris Mayr *

Agassiz Provincial Forest; Lake Minnewasta.

Formica oreas comptula Wheeler

Agassiz Provincial Forest; Aweme; Birds Hill; Birds Hill
Provincial Park; Carberry; Lake Minnewasta; Sandilands
Provincial Forest; Spruce Woods Provincial Forest (Oxbow
Lake Nature Trail); Whitemouth Lake.

Formica ulkei Emery

Cook's Creek.

Formica spatulata Buren

Rathwell.

Formica podzolica Francoeur

Aweme; Birds Hill; Birds Hill Provincial Park; Carberry;
Lewis; Lake Minnewasta; Northwest Angle Provincial Park (Moose
Lake); Atomic Energy Canada Limited Pinawa (FIG area); Rennie
Bird Sanctuary; Sandilands Provincial Forest; Stoney Mountain;
Thompson; UM Campus; Whitemouth Lake; Whiteshell Provincial
Park (Hanson Ck./Caddy Lake area); City of Winnipeg.

Formica subaenescens Emery

Agassiz Provincial Forest; Aweme; Birds Hill Provincial Park;
Northwest Angle Provincial Park (Moose Lake); Atomic Energy
Canada Limited Pinawa (FIG area); Richer; Sandilands Provincial
Forest; Whiteshell Provincial Park (Hanson Ck./Caddy Lake and
Lone Island Lake areas).

Formica montana Emery

UM Campus.

Formica densiventris Viereck

Sandilands Provincial Forest.

Formica hewitti Wheeler

Birds Hill Provincial Park; Hecla Island; Northwest Angle
Provincial Park (Moose Lake); Sandilands Provincial Forest.

Formica subsericea Say

Lewis; Sandilands Provincial Forest; Whitemouth Lake.

Formica neorufibarbis Emery

Churchill.

* Gregg (1972) reported the occurrence of F. obscuriventris
in Birds Hill Park, but he did not mention the presence of

APPENDIX D concluded.

F. oreas comptula therein. F. obscuriventris was not found in Birds Hill Park as a result of collections and monitoring discussed herein, but F. oreas comptula was found to be well represented. Identification of the latter species was confirmed upon examination of its alate reproductives.

APPENDIX E. Mean and Standard Deviation of Day of Season, Per Cent Relative Humidity, Barometric Pressure, Precipitation, Sky, Number of Ants Present at Aphid Colony, Stem Activity Up and Down, Ambient Temperature. and Number of Aphids in Aphid Colony for Three Aphid Species Monitored during Time Periods 1 to 8 from 8 June to 27 July, 1977.

Aphid Species*	Day (log)	%RH (arcsin \sqrt{p})	Barp (mmHg)	Rain (0-3)	Sky (1-5)	No. of Ants (Log ₁₀ (N+.1))	Stem Act Up (Log ₁₀ (N+.1))	Stem Act Down (Log ₁₀ (N+.1))	Temp (°C)	No. of Aphids (Log ₁₀ (N+.1))
A	<u>Time Period 1 (N=94)</u>									
Mean	1.33	81.1	762			0.432			13.8	2.02
SD**	0.262	11.8	4.84			0.894			2.52	0.538
A	<u>Time Period 2 (N=90)</u>									
Mean	1.31	60.4	759	0.0556	2.62	0.646	-0.412	-0.403	18.8	2.07
SD	0.262	15.7	12.1	0.230	1.75	0.730	0.553	0.525	2.60	0.490
A	<u>Time Period 3 (N=92)</u>									
Mean	1.32	50.6	757	0.0870	2.52	0.447	-0.336	-0.372	21.9	2.01
SD	0.313	17.8	5.35	0.283	1.63	0.813	0.532	0.553	3.77	0.547

Appendix E cont'd.

