

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

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by

Mary Catherine Anne Madder

In Partial Fulfillment of the

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of

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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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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