Ecological Entomology (1976) **1**, 139–142

Searching by *Adalia bipunctata* (L.) (Coleoptera : Coccinellidae) and escape behaviour of its aphid and cicadellid prey on lime (*Tilia* × *vulgaris* Hayne)

S. D. WRATTEN

Department of Applied Biology, University of Cambridge

Abstract

(1) The paper describes the behavioural interactions between searching larvae of *Adalia bipunctata* and its aphid and cicadellid prey on lime (*Tilia* × *vulgaris* Hayne).

(2) The frequency with which the predator achieves contact with cicadellid nymphs of differing ages is related to direction of predator approach and predator perception by the cicadellid.

(3) The success of a coccinellid in contacting and capturing its aphid prey is related to the predator's size and direction of approach, the perception of the predator by an aphid and the latter's ability to escape, the effectiveness of which is discussed.

Introduction

The well-developed escape responses of tree-dwelling aphids such as the sycamore aphid, *Drepanosiphum platanoides* (Schr.) and the lime aphid, *Eucallipterus tiliae* L. reduce the effectiveness of the coccinellid predators of these aphids (Dixon, 1958; Wratten, 1971). Coccinellids respond to potential prey individuals only after touching them (Hodek, 1967), whereas aphids and cicadellids usually respond to the sight of a predator also. The size of a coccinellid and its direction of approach may therefore have an important effect on the likelihood of its making contact with its prey, and on the reaction of the prey to the predator. A coccinellid catches small aphids more easily than large ones (Wratten, 1973). This is possibly a consequence of a change with age in the responsiveness of an aphid to an approaching predator. This paper investigates the influence of predator age, prey age and predator's direction of approach on the avoidance reaction of the prey and contact rate of the predator for larvae of *A.bipunctata* and its aphid and cicadellid (*Alnetoidia alneti* Dahlbom) prey on lime (*Tilia* × *vulgaris* Hayne).

Methods

Coccinellid larvae were reared as described by Wratten (1973) and were deprived of food for 24 h before each experiment. Lime aphids were cultured in summer on lime saplings in an insectary, and in winter in a glasshouse with daylight supplemented with artificial light to give a minimum daylength of 16 h. Cicadellids were collected in the field either as nymphs or, in winter, as eggs on dormant twigs; the latter were placed in moist peat under propagators in a glasshouse. Bud-burst and egg hatch occurred within 1–2 weeks of collection.

The procedure for recording prey and predator behaviour was as described by Wratten (1973). The angle of approach of the predator in relation to its potential prey was estimated and classified as occurring in the anterior 90°, posterior 90° or one or other of the two lateral 90° segments. Coccinellid larvae frequently made contact with prey items without succeeding in capturing them and all such instances were defined as 'contacts' and recorded so that they could be related to the size of the predator and prey and the direction of the predator's approach. Only the first three nymphal instars of *A.alneti* were used, as previous experiments showed that larger instars were never captured by *Adalia bipunctata* larvae (Wratten, 1973). Observations on the direction of approach of a predator and its

Correspondence: Dr S. D. Wratten, Department of Biology, Building 44, The University, Southampton SO9 5NH.

success in making contact with aphids were confined to fourth instar aphids; the responses of aphids to coccinellids were recorded for all aphid instars.

Analyses of variance were carried out on the data expressed as percentages, the reliability of which was tested in each case by comparing the results for main effects with those of a second, more reliable but less easily interpretable analysis of variance which used the logistic transformation.

Results

Frequency of coccinellid/cicadellid contact

There is an apparent trend in which small coccinellid larvae contact small cicadellid nymphs more often than large ones wheras large coccinellid larvae are most successful in contacting large nymphs (Fig. 1). The $F_{6,22}$-value for this predator age/prey age interaction does not quite reach significance ($P = 0{\cdot}08$) but the tests for main effects using logistically transformed data indicate that F-values for the percentage analyses are probably underestimates. It is likely therefore that the trend in Fig. 1 is significant. The likelihood that coccinellid larvae will contact potential cicadellid prey, averaged over the first three prey instars, declines from 18% for first instar larvae to 3% for fourth instars ($F_{3,22} = 3{\cdot}21$, $P < 0{\cdot}05$). The contention that such a trend is partly related to increasing visibility of the predator by the prey (see discussion) is supported by the trend from 1% contact achieved by the predator when cicadellids are approached from the anterior end, increasing to 13% when approached laterally and to 19% when a posterior approach is employed ($F_{2,22} = 18{\cdot}11$ averaged over predator and prey ages; $P < 0{\cdot}001$). In all cases the escape response of the cicadellid was to run, often on to the adaxial leaf surface, before settling and resuming feeding on the abaxial surface.

