

Behavioral interactions between three birch aphid species and *Adalia bipunctata* larvae

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Abstract

First and fourth instars of three birch aphid species were exposed to first and fourth instars of *Adalia bipunctata* (L.), the most common aphid predator on silver birch, *Betula pendula* Roth, in northern California. Defensive behavior differed by aphid species. *Euceraphis betulae* (Koch) (Eb), the most successful escapee, was highly mobile and frequently walked away from coccinellid larvae. *Betulaphis brevipilosa* Börner (Bb), a flat, sessile species, was the least successful aphid at actively escaping from *A. bipunctata* larvae, but could passively escape detection when coccinellid larvae walked over nymphs and did not perceive them. Active escape behavior was much safer for aphids than passive avoidance of detection. Both instars of Eb and fourth instars of *Callipterinella calliptera* (Hartig) (Cc) escaped from coccinellid larvae more frequently when approached from the front, apparently using vision for pre-contact detection of *A. bipunctata*. These aphids avoided physical contact with larger predators more often than with smaller predators. Level of predation by *A. bipunctata* on these three aphid species is dependent upon types of aphid defense.

Introduction

A critical attribute of a natural enemy that regulates prey populations is good searching ability (DeBach, 1974). Many predacious members of the Coccinellidae are important natural enemies of aphids and the searching behavior of several species has been studied (e.g., Dixon, 1959; Kaddou, 1960; Brown, 1972). To evaluate potential capture of prey species, however, defensive behavior of the prey must be investigated along with the predator's searching ability. Aphid defensive behavior in response to coccinellids has been examined in detail for *Schizaphis graminum* (Rondani) (Brown, 1974), *Microlophium evansi* (Theobald) (Dixon, 1958), *Eucallipterus tiliae* L.

(Wratten, 1976), *Acyrtosiphon pisum* (Harris) (Klingauf, 1967; Brodsky & Barlow, 1986), and *Myzus persicae* (Sulzer) and *Neomyzus circumflexus* (Buckton) (Klingauf, 1967). In only two of these studies (Klingauf, 1967; Wratten, 1976), coccinellid searching was evaluated simultaneously with aphid defensive behavior.

Prey behavior in response to coccinellid presence is especially important since coccinellid larvae do not recognize prey visually (Hagen, 1962; Hodek, 1967). Olfactory cues may be used for prey detection although this has only been demonstrated for crushed prey (Stubbs, 1980). *A. bipunctata* is thought to recognize prey only when palpal contact is made or when an aphid is contacted with the tips

of the foretarsi (Wratten, 1973). Therefore, prey that can avoid physical contact may escape capture.

In northern California, three aphid species (*Betulaphis brevipilosa* (Bb), *Callipterinella calliptera* (Cc) and *Euceraphis betulae* (Eb)) are frequently abundant on silver birch trees, *Betula pendula*. These aphid species vary in size, morphology and life history. The most common natural enemy of aphids on *B. pendula* is the polyphagous coccinellid, *Adalia bipunctata* (Hajek & Dahlsten, 1986). Feeding studies have shown that *A. bipunctata* larvae can mature on diets of each of these aphid species (Hajek, unpubl. data). During extensive field studies, it was noted that birch aphids are by far the most abundant potential prey for *A. bipunctata* larvae on birch trees (Hajek, 1984). Thus, these three aphid species constitute the major food source for coccinellid larvae on birches. It was hypothesized that the great variation in behavior exhibited by these aphids would differentially impact predation rates. This study compares the interactions between aphid defensive behavior and capture success of *A. bipunctata* larvae for these three aphid species.

