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Honeydew: an arrestant stimulus for coccinellids

M. C. CARTER and A. F. G. DIXON School of Biological Sciences, University of East Anglia, Norwich

ABSTRACT. 1. The presence and quantity of honeydew, produced by the cereal aphid, *Sitobion avenae* (Fab.), on the time *Coccinella septempunctata* L. larvae spent searching ears of wheat and on the number of aphids eaten, was investigated.

2. In the presence of honeydew larvae spent longer searching the ears, resulting in a greater exploitation of prey than in the absence of honeydew.

3. Larvae did not respond to differences in the amount of honeydew, so that the arrestment response would not result in aggregation in areas of high prey density.

Key words. Coccinellids, foraging, arrestment, honeydew, aggregation.

Introduction

In recent years the response of insect predators and parasitoids to the spatial heterogeneity of their prey has been widely studied and extensively reviewed (Curio, 1976; Hassell *et al.*, 1976; Wiens, 1976; Hassell, 1978; Hassell & Southwood, 1978). The problem facing a forager is twofold: finding patches of prey and allocating most of its foraging time to the most profitable ones.

Host finding in parasitoids typically involves an attractant stimulus that causes a parasitoid to orientate towards the source and an arrestant stimulus that causes it to reduce searching speed and/or increase turning rate, resulting in an intensive search of the area (Dethier *et al.*, 1960; Vinson, 1976; Waage, 1978). Many arrestant stimuli are contact chemicals, i.e. substances of low volatility deposited on the substrate by the host, e.g. in frass or mandibular gland secretion (Vinson, 1976; Waage, 1978).

Although an arrestment response will distinguish between areas where prey are present or absent, it will lead to aggregation in patches of high prey density only if prey density determines the concentration of arrestant stimulus and the differences in concentration can be detected by the forager. Such a response has been shown in the parasitoid *Nemeritis canescens* (Grav.) (Corbet, 1973; Waage, 1978, 1979).

In coccinellid larvae, as in many immature insect predators, however, the location of prey does not involve vision, olfaction or chemoreception but occurs only on physical contact (Fleschner, 1950; Banks, 1954, 1957; Putman, 1955; Dixon, 1959; Bansch, 1966; Kehat, 1968; Boldyrev & Wilde, 1969; Kesten, 1969; Storch, 1976). The exploitation of patchily distributed prey results from an intensive search of the area after each prey encounter (Curio, 1976; Hassell & Southwood, 1978), and has been shown theoretically (Hassell & May, 1974; Hassell, 1978) and experimentally (Carter, 1982; Carter & Dixon, 1982) to lead to aggregation in areas of high prey density.

Coccinellids, as well as other aphidophagous insects, however, have been reported

Correspondence: Professor A. F. G. Dixon, School of Biological Sciences, University of East Anglia, Norwich, Norfolk NR4 7TJ.

feeding on the sugary excretion, honeydew, of their prey (Simanton, 1916; Finney, 1948; Putman, 1955; Bogdanova, 1956; Zoebelein, 1956; Hagen, 1962). The spraying of crops with sucrose solution has also been found to increase the density of coccinellids (Ewert & Chiang, 1966; Smith, 1966), a result similar to that of increasing parasitism by the application of a contact chemical to plants in the field (Lewis *et al.*, 1972). But is honeydew a food for coccinellids or an arrestant stimulus, intensifing the search for prey? If it is an arrestant stimulus, does the amount of honeydew affect the time coccinellids spend searching a patch?

Materials and Methods

Coccinella septempunctata L. larvae were reared on the pea aphid, *Acyrthosiphon pisum* (Harris). Rearing and experiments took place at 20 ± 1°C, 70–75% r.h. and a photoperiod of 16 h.

The effect of honeydew on foraging behaviour

The foraging behaviour of forty fourth instar larvae, unfed since moulting the previous day, was investigated using defoliated wheat plants with ears approximately 6 cm long and at the milky ripe stage of development. The stems and ears were washed in warm water and when dry twenty to twenty-five apterous adults of the cereal aphid, *Sitobion avenae* (Fab.), were placed on half of the ears. After 3 days these aphids and the large number of nymphs and exuviae that had been produced were carefully removed. Coccinellid larvae were placed individually at the base of each stem and allowed to begin foraging in their own time. The time spent searching and stationary on the ears was recorded, and records were terminated when larvae had travelled 2 cm down a stem.

The quantity of honeydew and the exploitation of prey

Wheat plants at the milky ripe stage of development were again used but the ears were approximately 8 cm long and only the leaves on the upper part of the plant were removed. After washing the stems and ears in warm water, the ears were then subjected to one of three treatments in order to obtain three levels of honeydew contamination: (A) infested with twelve apterous adults of *S.avenae* for 6 days; (B) infested with four apterous adults of *S.avenae* for 6 days; (C) left uninfested for 6 days.

The adult aphids and the large number of nymphs and exuviae produced were then carefully removed and each ear infested with twenty first instar aphids. After allowing the aphids to settle overnight, fourth instar coccinellid larvae, unfed since moulting the previous day, were placed individually on the stems and allowed to search the ears in their own time. The time larvae spent on an ear, the number of aphids that walked or dropped off the ear, and the number of aphids remaining was recorded for fourteen larvae in each treatment.

The honeydew produced by the twenty first instar aphids is assumed to be negligible and treatment C was the control.

Results

The effect of honeydew on foraging behaviour

On the ears with honeydew larvae spent 2.49 ± 1.03 min (± SE) stationary, significantly longer than the 0.31 ± 0.21 min on the ears without honeydew (Mann-Whitney $U = 120.5$, $N_1 = 20$, $N_2 = 20$, $P < 0.05$). It is probable that during this time larvae were feeding on the honeydew.