Aphid Species	Day (log)	%RH (arcsin \sqrt{p})	Barp (mmHg)	Rain (0-3)	Sky (1-5)	No. of Ants (Log ₁₀ (N+.1))	Stem Act Up (Log ₁₀ (N+.1))	Stem Act Down (Log ₁₀ (N+.1))	Temp (°C)	No. of Aphids (Log ₁₀ (N+.1))
A	<u>Time Period 4 (N=93)</u>									
Mean	1.25	50.0	757	0.280	3.04	0.469	-0.354	-0.395	22.7	2.06
SD	0.368	22.7	5.33	0.682	1.66	0.830	0.529	0.544	5.05	0.489
A	<u>Time Period 5 (N=105)</u>									
Mean	1.25	49.5	757	0.152	3.06	0.465	-0.325	-0.308	23.0	2.03
SD	0.363	22.7	5.51	0.387	1.78	0.862	0.551	0.545	5.37	0.534
A	<u>Time Period 6 (N=97)</u>									
Mean	1.26	49.2	757	0.186	2.80	0.554	-0.310	-0.274	23.3	2.07
SD	0.323	22.1	5.30	0.391	1.80	0.810	0.603	0.546	5.43	0.489
A	<u>Time Period 7 (N=48)</u>									
Mean	1.05	50.8	758		2.83	0.875	0.0167	-0.132	19.7	2.20
SD	0.293	17.3	4.44		1.94	0.764	0.435	0.522	2.98	0.458

Appendix E cont'd.

Aphid Species	Day (log)	%RH (arcsin \sqrt{p})	Barp (mmHg)	Rain (0-3)	Sky (1-5)	No. of Ants (Log ₁₀ (N+.1))	Stem Act Up (Log ₁₀ (N+.1))	Stem Act Down (Log ₁₀ (N+.1))	Temp (°C)	No. of Aphids (Log ₁₀ (N+.1))
A <u>Time Period 8</u> (N=48)										
Mean	1.05	65.0	760		1.98	0.869	-0.319	-0.293	14.9	2.20
SD	0.293	14.6	5.05		1.45	0.863	0.551	0.482	2.65	0.458
B <u>Time Period 1</u> (N=105)										
Mean	1.35	80.4	762			-0.0732			13.6	2.18
SD	0.265	12.9	4.79			0.962			2.78	0.582
B <u>Time Period 2</u> (N=99)										
Mean	1.34	60.2	760	0.061	2.45	0.137	-0.679	-0.660	18.6	2.22
SD	0.268	15.5	5.28	0.240	1.71	0.920	0.461	0.424	2.91	0.544
B <u>Time Period 3</u> (N=101)										
Mean	1.34	50.0	758	0.0693	2.49	-0.00013	-0.535	-0.605	21.9	2.15
SD	0.339	17.5	5.45	0.255	1.69	0.881	0.470	0.418	4.03	0.579

Appendix E cont'd.

Aphid Species	Day (log)	%RH (arcsin \sqrt{p})	Barp (mmHg)	Rain (0-3)	Sky (1-5)	No. of Ants (Log ₁₀ (N+.1))	Stem Act Up (Log ₁₀ (N+.1))	Stem Act Down (Log ₁₀ (N+.1))	Temp (°C)	No. of Aphids (Log ₁₀ (N+.1))
B	<u>Time Period 4</u> (N=99)									
Mean	1.27	47.8	757	0.333	2.80	0.120	-0.542	-0.632	22.9	2.21
SD	0.383	21.6	5.39	0.742	1.63	0.875	0.470	0.461	4.86	0.543
B	<u>Time Period 5</u> (N=111)									
Mean	1.29	47.2	757	0.144	2.72	0.0385	-0.447	-0.520	23.8	2.18
SD	0.365	21.8	5.34	0.423	1.84	0.944	0.495	0.459	5.60	0.570
B	<u>Time Period 6</u> (N=104)									
Mean	1.29	47.0	757	0.154	2.65	0.183	-0.461	-0.506	23.7	2.22
SD	0.329	20.3	5.35	0.457	1.77	0.902	0.503	0.475	5.74	0.537
B	<u>Time Period 7</u> (N=47)									
Mean	1.06	50.5	758		2.94	0.799	-0.164	-0.327	20.2	2.47
SD	0.283	17.2	4.38		1.94	0.760	0.434	0.506	3.26	0.414

Appendix E cont'd.