Materials and methods

Petioles of freshly cut, field-collected leaves of *B. pendula* were tightly wrapped with cotton and placed in water-filled vials (1×4 cm). Laboratory experiments were conducted during August and September, 1983 with freshly-collected aphids from Albany and Berkeley, California. From 17 to 20 first instar (L1) or fourth instar (L4) individuals of Eb, Cc or Bb were transferred to each leaf and allowed to settle for at least 30 minutes before testing. Similar numbers of Cc and Bb were used although only five to eight L4 Eb were placed on each leaf. First instars of each species are approximately equal in size although L4 Eb are roughly three times larger than L4 of the other two species. Therefore, the areas of leaf covered by aphids of each species and instar tested were approximately equivalent in each trial. L4 Eb were the only group of aphids tested which walked off of leaves during trials since these aphids are extremely mobile. When this happened, they were picked up with a fine brush (#000) and replaced on leaves.

Larvae of *A. bipunctata* were reared from eggs collected in Berkeley and Albany, California or from eggs laid by field-collected adults. All larvae were fed *A. pisum* or Cc depending on the availability of these aphids. L1 and L4 coccinellids had hatched or molted, respectively, the day before their searching was observed. L1 coccinellids were starved for 6 to 8 hours and L4 coccinellids were starved for at least 24 h before being tested.

All searching trials were done in the laboratory (21 to 24 °C) and behavior was observed using a 10 × hand lens. During preliminary studies, it was found that coccinellid searching time per capture increased if leaves had previously been successfully searched by another coccinellid larva. Larvae of *Coccinella septempunctata* L. have also been reported as searching for longer periods in areas where an aphid had previously been captured, as well as searching for shorter intervals in unsuccessfully searched areas (Marks, 1977). Therefore, leaves used for trials were collected from trees apparently lacking coccinellids, based on cursory examination, and each leaf was only used once.

Twenty trials, each using a different coccinellid larva, were observed for each combination of L1 or L4 of each of the three aphid species (Eb, Cc, and Bb) with L1 or L4 *A. bipunctata* (total = 240 trials). Each trial began when a coccinellid larva was placed in the center of a leaf and ended with one of three events: one successful capture, 20 attacks by coccinellid larvae, or the passage of 15 min. At the end of each trial during which a capture was not made, the larva being tested was fed an aphid to ascertain that it had been hungry.

An "encounter" was recorded when a potential prey individual occurred in the direct path of a moving coccinellid larva and either the coccinellid or aphid altered its behavior or physical contact was made. An "attack" was recorded when a coccinellid exhibited intensified searching. Trial duration, physical contact between coccinellid and aphid, and outcome of encounters (escape or capture) were recorded for each trial. The angle of approach of the coccinellid was recorded (front or rear), as illustrated by Dixon (1958), since evidence suggests that some aphid species can detect the approach of coccinellids from the front but not the rear (Dixon, 1958; Wratten, 1976). As illustrated by Dixon (1958), aphids can

potentially use vision to detect predators approaching from the front or side. During feeding, antennae of aphids, which contain many chemoreceptors, are extended caudally, so antennal perception of anteriorly approaching predators was unlikely.

Active aphid defensive behavior was recorded as walking away, dropping from the leaf, pulling away or kicking. Dixon (1958) and Brown (1974) described these defenses although the kicking response recorded in this study is a combination of kicking and bucking as defined by Brown (1974). The associations of capture rate with passive and active escapes were calculated using arcsine transformations to normalize the percentages (Steel & Torrie, 1980). Associations were compared using a t-test for detection of significant differences between two non-independent r 's (Edwards, 1973).

Results

The outcome of total encounters between aphids and coccinellid larvae provides a comparison of these three aphid species as prey for *A. bipunctata* larvae (Table 1). Use of mobility by Eb and L4 Cc clearly provided protection from capture. The numbers of encounters were greatly increased for these mobile aphids, but only low percentages of encounters ended in capture (Table 1). In the extreme, no L4 Eb were captured by L1 *A. bipunctata*. The greater mobility of Eb even allowed this species to walk over coccinellid larvae usually without being perceived.