Larvae also spent longer searching the ears with honeydew, spending 5.61 ± 0.71 min compared with 2.30 ± 0.36 min on clean ears ($U = 63$, $N_1 = 20$, $N_2 = 20$, $P < 0.002$). The longer time spent searching in the presence of honeydew was due to the larvae intensively searching the whole ear, including deep down between the grains where *S.avenae* is generally found. Honeydew therefore acts as an arrestant stimulus, analagous to the contact chemicals produced by the hosts of many parasitoids.

The quantity of honeydew and the exploitation of prey

The time larvae spent on an ear, the number of aphids remaining, the number that walked or dropped off, and the number eaten is shown in Table 1. Comparing the results for the three treatments showed that there was a

TABLE 1. The effect of the quantity of honeydew on the exploitation of prey. See text for description of treatments.

	Treatment A	Treatment B	Treatment C
Total time spent on the ear (min ±1 SE)*	50.58 ± 6.33	70.60 ± 11.90	25.14 ± 4.90
No. of aphids falling or walking off ±1 SE	7.4 ± 0.54	7.5 ± 0.54	7.6 ± 0.83
No. of aphids remaining ±1 SE	3.6 ± 0.80	3.6 ± 0.64	6.3 ± 1.07
No. of aphids eaten ±1 SE	9.0 ± 0.96	8.9 ± 0.74	6.1 ± 0.69
N	14	14	14

* Note that this is not the time spent searching but total time, i.e. the time spent searching, stationary and handling prey.

difference in the time larvae spent on an ear (Kruskal-Wallis H = 14.95, 2 d.f., $P < 0.001$) and in the number of aphids eaten (H = 7.51, 2 d.f., $P < 0.05$). However, when treatment A was compared with treatment B to determine the effect of the quantity of honeydew, no difference was found in the time larvae spent on an ear ($U = 78, N_1 = 14, N_2 = 14$) nor in the number of aphids eaten ($U = 94$, $N_1 = 14$, $N_2 = 14$). Thus, the quantity of honeydew did not affect the average number of aphids eaten by the larvae.

By intensively searching an ear when honeydew was present larvae found and ate a greater number of aphids than when honeydew was absent (Mann-Whitney $N > 20$, $z = 2.72$, $P = 0.003$, treatments A and B combined). The presence of honeydew did not increase the probability of encountering the first prey time, however, as even without honeydew all larvae found at least one aphid. However, there was a greater tendency for larvae to re-search an ear when honeydew was present, 46.4% of larvae turning back onto the ear on reaching the stem compared with 7.1% when honeydew was absent ($\chi^2 = 4.83$, $P < 0.025$, one-tailed test).

Discussion

In common with many invertebrate predators, coccinellid larvae search along the prominent contours of plants (Dixon, 1959; Dixon & Russell, 1972; Wratten, 1973; Evans, 1976). Combined with a positive phototactic and a negative geotactic response this behaviour tends to lead coccinellid larvae to the preferred feeding sites of their prey (Hodek, 1973). Once there, however, searching behaviour before a prey encounter was thought to be random and unrelated to the presence or absence of prey (for example, Carter & Dixon, 1982). Despite observations of coccinellids feeding on honeydew, it has not been considered as a cue for the location of prey. However, it is not only a source of food, high in nutrients (Hagen, 1958; Way, 1963), as in its presence larvae foraged more intensively.

Banks (1957) found that *Propylea quatuordecimpunctata* (L.) larvae similarly moved more slowly on honeydew contaminated bean leaves than on clean bean leaves. His interpretation that the honeydew impeded movement is unlikely, however, in view of the intensive search in the presence of honeydew observed in this study. Similarly, the olfactory detection of prey by *C.septempunctata* larvae claimed by Stubbs (1980) is more likely to be the consequence of an arrestment response following contact with the haemolymph of the crushed prey. For syrphid adults honeydew is both an arrestant and oviposition stimulus (Bombosch & St Volk, 1966).

Arrestment in response to the presence of honeydew would increase the probability of locating a clump of aphids. This was not observed in this study as even in the absence of honeydew larvae found at least one aphid. The main outcome of the response to honeydew was the increased exploitation of prey patches. This resulted from a more intensive search and a tendency for larvae to re-search a patch. However, larvae did not respond to differences in the amount of honeydew resulting from different prey densities.

In *N.canescens* a response to the concentration of arrestant stimulus enables the parasitoid to exploit hosts that are patchily distributed (Waage, 1979). Unlike coccinellids and many parasitoids (Laing, 1937, 1938; Edwards, 1954; Hokyo & Kiritani, 1966; Chabora, 1967; Gerling & Schwartz, 1974; Vinson, 1976), however, *N.canescens* does not search intensively after an encounter with a host (Waage, 1978). A simple response to the presence of an arrestant stimulus but not its concentration, such as shown by coccinellid larvae, will not lead to aggregation in areas of high prey density, but intensive search following a prey encounter does (Carter & Dixon, 1982). However, it would be interesting to know how the presence of honeydew affects the aggregative response, since the increased searching intensity in the presence of honeydew is density independent.

The response of coccinellid larvae to honeydew is similar to the response of parasitoids to the contact chemicals of their hosts. However, for larvae it is not part of a hierarchy of responses leading to the recognition and acceptance of prey, as honeydew is a general arrestant stimulus associated with any of the honeydew producing insects.

Finally, honeydew is rarely confined to the immediate vicinity of prey and in many cases falls or is thrown onto the parts of plants where prey are absent, for example the upper surface of the leaves of trees. However, by searching more intensively in areas with honeydew larvae increase their chance of finding prey.

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