Aphid Species	Day (log)	%RH (arcsin \sqrt{p})	Barp (mmHg)	Rain (0-3)	Sky (1-5)	No. of Ants (Log ₁₀ (N+.1))	Stem Act Up (Log ₁₀ (N+.1))	Stem Act Down (Log ₁₀ (N+.1))	Temp (°C)	No. of Aphids (Log ₁₀ (N+.1))
B	<u>Time Period 8 (N=48)</u>									
Mean	1.05	64.0	760		2.33	0.884	-0.438	-0.467	15.1	2.47
SD	0.293	15.5	5.08		1.68	0.663	0.479	0.468	2.73	0.411
C	<u>Time Period 1 (N=81)</u>									
Mean	1.31	83.2	761			0.693			13.4	1.75
SD	0.261	11.1	4.31			0.453			2.50	0.464
C	<u>Time Period 2 (N=82)</u>									
Mean	1.28	62.0	759	0.0122	2.67	0.696	-0.347	-0.422	18.7	1.74
SD	0.256	16.8	4.88	0.110	1.69	0.502	0.417	0.463	2.73	0.468
C	<u>Time Period 3 (N=84)</u>									
Mean	1.25	51.3	757	0.0833	2.58	0.618	-0.423	-0.398	21.2	1.76
SD	0.393	18.0	5.03	0.318	1.66	0.574	0.458	0.462	3.90	0.454

Appendix E cont'd.

Aphid Species	Day (log)	%RH (arcsin \sqrt{p})	Barp (mmHg)	Rain (0-3)	Sky (1-5)	No. of Ants (Log ₁₀ (N+.1))	Stem Act Up (Log ₁₀ (N+.1))	Stem Act Down (Log ₁₀ (N+.1))	Temp (°C)	No. of Aphids (Log ₁₀ (N+.1))
C	<u>Time Period 4 (N=87)</u>									
Mean	1.17	49.7	757.0	0.414	2.90	0.659	-0.349	-0.356	22.4	1.72
SD	0.425	22.9	5.07	0.829	1.69	0.538	0.444	0.455	5.04	0.447
C	<u>Time Period 5 (N=94)</u>									
Mean	1.20	49.0	756.0	0.223	2.96	0.646	-0.200	-0.309	22.9	1.74
SD	0.404	22.6	5.14	0.490	1.88	0.576	0.410	0.458	5.32	0.448
C	<u>Time Period 6 (N=88)</u>									
Mean	1.22	49.4	756.0	0.205	2.97	0.665	-0.314	-0.378	22.7	1.72
SD	0.319	21.3	5.08	0.550	1.81	0.608	0.424	0.496	5.33	0.456
C	<u>Time Period 7 (N=48)</u>									
Mean	1.05	50.8	758.0	0.0208	2.79	0.884	-0.302	-0.316	19.8	1.65
SD	0.293	17.1	4.35	0.144	1.92	0.469	0.492	0.397	3.53	0.444

Appendix E concluded.

Aphid Species	Day (log)	%RH (arcsin \sqrt{p})	Barp (mmHg)	Rain (0-3)	Sky (1-5)	No. of Ants (Log ₁₀ (N+.1))	Stem Act Up (Log ₁₀ (N+.1))	Stem Act Down (Log ₁₀ (N+.1))	Temp (°C)	No. of Aphids (Log ₁₀ (N+.1))
C	Time Period 8 (N=48)									
Mean	1.05	64.8	759	0.0208	2.38	0.891	-0.560	-0.555	15.2	1.65
SD	0.293	15.7	5.07	0.144	1.76	0.503	0.443	0.459	3.02	0.444

* Aphid Species A = Symydobius americanus Baker on Dwarf Birch; B = Chaitophorus saliciniger (Knowlton) on Willow; C = Pterocomma smithiae (Monell) on Balsam Poplar.

** Standard Deviation.

APPENDIX F. Correlation Matrix of Day of Season, Ambient Temperature, Per Cent Relative Humidity, Barometric Pressure, Number of Ants Present at Aphid Colony, and Number of Aphids in Aphid Colony for Each Aphid Species Monitored during Time Period 1 from 8 June to 27 July, 1977.

