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OBSERVATIONS ON THE INTERRELATIONSHIPS AMONG ANTS, APHIDS AND APHID PREDATORS

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The literature concerning the interactions of these insect groups is as interesting as it is extensive. It has generally been accepted that the relationship between ants and aphids has been one of mutualism in which ants derive all or a large part of their nutrients from aphid honeydew and perform special functions in return, primarily that of protecting aphids from their enemies. Every aspect of these associations has been covered by the excellent reviews of Nixon (1951) and Way (1963). It now appears that the nature and effectiveness of the protective value afforded the attended aphids by ants cannot be reduced to a simple statement of symbiosis. Nixon (1951) pointed out numerous situations that are responsible for fluctuations in the ant-aphid relationship. The emphasis in the present study was on the protection extended to *Aphis rumicis* Linn., a small aphid found on spirea shoots by the common tending ants. This restriction allowed constant surveillance of the protection supplied to a single aphid species by ants against the seasonal succession of predators. Aphid parasites were ignored in this study.

These observations were made from June to mid-August, 1966, on four dispersed clumps of aphid-infested spirea bushes. Only two ants, *Lasius neoniger* Emery and *Formica fusca* Linnaeus were in regular attendance to *Aphis rumicis*. The responses of these ants to the aphid and to the five predator groups were so different that each ant was treated separately. The predator species were not identified in all instances. Species of Chrysopidae, Coccinellidae, Syrphidae, Chamaemyiidae, and Cecidomyiidae attacked the tended aphids. The predator protection provided by the ants was the prime object of the study. Therefore, opportunities to identify predaceous larvae were frequently sacrificed for potential observation of ant-predator encounters.

Lasius neoniger

Even though many syrphid larvae preyed upon tended aphids, in only one case was a syrphid larva attacked by *Lasius neoniger*, and in this instance the attack may have been precipitated by the actions of the observer as the larva was placed on a spirea twig. The interference by *L. neoniger* in the aphid feeding activities of *Aphidoletes* (Cecidomyiidae) and *Leucopis* (Chamaemyiidae) was even less than in the case of syrphids. On one spirea bush these predators completely killed the aphid population being tended. Ants often overran the larvae and tapped them with their antennae. Only one *Leucopis* larva was disturbed by these attentions and left the branch while the others remained undisturbed. *Leucopis* pupae were commonly found among tended aphids. These ants were never observed to disturb any dipteran eggs.

The responses of *Lasius neoniger* to coccinellid larvae seemed to depend upon the size of the larvae. Small larvae, 3 to 4 mm. long, were not attacked. The ants would, however, investigate their bodies with antennae and palps. These small larvae would remain perfectly quiet during these attentions, but would continue feeding or searching as soon as the ants would leave them. The larger coccinellid larvae were always attacked. One larva, about 8 mm. long, was dragged down a branch by three ants. However, the small *Lasius* workers were usually unable to inflict much damage on the large larvae. In all observed instances, the tending ants did succeed in driving large coccinellid larvae away from aphids.

Chrysopid (Neuroptera) larvae always excited *L. neoniger* whenever they were encountered near aphids. Some ants succeeded in biting a small chrysopid larvae and carried the struggling larva away to the nest. Many ants were required to interfere successfully with the searching and feeding activities of the larger lacewing larvae. Whenever the tending ants would attack, the larva would raise the tip of the abdomen and exude a droplet of brown liquid. The larva would then twist about trying to touch an ant with this droplet. Any ant touched by the droplet would flee from the scene. Soon all the nearby ants would gather and try to attack the larva. Many were repelled before the larva was finally driven away.

Whenever *L. neoniger* occurred in sufficient numbers, they seemed to be quite capable of protecting their tended aphids against the larger chrysopid and coccinellid larvae. However, they did not seem to recognize the Diptera larvae as intruders. These larvae were generally quite passive and ordinarily did not make excited movements when touched by the ants. These ants appeared to treat them as they would treat an aphid, tapping them with their antennae and often palpating them. These predators did not seem to be foreign to this *Lasius* species. Pontin (1959) lists two syrphid species and Chamaemyiidae and Cecidomyiidae larvae among the predators adapted to attack aphids tended by ants. Our observations support Pontin's claim that certain predators are tolerated by *Lasius* and *Formica* species.

Lasius neoniger was observed tending populations of a waxy coccid, *Planococcus citri* Risso, on chrysanthemums. Some spirea aphids were transferred to the 'mum' plants. After having settled on the plant, they were quickly seized and carried off to the nest by the ants. Within a few minutes all of the "immigrant" aphids were removed. Contradictory results were obtained when coccids were added to an aphid population on spirea. In this instance the "immigrants" were accepted by the ants which regularly solicited honeydew from them. The coccids remained on the spirea for several days. No explanation is evident for the different responses by *L. neoniger* toward these two homopteran species.

The response of *L. neoniger* to the presence of predators among tended aphids was not consistent with the observations made on other *Lasius* species. Way (1963) did not consider *Lasius* species to be especially predaceous or hostile. However, El-Ziady and Kennedy (1956) showed that *Lasius niger* carried off or drove away larvae of Syrphidae and of the coccinellid *Adalia bipunctata* Linn. but did not harm syrphid or coccinellid eggs. Adult coccinellids were also attacked by *L. niger* (Linn).

Banks (1962) confirmed that *L. niger* attacked syrphid and coccinellid larvae and drove away chrysopid larvae as well as adult and immature Anthocoridae (Hemiptera). Banks (1962) also observed the removal of eggs of syrphids and coccinellids by this species.

