THE ESCAPE RESPONSES SHOWN BY CERTAIN APHIDS TO THE PRESENCE OF THE COCCINELLID *ADALIA DECEMPUNCTATA* (L.)

By A. F. G. Dixon

(*Hope Department of Entomology, University of Oxford**)

[Communicated by Professor G. C. Varley]

Manuscript received 6th March, 1958

(Read 7th May, 1958)

With 4 Text-figures

Contents

I. Introduction

The general impression conveyed by the literature on aphids and their predators is typified by Imms (1947 : 129) who, in considering the prey of ladybird beetles, states " This consists of Aphids and related small insects which are all helpless sedentary and thin-skinned creatures that almost seem to invite the attention of any predator that comes along."

That aphids have defensive mechanisms has nevertheless been known since 1891, when Büsgen reported that several different species of aphid exuded an oily liquid from their siphunculi, which they smeared on to the head of an attacking predator, from which they then escaped. Furthermore, Davis (1914),

* Now at the Department of Zoology, University of Glasgow.

working on *Callipterus trifolii* Mon., and Haine (1955), working on *Drepanosiphum platanoides* (Schrk.), found that these aphids, when disturbed, readily leap from the plant on which they have been feeding, and both Davis and Haine concluded that the aphids could escape from certain of their parasites and predators by this means.

Larvae of the predatory coccinellid beetle *Adalia decempunctata* (L.) apparently respond to the presence of the nettle aphid *Microlophium evansi* (Theobald) only after touching it with the head or fore limbs. The necessity for physical contact with the prey, before recognition, has also been observed in *Stethorus picipes* Casey (Fleschner, 1950) and *A. bipunctata* (L.) (Banks, 1957). Although other species respond to form (Tischler, 1936) and movement (Gaffron, 1934), adults of *A. decempunctata* require actual palpal contact with prey before showing a response.

The present account is concerned with the behaviour of aphids when encountered by a coccinellid. The results were obtained during a study of the searching behaviour of *A. decempunctata* (to be published elsewhere).

II. Culturing Techniques

The nettle aphid was cultured on nettle plants (*Urtica dioica* L.) grown from rhizomes collected in the field. From these aphids of a suitable instar were removed for experimental use as required. Table I gives the mean length of individuals of each instar, the measurement taken being the distance from the base of the antennae to the base of the cauda. Rearing of individuals showed that assessment of instars according to size and general appearance is accurate. The relative sizes of each instar of aphid and coccinellid are shown in figure 1.

Table I.—*The average length of individuals of each instar of* Microlophium evansi.

Instar	Number of aphids measured	Average length of individuals (mm.)
First	200	$0\cdot87\pm0\cdot01$
Second	100	$1\cdot35\pm0\cdot02$
Third	102	$1\cdot71\pm0\cdot02$
Fourth	100	$2\cdot26\pm0\cdot02$
Adult	100	$2\cdot45\pm0\cdot02$

Larvae of *A. decempunctata* were obtained from eggs laid by adults which had been collected in the field and allowed to mate in the laboratory. Larvae and adults were each kept in individual 7·5 cm. × 2·5 cm. vials filled to a depth of 1·25 cm. with plaster of Paris and stoppered with a plug of cotton wool wrapped in muslin. The plaster of Paris was moistened every three days to maintain a relatively high humidity. To facilitate the removal of egg batches undamaged, the sides of the vials in which adult females were kept were lined with cambric. Aphids provided as food for coccinellid adults and larvae during rearing were placed on a nettle leaf in the vial, the leaf being replaced as necessary.