	Day (log)	Temp (°C)	% RH (arcsin \sqrt{p})	Barp (mmHg)	No. of Ants (log ₁₀ (N+.1))
<hr/>					
Aphid Species: <u>Symydobius americanus</u> (N=94)	Critical r (P= 0.10) = 0.171				
Temp (°C)	0.206				
% RH (arcsin p)	-0.354	-0.368			
Barp (mmHg)	-0.060	-0.456	-0.249		
No. of Ants (log ₁₀ (N+.1))	-0.429	0.045	0.043	0.274	
No. of Aphids (log ₁₀ (N+.1))	-0.357	-0.027	0.058	0.114	0.586
Aphid Species: <u>Chaitophorus saliciniger</u> (N=105)	r = 0.162				
Temp (°C)	0.337				
% RH (arcsin p)	-0.383	-0.504			
Barp (mmHg)	-0.090	-0.543	-0.128		
No. of Ants (log ₁₀ (N+.1))	-0.812	-0.209	0.231	0.161	
No. of Aphids (log ₁₀ (N+.1))	-0.478	-0.333	0.196	0.071	0.618
Aphid Species: <u>Pterocomma smithiae</u> (N=81)	r = 0.184				
Temp (°C)	0.238				
% RH (arcsin p)	-0.322	-0.328			
Barp (mmHg)	-0.143	-0.520	-0.227		
No. of Ants (log ₁₀ (N+.1))	-0.508	-0.075	0.214	0.159	
No. of Aphids (log ₁₀ (N+.1))	0.245	0.107	-0.093	-0.028	0.419

APPENDIX G. Correlation matrix of Day of Season, Per Cent Relative Humidity, Barometric Pressure, Precipitation, Sky, Number of Ants Present at Aphid Colony, Stem Activity Up, Stem Activity Down, Ambient Temperature, and Number of Aphids in Aphid Colony for Each Aphid Species during Each of Time Periods 2 to 8 Monitored from 8 June to 27 July, 1977.

Day (log)	% RH ($\arcsin \sqrt{P}$)	Barp (mmHg)	Rain (Coded 0 to 3)	Sky (Coded to 5)	No. of Ants (\log_{10} (N+.1))	Stem Act Up (\log_{10} (N+.1))	Stem Act Dn (\log_{10} (N+.1))	Temp (°C)
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Aphid Species: Symydobius americanus

Critical r (P = 0.10) = 0.175

Time Period 2 (N=90)

% RH	-0.499								
Barp	-0.067	-0.085							
Rain	-0.490	0.461	0.100						
Sky	-0.502	0.744	-0.209	0.332					
No. of Ants	-0.485	0.113	0.132	0.200	0.073				
Stem Act Up	-0.175	-0.087	0.053	-0.087	-0.219	0.552			
Stem Act Down	-0.176	-0.067	0.166	-0.103	-0.206	0.649	0.698		
Temp	0.432	-0.524	-0.132	-0.473	-0.474	0.021	0.262	0.289	
No. of Aphids (\log_{10} (N+.1))	-0.353	0.005	0.040	0.085	0.015	0.635	0.425	0.394	0.054

APPENDIX G cont'd.

	Day (log)	% RH (arcsin \sqrt{p})	Barp (mmHg)	Rain (Coded 0 to 3)	Sky (Coded 1 to 5)	No. of Ants (log ₁₀ (N+.1))	Stem Act Up (log ₁₀ (N+.1))	Stem Act Dn (log ₁₀ (N+.1))	Temp (°C)
Time Period 3 (N=92)						r = 0.173			
% RH	-0.241								
Barp	-0.221	0.013							
Rain	-0.371	0.320	0.055						
Sky	-0.160	0.776	-0.184	0.473					
No. of Ants	-0.400	-0.017	0.316	0.342	-0.057				
Stem Act Up	-0.059	-0.088	0.079	0.184	-0.136	0.594			
Stem Act Down	-0.047	-0.185	0.154	0.073	-0.276	0.649	0.753		
Temp	0.464	-0.750	-0.325	-0.365	-0.671	-0.019	0.142	0.246	
No. of Aphids (log ₁₀ (N+.1))	-0.150	-0.141	0.095	0.181	-0.126	0.673	0.458	0.450	0.211
Time Period 4 (N=93)						r = 0.172			
% RH	-0.517								
Barp	-0.206	-0.018							
Rain	-0.575	0.730	0.120						
Sky	-0.231	0.783	-0.426	0.489					
No. of Ants	-0.371	0.146	0.424	0.262	-0.086				
Stem Act Up	-0.068	-0.144	0.222	-0.083	-0.182	0.643			
Stem Act Down	-0.041	-0.265	0.305	-0.118	-0.379	0.701	0.741		
Temp	0.569	-0.815	-0.143	-0.658	-0.601	-0.017	0.203	0.336	
No. of Aphids (log ₁₀ (N+.1))	-0.082	-0.024	0.078	0.072	-0.087	0.579	0.503	0.437	0.126

APPENDIX G cont'd.