Conflicting with these observations are the investigations of Herzig (1938) and Pontin (1959). Herzig concluded that ants react to swift moving bodies as a threat to themselves and do not fight intruders to protect their aphids. His experiments included observations of three *Lasius* species. Pontin found aphid predators in the nests of *L. niger* and *L. flavus* (Fab.).

Formica fusca

During the early summer, syrphid, *Leucopis*, chrysopid, and coccinellid eggs were found on an aphid-infested spirea bush tended by a large colony of *Formica fusca*. However, during this period predators were rarely seen. When larvae were transferred to the bush they were attacked as soon as discovered. These larger ants swiftly bit and carried to the nest all introduced syrphid, *Leucopis*, and *Aphidoletes* larvae. All chrysopid and large coccinellid larvae were also promptly attacked. The ants were often repelled by larger chrysopids in the same manner that they discouraged *L. neoniger*. One *Formica* was repulsed by a secretion from a wounded coccinellid larva. A similar response was noted when a *Formica* which became agitated retreated from a wounded *Leucopis*. The coccinellid larvae usually escaped the attacking ants by dropping to the ground. In one instance several small coccinellid larvae were observed among the tended aphids and were not attacked. In this instance *F. fusca* behaved as *L. neoniger*.

Aside from the small coccinellids, *F. fusca* had no difficulty recognizing and dealing with aphid predators. During this period the aphid population was quite stable. The effectiveness of their protection became apparent when they abruptly ceased tending the aphids near the end of July, several days before the winged ants appeared in August. This spirea bush was rapidly colonized by the Diptera predators, a coccinellid and a debris-collecting chrysopid. Thereafter, the aphid population was shortly decimated.

In the only observed instance of egg predation, a *F. fusca* was seen devouring a chrysopid egg from a bent egg stalk.

The ants were also of benefit to the aphids by keeping them clean. In untended areas the aphids on stem tips became sticky and clogged with cast skins and debris.

The literature does not indicate that European *Formica* are formidable aphid protectors. Nixon (1951) does not provide evidence of aggressive protection by *Formica*. Pontin (1959) cites tolerance of *Coccinella divaricata* Ol. by *Formica sanguinea* Latr. *Formica rufa* Linn. is regarded by Way (1963) as only a partially successful syrphid predator.

Both ant species observed in this study appeared to exhibit some form of ownership toward the attended aphids. A *Lasius neoniger*, captured on a bush and transferred to another bush 15 feet away, was killed by the native *L. neoniger* population. A *Lasius* introduced onto the *Formica*-tended bush was also killed with dispatch.

Collateral evidence of aphid "ownership" may be inferred from the reactions of these ants to aphid predators in the absence of aphids. A large coccinellid larva was placed on the ground near the *Formica fusca* nest. It was completely ignored by the ants as it crawled on the ground. When this larva was placed on a tended branch it was promptly attacked and forced to drop to the apparent safety of the ground. Chrysopid larvae on the ground responded defensively toward *Lasius* which in turn ignored the larvae. The aggressive behavior seems to be exhibited only under conditions in which ownership of territory exists.

Undoubtedly some populations of *Aphis rumicis* prospered through the attentions of *F. fusca* and *L. neoniger*. *Formica fusca* was very effective in protecting the aphids and kept a stable population of aphids until August. *Lasius neoniger* appeared to be more erratic in tending and would desert the aphids for days. They were not nearly so effective as protectors against predators. The nature of this protection may or may not be a defense of "owned" aphids. The variability of the data presented by responsible observers certainly indicates that these interrelationships among ants, aphids, and aphid predators fluctuate. More study is needed to define the reasons for these fluctuations. Perhaps the ant species involved is chiefly responsible for the variety of effects observed in these interspecific relationships.

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REVIEWS OF RECENT LITERATURE

TRAP-NESTING WASPS AND BEES: LIFE HISTORIES, NESTS, AND ASSOCIATES. Karl V. Krombein. Washington, D.C.: The Smithsonian Institution, 1957. Smithsonian Publ. 4670. vi, 570 pp. $12.50.

The technique of "trap-nesting" for wasps and bees by putting out strips of wood having a hole bored in one end is not exactly new, but only within the last 15 years has it been widely employed in this country. This new book by Karl V. Krombein, chairman of the Department of Entomology at the U.S. National Museum, reveals how enormously productive the technique can be. It is, of course, useful only for species that normally nest in hollow twigs. Species that bore in pith (such as many crabronine wasps) do not usually accept the traps, nor do ground-nesters (which make up the majority of wasps and bees).

Despite its limitations, the trap-nesting technique is extremely valuable, as it allows one to follow the development of the cell contents closely once the nest has been split open, and also because the nests are so simple and inexpensive that it is practicable to use large numbers of them, thus obtaining information on ecology and population phenomena not available from isolated nests. The technique is also useful in summer programs for young people; there is probably no equally simple method for demonstrating some of the complexities in natural environments.

Krombein's study is based on data gained from about 3400 trap-nests put out over a 12-year period in several eastern states and Arizona. In all, he treats 75 species of wasps that accepted his traps, as well as 43 species of bees and 83 species of parasites and predators of diverse groups. Previous knowledge of these insects is reviewed, but in a great many cases nothing at all was known about them. In fact, 5 species of wasps had to be described as new from the Washington area alone, and the symbiotic mites included 2 new genera and 17 new species! If there are persons who feel that descriptive natural history has "run its course" (and there are), they should be closeted with this book for a few days.

Krombein is known for his meticulous attention to detail, and this book is no exception. It is a great compendium of facts, gathered with great