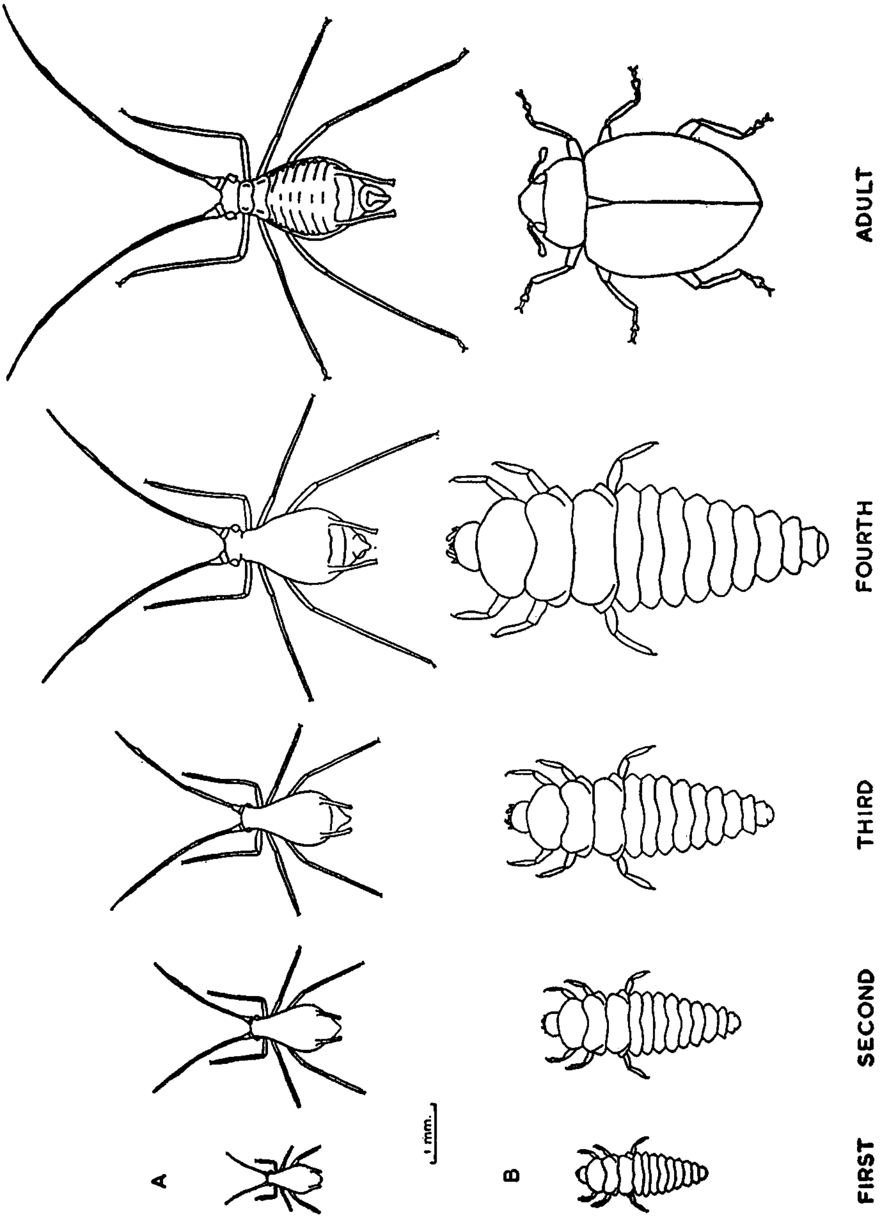

FIG. 1.—The relative sizes of each instar of *Microlophium evansi* and *Adalia decempunctata*.

III. Experimental Method

Corked vials were filled with water, and the petiole of a freshly cut nettle leaf was inserted through a hole in each cork. The leaves were then left for several hours in order to accommodate to the change. Aphids of a selected instar were then placed on each leaf and left to settle and insert their stylets. If the aphids started to move about the leaf during an experiment, their records were rejected.