	Day (log)	% RH (arcsin \sqrt{p})	Barp (mmHg)	Rain (Coded 0 to 3)	Sky (Coded 1 to 5)	No. of Ants (log ₁₀ (N+.1))	Stem Act Up (log ₁₀ (N+.1))	Stem Act Dn (log ₁₀ (N+.1))	Temp (°C)
<hr/>									
Time Period 5 (N=105)						r = 0.162			
% RH	-0.447								
Barp	-0.231	0.081							
Rain	-0.160	0.435	-0.182						
Sky	-0.275	0.753	-0.149	0.420					
No. of Ants	-0.418	0.042	0.336	-0.085	-0.023				
Stem Act Up	-0.075	-0.168	0.331	-0.206	-0.202	0.656			
Stem Act Down	-0.051	-0.259	0.218	-0.212	-0.246	0.728	0.820		
Temp	0.486	-0.837	-0.270	-0.415	-0.736	-0.022	0.148	0.249	
No. of Aphids (log ₁₀ (N+.1))	-0.149	-0.101	0.131	0.055	-0.074	0.605	0.530	0.512	0.137
<hr/>									
Time Period 6 (N=97)						r = 0.168			
% RH	-0.359								
Barp	-0.217	-0.198							
Rain	0.014	0.503	0.064						
Sky	-0.293	0.593	0.045	0.437					
No. of Ants	-0.511	-0.039	0.398	-0.192	0.077				
Stem Act Up	-0.331	-0.102	0.330	-0.262	-0.034	0.664			
Stem Act Down	-0.289	-0.184	0.271	-0.273	-0.052	0.761	0.736		
Temp	0.500	-0.772	-0.201	-0.547	-0.727	-0.008	0.095	0.133	
No. of Aphids (log ₁₀ (N+.1))	-0.266	-0.020	0.097	-0.080	0.125	0.697	0.479	0.528	0.027

APPENDIX G cont'd.

	Day (log)	% RH (arcsin \sqrt{p})	Barp (mmHg)	Rain (Coded 0 to 3)	Sky (Coded 1 to 5)	No. of Ants (log ₁₀ (N+.1))	Stem Act Up (log ₁₀ (N+.1))	Stem Act Dn (log ₁₀ (N+.1))	Temp (°C)
<hr/>									
Time Period 7 (N=48)							r = 0.240		
% RH	-0.424								
Barp	-0.338	-0.048							
Rain	—	—	—						
Sky	-0.023	0.793	0.016	—					
No. of Ants	-0.579	0.213	0.444	—	0.198				
Stem Act Up	-0.267	0.003	0.269	—	0.165	0.707			
Stem Act Down	-0.268	-0.051	0.272	—	0.075	0.759	0.828		
Temp	0.291	-0.784	-0.228	—	-0.659	-0.052	0.154	0.186	
No. of Aphids (log ₁₀ (N+.1))	-0.020	-0.173	0.179	—	0.089	0.649	0.643	0.695	0.318
<hr/>									
Time Period 8 (N=48)							r = 0.240		
% RH	-0.509								
Barp	-0.301	-0.322							
Rain	—	—	—						
Sky	0.207	0.225	-0.419	—					
No. of Ants	-0.611	0.232	0.391	—	0.015				
Stem Act Up	-0.178	0.076	0.014	—	0.208	0.575			
Stem Act Down	-0.121	-0.034	0.136	—	0.231	0.663	0.708		
Temp	0.244	0.214	-0.642	—	0.719	0.018	0.269	0.257	
No. of Aphids (log ₁₀ (N+.1))	-0.020	-0.111	0.161	—	0.072	0.484	0.567	0.459	0.308

APPENDIX G cont'd.