In many instances, an *A. bipunctata* larva walked directly over a stationary aphid but did not exhibit

intensified searching behavior. Such passive escapes by both Bb and Cc provided a high degree of protection, especially for Bb (Table 1). Coccinellids walking over aphids were recorded in over 50% of encounters between Bb and *A. bipunctata* when larvae differed in instar, and therefore, size. However, all trials for Bb and Cc always ended in capture and, summing all instar combinations, Bb was captured most quickly and Eb was captured most slowly (t-tests; $p \leq 0.05$). Capture efficiency (captures/encounters) had a positive association with passive escapes ($r = 0.75$) and a negative association with active escapes ($r = -0.82$). Comparing the capture efficiency associated with these two types of escapes, active escapes are clearly safer for aphids than passive escapes ($t = 4.216 \geq t_{9,0.05}$).

The percentages of captures per encounter for L4 *A. bipunctata* were always greater than for L1 *A. bipunctata* (χ^2 ; $p \leq 0.05$) except against the very active L4 Eb. Wratten (1973) showed that the area traversed per time by L4 *A. bipunctata* is roughly 20 times greater than the area covered by L1s. The disparity in capture times between different coccinellid larval instars (e.g., L1 *A. bipunctata*/L4 Cc = 5.00 min. \pm 1.01 SE; L4 *A. bipunctata*/L4 Cc = 0.36 min. \pm 0.10 SE) could easily be explained by differences in the areas which were searched. In all instances, L1 aphids were captured more frequently than L4 aphids (χ^2 ; $p \leq 0.05$).

When aphid escape behavior was elicited, the most frequent type of behavior was walking away from coccinellid larvae. Among only L4 Eb, aphids frequently continued walking and proceeded down the petiole and off of the leaf after an encounter with

Table 1. Results of encounters between three species of birch aphids (Bb, Cc, Eb, see text) and larvae of *Adalia bipunctata*.

	L1 <i>Adalia bipunctata</i>					L4 <i>Adalia bipunctata</i>				
	Total encounters	% Captures	% Active escapes	% Passive escapes	% Aphid over coccinellid	Total encounters	% Captures	% Active escapes	% Passive escapes	% Aphid over coccinellid
L1 Bb	33	60.6	0.0	39.4	0.0	65	30.8	1.5	67.7	0.0
L4 Bb	56	35.7	8.9	55.4	0.0	38	52.6	0.0	47.4	0.0
L1 Cc	51	39.2	41.2	19.6	0.0	33	60.6	9.1	30.3	0.0
L4 Cc	214	8.4	71.5	20.1	0.0	66	30.3	60.6	9.1	0.0
L1 Eb	216	6.9	75.5	0.0	17.6	104	19.2	78.8	1.0	1.0
L4 Eb	260	0.0	71.5	0.0	28.5	375	1.9	82.6	0.0	15.5

a coccinellid (L1 Ab=93.01%; L4 Ab=23.42%). Very low percentages of L4 Cc and L1 Eb approached by L1 *A. bipunctata* dropped off leaves. L4 Eb dropped from leaves more frequently after encountering a coccinellid (L1 Ab = 8.60%; L4 Ab = 8.54%) while only one L1 Eb dropped from a leaf. A kicking response was very weakly developed in L4 Cc and L1 Eb although it was used by L4 Eb against L1 *A. bipunctata* in 11.15% of encounters.

One-third of captures of L4 Cc by L1 coccinellids were initiated by grabbing an aphid's leg. The coccinellid larvae tenaciously held onto the aphids which tried to pull away, and, in all cases, the predator eventually ate the entire aphid. In the instances when L1 *A. bipunctata* caught Eb nymphs, a leg or rostrum of an L4 aphid was grasped. L1 *A. bipunctata* did not hold L4 Eb long before the aphids simply pulled away with no evidence of impairment.

The angle at which coccinellid larvae approached aphids had an impact on aphid capture or escape, but this differed by aphid species. Both instars of Bb seldom displayed active evasive behavior regardless of the approach angle, although coccinellid larvae captured both instars of Bb more often when approaching them from the rear (Table 2). Passive escape may have been aided by vision, with aphids remaining stationary as a coccinellid larva walked over them.