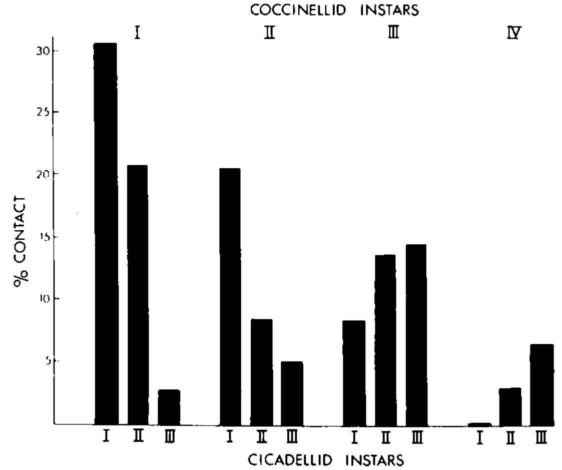

Fig. 1. Frequency with which searching larvae of *A.bipunctata* contact nymphs of the cicadellid *A.alneti*.

Frequency of coccinellid/aphid contact

The direction from which each coccinellid larval instar approached fourth instar lime aphids had a significant effect on the likelihood of predator/prey contact (Table 1, $P < 0{\cdot}001$ for each instar). There was also a significant difference in the mean contact rate between coccinellid instars averaged over direction of approach ($F_{3,6} = 7{\cdot}92$, $P < 0{\cdot}05$) and on average, coccinellid larvae were most successful when they approached aphids from the rear (Table 1; $F_{2,6} = 36{\cdot}88$ for the comparison of contact rates for the three directions of approach, averaged over all larval instars; $P < 0{\cdot}001$). There was no significant interaction, however, between predator age and contact rate ($F_{6,12} = 2{\cdot}15$, $P > 0{\cdot}05$), i.e. the percentage units change in contact rate for each direction did not differ significantly between larval instars.

Table 1. The effects of age and direction of approach of searching coccinellid larvae on the percentage of encounters with fourth instar aphids which result in predator/prey contact (see text)

	Approach direction			
Larval instar	Anterior	Lateral	Posterior	Mean
I	58	79	100	79
II	61	92	97	83
III	26	44	83	51
IV	50	66	100	72

Aphid responses to searching larvae of A.bipunctata

All lime aphid instars can respond in a variety of ways to the presence of a searching larva of *A. bipunctata* but some responses are almost wholly confined to particular aphid instars irrespective of the size of the predator which approaches them. The possible responses are: *jumping*—using the enlarged femora on the first pair of legs; *running*—the stylets are removed rapidly and the aphid runs away from the predators; *kicking*—the stylets are left in the leaf and the aphid kicks rhythmically with the hind legs, sometimes swivelling on the mouth parts at the same time. Coccinellid larvae may also fail to capture lime aphid prey when the aphid is so small relative to the predator that it passes undetected beneath the larva's head and between the tips of its fore-tarsi, usually making no movement and continuing to feed. The ability of the lime aphid to change its response according to the size of the predator which encounters it was investigated in detail for fourth instar aphids. These become increasingly likely to jump as the age of the predator larva increases (Table 2; $F_{3,3} = 36{\cdot}96$ for the comparison of jumping frequency for the four larval ages, averaged over contact/no contact, $P < 0{\cdot}01$). There is a parallel trend in which the frequency of running declines as predator size increases, but this trend is not significant ($F_{3,3} = 3{\cdot}48$, $P > 0{\cdot}05$). It is notable that the frequency with which fourth instar aphids jump in response to the four coccinellid larval instars was similar when tested under the same conditions but in different places and with different aphid and coccinellid cultures (Table 2 (Cambridge) and Fig. 2 (Glasgow)).

Table 2. Effects of the age of searching coccinellid larvae on the percentage frequency of jumping and running by fourth instar aphids which they encounter (see text)

	Percentage of aphids	
Larval instar	Jumping	Running
I	36	48
II	69	28
III	87	12
IV	77	23

The ways in which all aphid instars avoid capture by coccinellid larvae are summarized in Fig. 2, which also includes the frequency with which passive avoidance occurred, i.e. situations where larvae walked over their potential prey. Kicking occurred only in response to first and second instar larvae, and passive avoidance was rare for aphid instars larger than the third. The frequency of running and jumping also appeared to reflect the size ratio and relative speeds of predator and prey, in that running occurred most frequently when the predator was