	Day (log)	% RH (arcsin \sqrt{p})	Barp (mmHg)	Rain (Coded 0 to 3)	Sky (Coded 1 to 5)	No. of Ants (log ₁₀ (N+.1))	Stem Act Up (log ₁₀ (N+.1))	Stem Act Dn (log ₁₀ (N+.1))	Temp (°C)
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Aphid Species: Chaitophorus saliciniger

Time Period 2 (N=99)

r = 0.167

% RH	-0.542								
Barp	-0.043	-0.201							
Rain	-0.204	0.308	-0.012						
Sky	-0.551	0.775	-0.283	0.380					
No. of Ants	-0.813	0.257	-0.005	-0.062	0.269				
Stem Act Up	-0.446	0.023	0.036	-0.178	0.020	0.576			
Stem Act Down	-0.552	0.112	0.079	-0.078	0.126	0.714	0.646		
Temp	0.473	-0.585	-0.329	-0.215	-0.457	-0.206	0.055	-0.041	
No. of Aphids (log ₁₀ (N+.1))	-0.472	0.006	-0.054	0.017	0.125	0.636	0.443	0.469	-0.118

Time Period 3 (N=101)

r = 0.165

% RH	-0.240								
Barp	-0.177	-0.031							
Rain	-0.375	0.532	0.138						
Sky	-0.161	0.793	-0.226	0.408					
No. of Ants	-0.672	0.160	0.085	0.391	0.134				
Stem Act Up	-0.444	0.075	0.061	0.267	0.150	0.604			
Stem Act Down	-0.294	-0.096	0.042	0.087	-0.022	0.590	0.660		
Temp	0.469	-0.713	-0.291	-0.417	-0.645	-0.251	-0.184	0.017	
No. of Aphids (log ₁₀ (N+.1))	-0.289	-0.118	-0.036	0.163	0.002	0.662	0.521	0.455	-0.003

APPENDIX G cont'd.

	Day (log)	% RH (arcsin \sqrt{p})	Barp (mmHg)	Rain (Coded 0 to 3)	Sky (Coded 1 to 5)	No. of Ants (log ₁₀ (N+.1))	Stem Act Up (log ₁₀ (N+.1))	Stem Act Dn (log ₁₀ (N+.1))	Temp (°C)
<u>Time Period 4 (N=99)</u>						r = 0.167			
% RH	-0.472								
Barp	-0.182	-0.028							
Rain	-0.462	0.798	0.037						
Sky	-0.256	0.783	-0.274	0.561					
No. of Ants	-0.698	0.322	0.218	0.328	0.205				
Stem Act Up	-0.358	0.070	0.165	0.039	0.046	0.489			
Stem Act Down	-0.288	-0.114	0.224	-0.108	-0.089	0.529	0.579		
Temp	0.566	-0.835	-0.141	-0.743	-0.676	-0.415	-0.104	0.055	
No. of Aphids (log ₁₀ (N+.1))	-0.256	0.043	-0.055	0.089	0.091	0.639	0.505	0.347	-0.107
<u>Time Period 5 (N=111)</u>						r = 0.157			
% RH	-0.363								
Barp	-0.186	0.107							
Rain	-0.078	0.416	-0.089						
Sky	-0.269	0.771	-0.141	0.425					
No. of Ants	-0.726	0.270	0.179	0.043	0.248				
Stem Act Up	-0.548	0.145	0.258	-0.034	0.094	0.632			
Stem Act Down	-0.486	0.072	0.242	0.019	0.070	0.647	0.769		
Temp	0.481	-0.835	-0.216	-0.408	-0.784	-0.344	-0.181	-0.126	
No. of Aphids (log ₁₀ (N+.1))	-0.295	0.017	-0.002	0.161	0.092	0.583	0.443	0.425	-0.072

APPENDIX G cont'd.