The angle of coccinellid approach did not influence behavior of L1 Cc (Table 2). By contrast, approach from the front frequently resulted in successful escape of L4 Cc from L1 *A. bipunctata* ($p \leq 0.05$), and increased captures occurred with approach from the rear (Table 2). Both instars of Eb escaped more frequently from both coccinellid instars when approached from the front ($p \leq 0.05$) and all captures of L4 Eb occurred when approach was from the rear. These results suggest that visual perception aids Cc and Eb in escape behavior.

Active aphid escapes occurred both with and without coccinellid contact, although this varied by aphid species and instar and coccinellid instar. Bb seldom actively escaped from coccinellid larvae. For Cc, over 65% of encounters for each instar required physical contact with the small L1 coccinellid larvae before aphids walked away (Table 3). Although L1 Cc did not demonstrate use of vision for escape, old-

Table 2. Effect of approach angle on capture of three birch aphid species by *Adalia bipunctata* larvae.

	L1 <i>A. bipunctata</i>		L4 <i>A. bipunctata</i>	
	No. active escapes	No. captures	No. active escapes	No. captures
L1 Bb				
Front	0	3	0	2
Rear	0	9	0	9*
L4 Bb				
Front	2	3	0	6
Rear	1	9	0	10
L1 Cc				
Front	4	5	0	5
Rear	7	5	0	5
L4 Cc				
Front	50	5	8	3
Rear	28*	9	6	9
L1 Eb				
Front	54	4	20	5
Rear	31*	6	17	4
L4 Eb				
Front	56	0	100	0
Rear	32*	0	52*	7*

* χ^2 test used to compare front vs. rear approach. Significant at $\alpha = 0.05$.

er aphids may see coccinellids (Table 2) but do not avoid coccinellid larvae before contact. L4 Cc avoided L4 predators in most encounters before being physically contacted (Table 3). Approached by a large, fast-moving coccinellid larva, these L4 aphids usually walked away before contact.

Table 3. Relation between physical contact with attacking *Adalia bipunctata* larvae and active escapes by birch aphid nymphs.

	L1 <i>A. bipunctata</i>		L4 <i>A. bipunctata</i>	
	Total active escapes	% escapes after contact	Total active escapes	% escapes after contact
L1 Bb	-	-	5	40.0
L4 Bb	1	100.0	-	-
L1 Cc	21	76.2	3	66.7
L4 Cc	163	66.7	40	17.5
L1 Eb	163	76.1	82	58.5
L4 Eb	196	79.1	309	53.4

Escapes of both instars of Eb from L1 coccinellid larvae occurred after contact in over 75% of encounters (Table 3). Behavior changed toward L4 *A. bipunctata*, since less than 60% of Eb escapes occurred after contact with coccinellid larvae.

Discussion

Aphid defensive behavior. Three species of sympatric aphids, all common on *B. pendula* in northern California, exhibit very different adaptations and behavior which enhance escape from *A. bipunctata*. The extreme mobility of the long-legged Eb and the perception of predators by this species make capture of this aphid very time- and energy-consuming for both instars of coccinellids tested. Both instars of Eb were able to perceive the approach of coccinellids, probably a visual response, and thus avoid contact with predators when necessary. Klingauf (1967) noted that aphids can perceive prey from 4–10 mm away giving them an advantage over predators that are dependent on tactile stimulation. The long legs of Eb enhance its mobility and may also provide an early warning system for this aphid species, as suggested by Kaddou (1960) and Brown (1974). In addition, aphids may respond to plant vibration and coccinellid beetles can cause plant vibration when foraging vigorously (Brodsky & Barlow, 1986). Plant vibration is known to heighten the response of *A. pisum* to alarm pheromones (Clegg & Barlow, 1982).