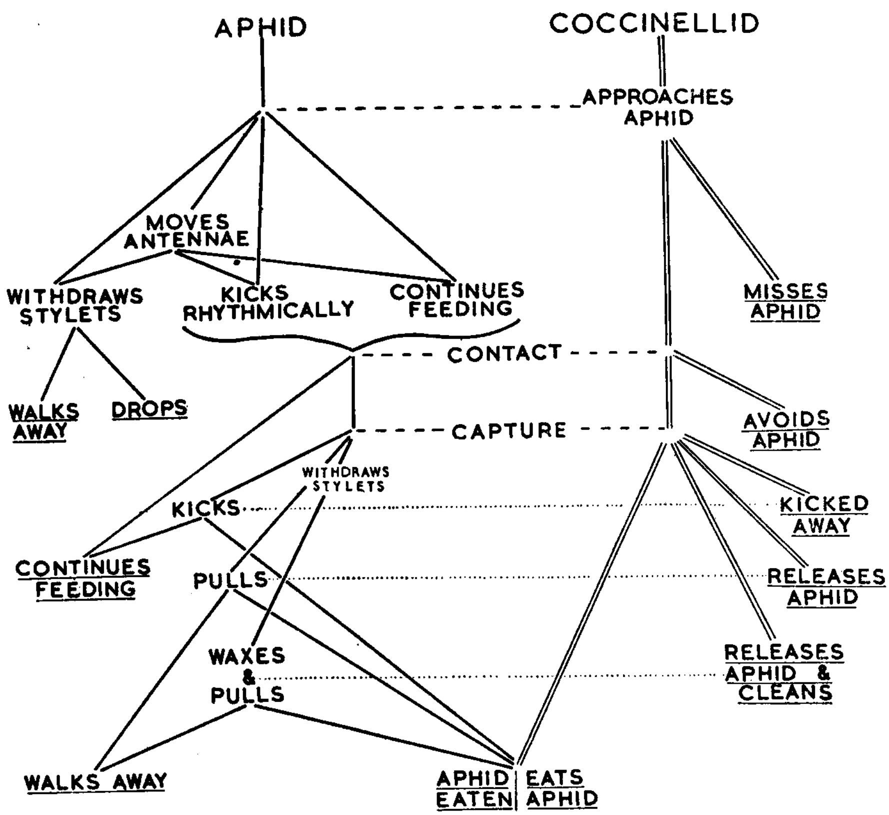

Fig. 2.—Diagrammatic representation of the possible interactions between the behaviour patterns of *Microlophium evansi* and *Adalia decempunctata* during an encounter.

A larva of *A. decempunctata* of a selected instar, and which had recently moulted and was actively moving about its vial, was placed on each leaf, and continuous observations of aphids and coccinellids began. If an aphid avoided a coccinellid larva the method of avoidance was noted. Records were restricted to aphids in the direct path of the coccinellid, and which had settled and inserted their stylets, this constituting an *encounter*. A maximum of 20[1] encounters was allowed for each coccinellid larva, but if it captured an aphid in less than 20 encounters, recording ceased with the capture. Larvae failing to make a capture by the twentieth encounter were offered an aphid held with a pair of forceps, and if they did not readily accept it, their records were rejected. In experiments with adult coccinellids, aphids were placed on nettle plants. The adults were kept for 24 hours without food before testing. Figure 2 gives a diagrammatic representation of the possible interactions of aphid and coccinellid behaviour patterns for these species.

IV. Responses of *Microlophium evansi* (Theobald) to *Adalia decempunctata* (L.)

(1) *Walking and Dropping*

At the approach of a coccinellid, *M. evansi* may first make exploratory movements of the antennae towards the intruder. When the coccinellid is close the aphid often withdraws the stylets and either walks out of the path of the coccinellid, or drops off the plant.

Figure 3 shows that third and fourth instar and adult aphids do not drop from the plant when encountered by first instar coccinellid larvae, but do so when encountered by later instars of coccinellid. There is an increase in the percentage of aphids in each instar which drop from the plant in response to each successive instar of coccinellid (fig. 3). This could be due to the fact that aphids move relatively more slowly compared with each successive instar of coccinellid, and therefore aphids which try to avoid capture by walking away may fail.

However, considering the fate of all the adult aphids, including those aphids that were captured (which possibly attempted to walk away), the ratio of the number of aphids which dropped to all the others (which walked away, or kicked, or were captured) when encountered by a second instar coccinellid differs significantly from that obtained when they are encountered by an adult coccinellid ($P < 0{\cdot}01$) (Table II). Therefore, the dropping response is most readily evoked by relatively big predators.

Table II.—*Fate of adults of* Microlophium evansi *when encountered by second instar and adult individuals of* Adalia decempunctata

Instar of coccinellid	Fate of adult aphids: Number of aphids which dropped	Total number which walked away, kicked, or were eaten
Second	1	202
Adult	38	110

[1] A few first and second instar coccinellid larvae were allowed more than 20 encounters with second instar and adult aphids.