	Day (log)	% RH (arcsin \sqrt{p})	Barp (mmHg)	Rain (Coded 0 to 3)	Sky (Coded 1 to 5)	No. of Ants (log ₁₀ (N+.1))	Stem Act Up (log ₁₀ (N+.1))	Stem Act Dn (log ₁₀ (N+.1))	Temp (°C)
<u>Time Period 6 (N=104)</u>						r = 0.162			
% RH	-0.522								
Barp	-0.168	-0.121							
Rain	0.002	0.431	-0.312						
Sky	-0.369	0.694	-0.102	0.451					
No. of Ants	-0.756	0.270	0.286	-0.093	0.277				
Stem Act Up	-0.479	0.167	0.315	-0.128	0.065	0.619			
Stem Act Down	-0.462	0.136	0.346	-0.097	0.044	0.686	0.753		
Temp	0.533	-0.799	-0.159	-0.413	-0.745	-0.342	-0.235	-0.150	
No. of Aphids (log ₁₀ (N+.1))	-0.381	0.174	0.020	0.019	0.271	0.622	0.537	0.494	-0.257
<u>Time Period 7 (N=47)</u>						r = 0.243			
% RH	-0.423								
Barp	-0.373	-0.092							
Rain	—	—	—						
Sky	-0.112	0.802	0.060	—					
No. of Ants	-0.603	0.084	0.505	—	0.112				
Stem Act Up	-0.260	-0.134	0.245	—	-0.048	0.527			
Stem Act Down	-0.153	-0.281	0.096	—	-0.187	0.495	0.650		
Temp	0.393	-0.787	-0.262	—	-0.583	-0.098	0.135	0.307	
No. of Aphids (log ₁₀ (N+.1))	0.196	-0.100	-0.054	—	0.025	0.435	0.513	0.434	0.083

APPENDIX G cont'd.

	Day (log)	% RH (arcsin \sqrt{P})	Barp (mmHg)	Rain (Coded 0 to 3)	Sky (Coded 1 to 5)	No. of Ants (log ₁₀ (N+.1))	Stem Act Up (log ₁₀ (N+.1))	Stem Act Dn (log ₁₀ (N+.1))	Temp (°C)
<u>Time Period 8 (N=48)</u>						r = 0.240			
% RH	-0.421								
Barp	-0.300	-0.325							
Rain	—	—	—						
Sky	0.047	0.338	-0.282	—					
No. of Ants	-0.620	0.198	0.427	—	0.124				
Stem Act Up	-0.254	-0.069	0.179	—	0.304	0.537			
Stem Act Down	-0.328	-0.016	0.240	—	0.269	0.555	0.642		
Temp	0.318	0.034	-0.635	—	0.618	-0.156	0.265	0.134	
No. of Aphids (log ₁₀ (N+.1))	0.216	-0.073	-0.061	—	0.032	0.445	0.279	0.222	0.061
<u>Aphid Species: <i>Pterocomma smithiae</i></u>									
<u>Time Period 2 (N=82)</u>						r = 0.183			
% RH	-0.518								
Barp	-0.292	-0.068							
Rain	-0.218	0.186	0.100						
Sky	-0.503	0.775	-0.185	0.154					
No. of Ants	-0.558	0.271	0.286	0.153	0.155				
Stem Act Up	-0.162	0.065	0.149	-0.005	-0.036	0.344			
Stem Act Down	0.009	0.003	-0.052	-0.140	-0.039	0.383	0.600		
Temp	0.527	-0.610	-0.441	-0.192	-0.532	-0.251	-0.013	0.104	
No. of Aphids (log ₁₀ (N+.1))	0.210	-0.080	-0.036	0.026	-0.118	0.366	0.299	0.369	0.096

APPENDIX G cont'd.

	Day (log)	%RH (arcsin \sqrt{P})	Barp (mmHg)	Rain (Coded 0 to 3)	Sky (Coded 1 to 5)	No. of Ants (log ₁₀ (N+.1))	Stem Act Up (log ₁₀ (N+.1))	Stem Act Dn (log ₁₀ (N+.1))	Temp (°C)
Time Period 3 (N=84)						r = 0.181			
% RH	-0.105								
Barp	-0.376	0.074							
Rain	-0.229	0.464	0.123						
Sky	0.038	0.802	-0.246	0.386					
No. of Ants	-0.526	0.082	0.374	0.227	-0.061				
Stem Act Up	0.016	-0.086	0.060	0.164	-0.057	0.280			
Stem Act Down	0.000	-0.168	-0.040	0.213	-0.112	0.240	0.574		
Temp	0.544	-0.672	-0.446	-0.372	-0.540	-0.259	0.120	0.203	
No. of Aphids (log ₁₀ (N+.1))	0.229	0.015	-0.049	-0.128	0.061	0.308	0.341	0.172	0.037
Time Period 4 (N=87)						r = 0.178			
% RH	-0.383								
Barp	-0.359	0.082							
Rain	-0.368	0.789	0.052						
Sky	-0.121	0.804	-0.277	0.628					
No. of Ants	-0.537	0.284	0.478	0.262	0.042				
Stem Act Up	-0.155	-0.108	0.058	-0.223	-0.164	0.340			
Stem Act Down	0.003	-0.248	0.093	-0.282	-0.317	0.401	0.656		
Temp	0.567	-0.842	-0.239	-0.730	-0.703	-0.384	0.066	0.249	
No. of Aphids (log ₁₀ (N+.1))	0.320	-0.155	-0.105	-0.181	-0.099	0.169	0.303	0.293	0.174

APPENDIX G cont'd.