Eb used the most active avoidance behavior observed among the aphids studied; walking away, kicking, dropping and pulling away. Dropping from plants is a fairly common behavior among aphids (Dixon, 1958; Niku, 1975) but is not without risk. Among *A. pisum*, young instars that dropped from herbaceous plants frequently could not find host plants again (Roitberg *et al.*, 1979). The dropping response was more highly developed in older than younger Eb, agreeing with the interpretation that dropping from the plant is riskier for smaller aphids. Bb and Cc, smaller and less mobile aphids, generally did not drop from birch leaves to escape predation.

Cc was not as efficient at avoiding capture as Eb. Cc seldom kicked predators or dropped from leaves, although predators were often sensed by aphids

without contact and aphids usually just walked away from them. Nevertheless, both aphid instars were readily captured by L4 coccinellids.

In contrast, the sessile Bb displayed virtually no active defensive behavior. This aphid species escaped capture predominantly through passive avoidance; by not being perceived when coccinellids walked over them. Cc exhibited passive escape to a lesser extent and this type of escape has also been noted from *E. tiliae* (Wratten, 1976). The flat shape of Bb helps make passive avoidance behavior possible. Whether Bb actually uses vision to passively escape is unknown; since there is no measurable reaction, it is impossible to know whether a stationary aphid sees an approaching coccinellid larva. Protection of Bb through passive avoidance was not as successful as the active escape behavior of Eb and Cc. Coccinellid larvae still found and captured Bb most readily of the three aphid species.

In Denmark, where Bb is native, it is not ant tended, and Eb is never tended (Heie, 1982). By contrast, in both California and Denmark, Cc is often tended by ants (Heie, 1972; Hajek, 1984). Myrmecophilous aphid species are known to display weak defensive behaviors that act to decrease dispersal (Nault *et al.*, 1976). Cc displayed a limited defensive behavior as would be characteristic of a myrmecophile. Protection by ants would clearly add to the intermediate level of defense exhibited by Cc. It is inconsistent with previous suggestions regarding defensive behavior of myrmecophilous aphids (Nault *et al.*, 1976) that Bb utilized an even less active defensive behavior but is not ant tended.

Dixon (1958) suggested that "aphids exhibit two main trends in the evolution of their behavior in relation to enemies." One trend describes Eb well, with cryptically colored, active aphids, occurring in diffuse colonies and avoiding natural enemies. The second trend describes inactive species which are myrmecophilous and often conspicuously colored. These aphids usually feed in dense colonies, may be unpalatable or toxic and some use siphuncular wax for defense. Cc fits well in this category. Although it is not always inactive, it is ant tended in California, conspicuously colored and occurs in dense colonies. Bb does not fit exactly into either category but provides an example of a third trend, these aphids using

cryptic form and habit to escape predation. Although Bb is inactive and forms dense colonies, a major defense of this species seems to lie in its flat morphology, sessile behavior, and leaf-like coloration. Aphids are a very diverse family and further trends in defensive behavior, predominantly including aggression, have also been described (see Dixon, 1985).

Coccinellid searching behavior and capture efficiency. Coccinellid larvae do not select prey species but appear to attack what they encounter and sense (Blackman, 1967; Murdoch & Marks, 1973). Attempts to train coccinellids to search for specific food sources have been unsuccessful (Murdoch & Marks, 1973). It seems unlikely then that *A. bipunctata* larvae would specialize in capturing Bb, the most easily captured aphid, and switch to the other two aphid species when Bb density decreased. Apparently, coccinellid larvae consume those aphid individuals which are randomly encountered (usually from the rear) and easily captured. Survival of *A. bipunctata* larvae most likely depends on aphid density and aphid species composition. All three aphid species studied exhibit a patchy distribution both within and between trees in urban, northern California (Hajek, 1984). A birch tree inhabited only by Eb might not support a population of *A. bipunctata* due to the superior defensive behavior of this aphid.

