

THE INFLUENCE OF APHIDS ON THE BEHAVIOUR OF ADULTS OF
THE LADYBIRD BEETLE, *HARMONIA AXYRIDIS* (COL.:
COCCINELLIDAE)

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The mechanism of prey finding by adult *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae) was investigated in the laboratory by offering beetles small gauze or polyethylene bags containing either aphid-infested leaves or uninfested leaves along with empty control bags. The beetles were attracted to bags containing aphid-infested leaves. It is suggested that adults of *H. axyridis* use olfactory and visual cues to detect prey. Mate-searching by males and the mating receptivity of females were enhanced in the presence of an abundance of aphids. The presence of aphids, perceived by the sensory organs of the beetles, possibly influence behaviour other than prey-searching.

KEY-WORDS: *Harmonia axyridis*, prey-searching behaviour, mating receptivity, mate-searching behaviour, prey detection.

Harmonia axyridis (Pallas) is one of the two most common species of aphidophagous ladybirds in Japan, and has polymorphic elytral patterns, like *Adalia bipunctata* (L.).

I have studied the adult biology of *H. axyridis*, particularly their behaviour. By observation and experiment, I have investigated its ability to detect aphids by means of olfactory and visual cues (Obata, 1986), its mating behaviour and sperm transfer by a spermatophore (Obata, 1987), its mating receptivity of females, with particular reference to internal and environmental conditions (Obata, 1988), and their distribution and behaviour in the field relative to aphid abundance (Obata & Johki, 1990). In this paper, this work is reviewed and the influence of aphids on the behaviour of adult *H. axyridis* is discussed. Apart from being prey, aphids might also be an important source of information for aphidophagous predators.

DETECTION OF APHIDS

In a laboratory experiment, the beetles were offered small gauze or polyethylene bags containing either aphid-infested leaves or healthy uninfested leaves together with empty control bags (Obata, 1986). The beetles were attracted to the bags by olfactory and visual cues indicating the presence of aphids: the odour of aphid-infested leaves, the odour of aphids, the odour of healthy leaves, and the sight of leaves. The odour of aphid-infested leaves was particularly effective in prolonging the beetles' stay on the visited bags. It is suggested that adults of *H. axyridis* use olfactory and visual cues to detect prey from a distance.

The searching behaviour of predacious coccinellids is generally assumed to be random (e.g. Dixon, 1959). But, there are some reports that suggest coccinellid beetles can perceive aphids sensually. For example, Colburn & Asquith (1970) found that adults of *Stethorus punctum* were attracted to their prey by smell, and Nakamuta (1984) reported that *Coccinella septempunctata* (L.) orientated visually towards its prey. The results of these studies and my own indicate that coccinellid beetles are able to detect their prey, at least from a short distance, by means of olfactory and/or visual cues.

INFLUENCE OF THE PRESENCE OF APHIDS ON THE BEHAVIOUR OF ADULT *H. AXYRIDIS*

Prey-searching

Hodek (1993) indicated that adult coccinellids are capable of responding to aphid odours, and asked: Why they should search at random? Based on my experiments, I explain the mechanisms of prey-searching and finding by adults of *H. axyridis* as follows. Beetles searching for aphids do not visit sites at random, but tend to visit those where aphids are likely to be present. Olfactory cues including the odour of the aphid-infested plant help the beetles to select sites to visit. Responding both to the odour of healthy leaves and to the odour of aphids can make beetles' search for prey more effective. The beetles also appear capable of utilizing visual cues such as the view of green leaves in deciding to visit a site. Banks (1955) described that few coccinellids immigrated into a field with abundant aphids, which was surrounded by woods or buildings. This fact suggests that open fields are found more easily by the beetles because of some cue, the odour, the visual appearance, etc..., of the aphid-infested plants that can be perceived by them.

Mate-searching by males

When field investigation was performed (Obata & Johki, 1990), the contagious distribution of *H. axyridis* in our study area was not satisfactorily explained solely in terms of the heterogeneity in aphid infestation. Beetles were clumped even on trees of the same grade of aphid infestation. It is highly probable that a factor other than aphid density, such as the attractiveness between males and females, also regulate the distribution pattern. A group of *H. axyridis* on a tree is usually made up of both sexes, and male-only or female-only groups are rare. Furthermore, males seldom or never stayed alone on a tree, unlike females. This distribution indicates that there is some mechanism, which results in the coexistence of both sexes on a tree. Probably it is the active attraction of males to females, and not a mutual attraction. The reason is that there are marked sex-related differences in behaviour: females usually rest or feed, while most males walk restlessly. Even if these males encountered an aphid colony, they did not attack but passed it by. The males' behaviour, fast walking in the vicinity of aphid colonies can be seen as mate-searching behaviour.