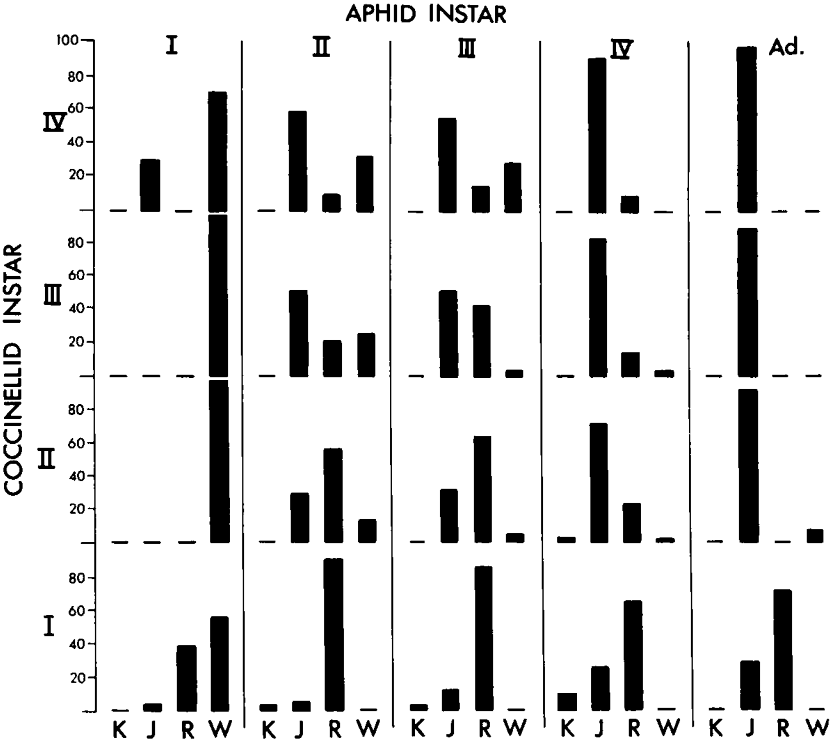

Fig. 2. The frequency of the responses by which nymphal and adult viviparous lime aphids avoid capture by searching coccinellid larvae of four instars. K = kicking; J = jumping; R = running; W = walked over (see text).

small relative to the aphid whereas jumping was used most frequently as a means of avoiding large larvae.

Discussion

Because of its low density in the field and efficient means of escape, the cicadellid *Alnetoidia alneti* forms a negligible proportion of the prey of *A. bipunctata* on lime and the coccinellid exerts no significant influence on the cicadellid's numbers (Wratten, 1973). Although few cicadellids are caught, coccinellid larvae which approach from the rear are more likely to contact (and presumably capture) the cicadellid nymphs. However, there appears to be no way that either predator or prey can exploit this tendency, as the predator was unaware of the presence of its prey until contact had occurred, and it was not consistent in the relative direction from which it approached the cicadellid. Larger instars of *A.bipunctata* move more rapidly than small ones (Wratten, 1973) but this advantage is offset by their conspicuousness to the aphids. The fact that first instar coccinellids were most successful in contacting cicadellid prey while third instars had the highest capture efficiency, suggests that capture success rate is an interaction between the relative speed of movement of predator and prey, predator visibility (related to larval size), and some other factor such as rapidity of predator response following prey contact. Third instar larvae appear to have the best combination of these conflicting characteristics. In this context, the shape, shininess and coloration of adults of *Adalia decempunctata* (L.) were considered by Dixon (1959) to be the main reasons why the efficiency of capture by adults lay between that of second and third instar larvae.

Although the lime aphid depends more on physical contact than on vision as the stimulus for predator avoidance behaviour, coccinellid larvae still achieve the highest contact rate when they approach fourth instar aphids from the rear (Table 1), suggesting that vision is also important in predator avoidance in the lime aphid.

Feeding aphids normally hold their antennae directed backwards, suggesting that a predator approaching from the front is detected by visual rather than antennal means.

The lime aphid's jumping response occurred most often against large coccinellid larvae; although always effective, irrespective of predator size, it involves a risk to the aphid, which has no control over where it will land. Running involves less risk but would be less effective against a larger and faster predator. Kicking does not even involve cessation of feeding but was only observed when aphids were approached by small larvae; larger instars would be undeterred by this response.

Capture rates of a particular aphid instar by large and small coccinellid larvae were often similar when the ratio of the frequency of the two main responses, jumping and running was reversed. This suggests that a change in the proportion of aphids responding by running was due to a change in the aphids' behaviour related to increasing predator size, and not because larger coccinellid larvae capture more aphids that run.

In common with many other monoecious, arboreal aphids, *Eucallipterus tiliae* does not form dense aggregations on the leaves of its host plant, and this behaviour, together with its varied and labile predator escape responses, helps to ensure the population's survival in the face of predation pressure which can sometimes be intense.

Acknowledgments

The above work was carried out in the Department of Zoology, University of Glasgow, where it was financed by an N.E.R.C. Research Studentship, and in the Department of Applied Biology, University of Cambridge. I am grateful to P. M. Lerman for valuable statistical advice and to Professor A. F. G. Dixon for useful comments.

References

DIXON, A.F.G. (1958) The escape responses shown by certain aphids to the presence of the coccinellid *Adalia decempunctata* (L.). *Trans. R. Ent. Soc. Lond.* **110,** 319–334.

DIXON, A.F.G. (1959) An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). *J. Anim. Ecol.* **28,** 259–281.

HODEK, I. (1967) Bionomics and ecology of predacious Coccinellidae. *A. Rev. Ent.* **12,** 79–104.

WRATTEN, S.D. (1971) The role of the predatory coccinellid beetle, *Adalia bipunctata* (L.) in regulating the numbers of the lime aphid, *Eucallipterus tiliae* L. Unpublished Ph.D. thesis, University of Glasgow.

WRATTEN, S.D. (1973) The effectiveness of the coccinellid beetle *Adalia bipunctata* (L.) as a predator of the lime aphid, *Eucallipterus tiliae* L. *J. Anim. Ecol.* **42,** 785–802.

Received 12 November 1975