Survival of first instars has often been considered a limiting factor in establishment of coccinellid populations (Banks, 1954; Dixon, 1970; Wratten, 1973). L1 *A. bipunctata* experienced much more difficulty in capturing aphids than L4 *A. bipunctata*, a situation observed in other coccinellid species (Dixon, 1959; Brown, 1972; Wratten, 1976). However, L1 can survive on alternate foods, frequently cannibalizing the unhatched eggs of their siblings. *A. bipunctata* can even develop to adulthood feeding solely on coccinellid eggs (Dimetry, 1974). L1 *A. bipunctata* must consume aphids when coccinellid eggs are not abundant on birch trees. L1 *A. bipunctata* would have difficulty surviving on a tree with only older individuals of Eb and L4's would also experience difficulty capturing Eb. Bb and Cc were readily captured by both ages of coccinellids and

thus provide an accessible food supply for L1 coccinellids. However, ant attendance of Cc may limit the ability of *A. bipunctata* to capture this aphid species. Survival of coccinellid populations may depend on oviposition by *A. bipunctata* adults on trees where adequate populations of Bb and/or Cc are available for development of young coccinellid larvae.

Clearly, predator-prey relationships between coccinellids and aphids are influenced by relative ages of predator and prey, presence of ants or alternative prey, and those defenses utilized by aphid prey.

Résumé

Interactions entre les comportements de trois espèces de pucerons du bouleau et celui des larves d'Adalia bipunctata

Des larves de premier et troisième stades de 3 espèces de pucerons du bouleau: *Betulaphis brevopilosa*, *Callipterinella calliptera* et *Euceraphis betulae* ont été exposées aux attaques des larves du premier et du quatrième stades d'*Adalia bipunctata*, prédateur le plus fréquent de pucerons sur *Betula pendula* en Californie du Nord. Le comportement défensif dépend beaucoup de l'espèce de puceron. *E. betulae*, qui s'échappe avec le plus de succès, est très mobile et s'écarte fréquemment des larves agressives de coccinelles. *B. brevopilosa*, espèce plate, sessile, a le moins de succès dans la protection active contre les attaques des larves de *A. bipunctata*, mais elle peut échapper passivement à la détection des larves de coccinelles qui ne peuvent pas les discerner lorsqu'elles circulent parmi les larves de pucerons. *E. betulae* (aux deux stades) et *C. calliptera* (au quatrième) échappent le plus aux larves de coccinelles qui attaquent de front, ce qui laisse supposer que la vision permet de détecter *A. bipunctata* avant le contact. Le succès des larves de coccinelles varie selon les stades du puceron et de la coccinelle. Les possibilités d'obtention de niveaux de prédation élevés de ces 3 pucerons par *A. bipunctata* dépend du type de protection du puceron.