In order to attain sexual maturation the newly emerged adults of *H. axyridis* need to feed on aphids. For mature adults, however, aphids seem to have an additional significance. Under laboratory condition it was confirmed that aphid consumption by mature male coccinellids was less than the half of that of the females (Smith, 1965; Kawai, unpublished data). I think that mature males are motivated to search for females by the presence of aphids. For him, aphids suggest "there is a female around here".

Oviposition

Mature females of *H. axyridis* are less active than the males in the field when aphids are, as in the case for *C. septempunctata* (Honek, 1985). Generally, coccinellid females remain in a habitat with a high density of aphid prey, and oviposit where they are well fed. This

behaviour of females leads to their ovipositing near an aphid colony, which is advantageous for the survival of larvae (Banks, 1956; Dixon, 1959). However, is ovipositing near an aphid colony nothing but a result of the tendency of females to remain in the place where they have caught and eaten prey? For females, aphids are the cue indicating a favourable oviposition site. That is, females select oviposition sites positively, using their ability to detect the presence of aphids.

Mating receptivity of mated females

In *H. axyridis*, refusal to mate was not restricted to young virgin females but also occurred in mated females, despite this being a multiple-mating species. Mating receptivity in mated females was investigated with reference to internal and environmental conditions (Obata, 1988). Females, which were continuously fed on aphids accepted copulation every day, while females which were sometimes given honey solution rejected copulation more frequently. This suggests that mating refusal in this species is induced by unfavourable food conditions. It is possible that it is the decline in egg production under such unfavourable food conditions which causes the female to reject copulation. Dissections revealed that the acceptors had a greater number of mature eggs, whose oviposition was imminent, than the rejecting females.

The food conditions may indirectly control mating receptivity in females of *H. axyridis* through the development of mature eggs. My results also suggested that the food conditions directly controlled mating receptivity. Females laid more eggs when at least 2 days of aphid diet were included within the last 3 days, when compared with those where only 1 day of aphid diet was included. The order of diet, however, had no influence on the number of eggs: the value for HAH, HHA and AHH (A: aphid diet; H: honey diet) were almost identical. However, the rate of mating refusal was influenced by the order of diet: the rate of mating refusal of females on HAH, HHA and AHH food regimes were different from one another. It is likely that the female can detect small changes in food availability or quality by sensory cues and/or the hunger level, and thus mating receptivity is regulated. Under unfavourable food conditions, copulation represents only a loss of time and energy, because it delays the female from searching for and migrating to a new habitat. Perhaps this is the explanation for mating refusal by mated females in *H. axyridis*.

CONCLUSION

Adult *H. axyridis* is able to perceive the presence of aphids using some olfactory and/or visual cues, at least over a short distance. It seems that such an ability makes the beetles' prey-searching more effective than random search. Furthermore I assume that the presence of aphids, perceived by the sensory organs of the beetles, may influence their mating behaviour, oviposition, etc., as well as prey searching. On aphid-infested plants, males search mainly for females and may neglect aphids. Females accept copulation repeatedly and lay a number of eggs. In other words, in addition to their nutritional function aphids may be an important source of information for aphidophagous coccinellids. More investigations are required to confirm this idea, but it is a new aspect in the behaviour studies of aphidophagous coccinellids.

RÉSUMÉ

Influence des pucerons sur le comportement des adultes d'*Harmonia axyridis* (Col. : Coccinellidae)

Les mécanismes impliqués dans la découverte de la proie par des adultes d'*Harmonia axyridis* (Col. : Coccinellidae) ont été étudiés en laboratoire en présentant aux adultes de petits sacs de gaze

ou de polyéthylène contenant soit des feuilles infestées de pucerons, soit des feuilles non infestées, en même temps que des sacs témoins vides. Les coccinelles sont attirées par les sacs contenant des feuilles infestées. Il est suggéré que les adultes d'*H. axyridis* utilisent des repères olfactifs et visuels pour détecter leur proie. La recherche des femelles par les mâles et la réceptivité des femelles à l'accouplement étaient favorisées par la présence abondante de pucerons. La présence de pucerons, perçue par les organes sensoriels des coccinelles, influence probablement aussi d'autres comportements que celui de la recherche de la proie.

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