	Day (log)	% RH (arcsin \sqrt{P})	Barp (mmHg)	Rain (Coded 0 to 3)	Sky (Coded 1 to 5)	No. of Ants (log ₁₀ (N+.1))	Stem Act Up (log ₁₀ (N+.1))	Stem Act Dn (log ₁₀ (N+.1))	Temp (°C)
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Time Period 5 (N=94)							r = 0.171		
% RH	-0.240								
Barp	-0.356	0.172							
Rain	0.023	0.381	-0.315						
Sky	-0.043	0.722	-0.091	0.502					
No. of Ants	-0.563	0.183	0.431	-0.077	0.131				
Stem Act Up	-0.359	-0.076	0.125	-0.123	-0.137	0.364			
Stem Act Down	-0.363	-0.191	0.229	-0.093	-0.141	0.510	0.661		
Temp	0.403	-0.837	-0.300	-0.430	-0.726	-0.303	0.026	0.053	
No. of Aphids (log ₁₀ (N+.1))	0.311	-0.095	-0.110	-0.001	0.024	0.215	0.125	0.079	0.090
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Time Period 6 (N=88)							r = 0.177		
% RH	-0.466								
Barp	-0.344	-0.085							
Rain	0.042	0.461	-0.278						
Sky	-0.318	0.702	-0.056	0.423					
No. of Ants	-0.511	0.139	0.299	-0.041	0.112				
Stem Act Up	-0.249	-0.137	0.208	-0.135	-0.064	0.576			
Stem Act Down	-0.125	-0.259	-0.026	-0.182	-0.150	0.487	0.552		
Temp	0.514	-0.813	-0.209	-0.435	-0.765	-0.167	0.030	0.268	
No. of Aphids (log ₁₀ (N+.1))	0.322	-0.131	-0.090	0.120	-0.062	0.302	0.286	0.255	0.094

APPENDIX G concluded.

	Day (log)	% RH (arcsin \sqrt{p})	Barp (mmHg)	Rain (Coded 0 to 3)	Sky (Coded 1 to 5)	No. of Ants (log ₁₀ (N+.1))	Stem Act Up (log ₁₀ (N+.1))	Stem Act Dn (log ₁₀ (N+.1))	Temp (°C)
Time Period 7 (N=48)						r = 0.240			
% RH	-0.398								
Barp	-0.341	-0.115							
Rain	0.147	0.215	-0.276						
Sky	-0.045	0.787	0.053	0.169					
No. of Ants	-0.648	0.195	0.457	-0.177	0.138				
Stem Act Up	-0.221	-0.332	0.081	-0.209	-0.371	0.446			
Stem Act Down	-0.104	-0.391	0.171	-0.019	-0.343	0.338	0.472		
Temp	0.331	-0.695	-0.322	-0.159	-0.615	-0.175	0.289	0.158	
No. of Aphids (log ₁₀ (N+.1))	0.358	-0.193	-0.102	0.112	0.040	0.271	0.290	0.198	0.171
Time Period 8 (N= 48)						r = 0.240			
% RH	-0.427								
Barp	-0.329	-0.269							
Rain	-0.074	0.160	-0.069						
Sky	0.107	0.441	-0.384	0.220					
No. of Ants	-0.646	0.284	0.296	0.154	0.034				
Stem Act Up	-0.284	-0.127	0.013	-0.147	-0.005	0.461			
Stem Act Down	-0.070	-0.155	0.024	0.140	0.156	0.329	0.564		
Temp	0.226	-0.023	-0.569	0.223	0.575	0.036	0.218	0.277	
No. of Aphids (log ₁₀ (N+.1))	0.358	-0.227	-0.082	0.101	0.085	0.320	0.355	0.275	0.181