References

- Banks, C. J., 1954. The searching behaviour of coccinellid larvae. *Brit. J. Anim. Behav.* 2, 37–38.
- Blackman, R. L., 1967. Selection of aphid prey by *Adalia bipunctata* L. and *Coccinella 7-punctata* L. *Ann. appl. Biol.* 59: 331–338.
- Brodsky, L. M. & C. A. Barlow, 1986. Escape responses of the pea aphid, *Acyrtosiphon pisum* (Harris) (Homoptera: Aphididae): influence of predator type and temperature. *Can. J. Zool.* 64: 937–939.
- Brown, H. D., 1972. Predacious behaviour of four species of Coccinellidae (Coleoptera) associated with the wheat aphid, *Schizaphis graminum* (Rondani), in South Africa. *Trans. R. Entomol. Soc. Lond.* 124: 21–36.
- Brown, H. D., 1974. Defensive behaviour of the wheat aphid, *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae), against Coccinellidae. *J. Entomol. (A)* 48: 157–165.
- Clegg, J. M. & C. A. Barlow, 1982. Escape behaviour of the pea aphid *Acyrtosiphon pisum* (Harris) in response to alarm pheromone and vibration. *Can. J. Zool.* 60: 2245–2252.
- DeBach, P., 1974. *Biological Control by Natural Enemies*. Cambridge Univ. Press. London: 323 pp.
- Dimetry, N., 1974. The consequences of egg cannibalism in *Adalia bipunctata* (Coleoptera: Coccinellidae). *Entomophaga* 19: 445–451.
- Dixon, A. F. G., 1958. The escape responses shown by certain aphids to the presence of the coccinellid *Adalia decempunctata* (L.). *Trans. R. Entomol. 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.
- Dixon, A. F. G., 1970. Factors limiting the effectiveness of the coccinellid beetle, *Adalia bipunctata* (L.), as a predator of the sycamore aphid, *Drepanosiphum platanooides* (Schr.). *J. Anim. Ecol.* 39: 739–751.
- Dixon, A. F. G., 1985. *Aphid Ecology*. Blackie. Glasgow: 157 pp.
- Edwards, A. L., 1973. *Statistical Methods*, 3rd Edition. Holt, Rinehart & Winston, Inc. New York: 312 pp.
- Hagen, K. S., 1962. Biology and ecology of predaceous Coccinellidae. *Ann. Rev. Entomol.* 7: 289–326.
- Hajek, A. E., 1984. The population ecology of three aphid species on *Betula pendula* Roth in northern California. Unpublished Ph.D. Thesis, University of California, Berkeley.
- Hajek, A. E. & D. L. Dahlsten, 1986. Regulation of aphids on European white birch in northern California by natural enemies. In: I. Hodek (ed.), *Ecology of Aphidophaga*, II. Academia, Prague & Junk, Dordrecht: 391–396.
- Heie, O. E., 1972. Bladlus på birk i Danmark (Hom., Aphidoidea). *Entomol. Meddr.* 40: 81–105.
- Heie, O. E., 1982. The Aphidoidea (Hemiptera) of Fennoscandia and Denmark. II. The Family Drepanosiphidae. *Scand. Sci. Press. Klampenborg, Denmark*: 176 pp.
- Hodek, I., 1967. Bionomics and ecology of predaceous Coccinellidae. *Ann. Rev. Entomol.* 12: 79–104.
- Kaddou, I. K., 1960. The feeding behavior of *Hippodamia quinquesignata* (Kirby) larvae. *Univ. Calif. Publ. Entomol.* 16: 181–232.
- Klingauf, F., 1967. Abwehr- und Meidereaktionen von Blattläusen (Aphididae) bei Bedrohung durch Rauber und Parasiten. *Z. angew. Entomol.* 60: 269–317.
- Marks, R. J., 1977. Laboratory studies of plant searching behavior by *Coccinella septempunctata* L. larvae. *Bull. Ent. Res.* 67: 235–241.
- Murdoch, W. W. & R. J. Marks, 1973. Predation by coccinellid beetles: experiments on switching. *Ecology* 54: 160–167.
- Nault, L. R., M. E. Montgomery & W. S. Bowers, 1976. Ant-aphid association: role of aphid alarm pheromone. *Science* 192: 1349–1351.
- Niku, B., 1975. Verhalten und fruchtbarkeit ungeflugelter erbsenläuse (*Acyrtosiphon pisum*) nach einer fallreaktion. *Ent. exp. appl.* 18: 17–30.
- Roitberg, B. D., J. H. Myers & B. D. Frazer, 1979. The influence of predators on the movement of apterous pea aphids between plants. *J. Anim. Ecol.* 48: 111–122.
- Steel, R. G. D. & J. H. Torrie, 1980. *Principles and Procedures of Statistics: A Biometrical Approach*, 2nd Edition. McGraw-Hill. New York: 633 pp.
- Stubbs, M., 1980. Another look at prey detection by coccinellids. *Ecol. Entomol.* 5: 179–182.
- Wratten, S. D., 1973. The effectiveness of the coccinellid beetle, *Adalia bipunctata* (L.), as a predator of the lime aphid, *Eucalyppterus tiliae* L. *J. Anim. Ecol.* 42: 785–792.
- Wratten, S. D., 1976. Searching by *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae) and escape behaviour of its aphid and cicadellid prey on lime (*Tilia × vulgaris* Hayne). *Ecol. Entomol.* 1: 139–142.