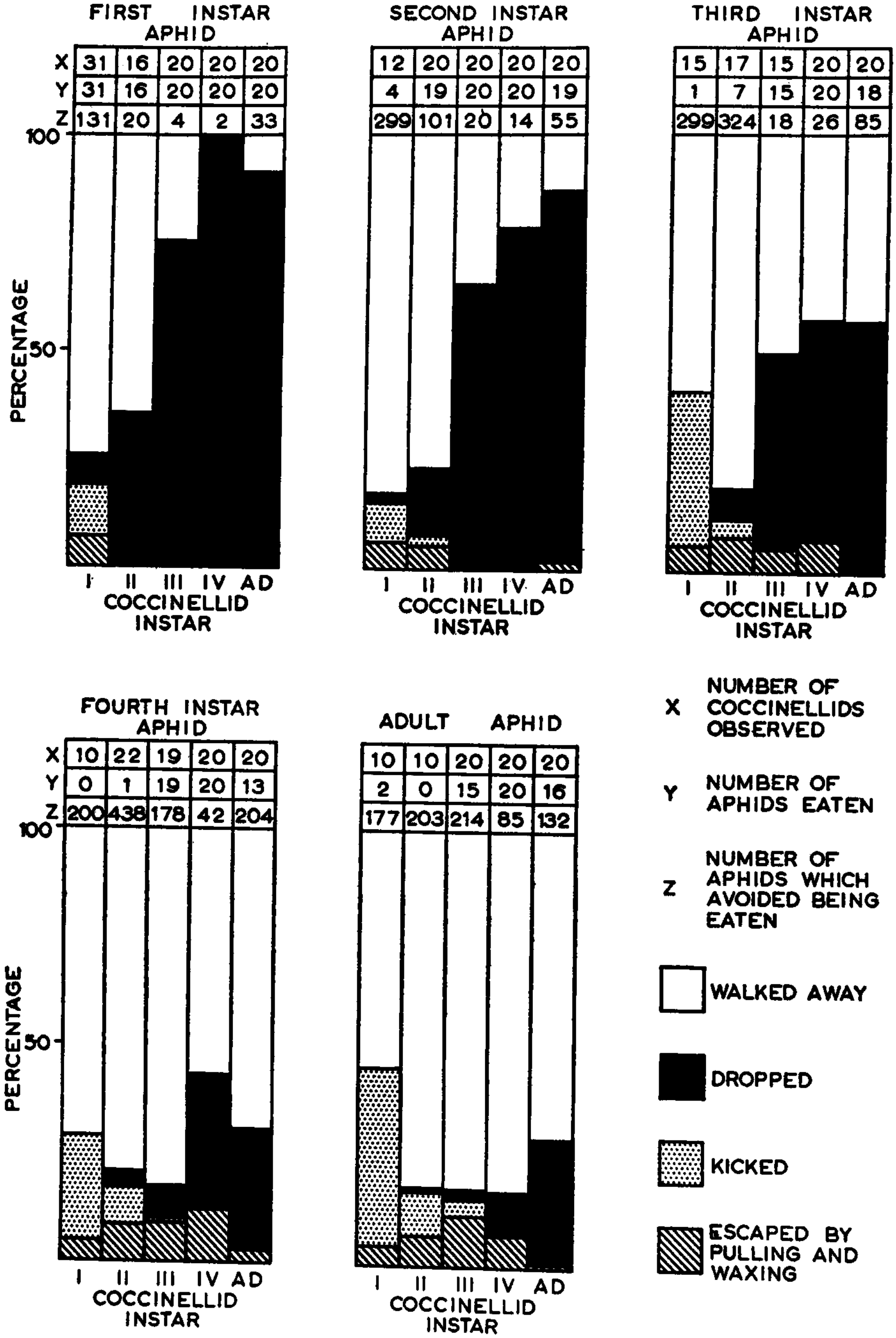

FIG. 3.—Responses of *Microlophium evansi* to the presence of *Adalia decempunctata* larvae and adults.

(2) *Kicking*

If a first instar coccinellid larva touches the leg of an adult aphid the latter may kick the larva off the plant with the leg which has been touched. As a first instar coccinellid is extremely small it is difficult to see whether it actually seizes the aphid first.

More frequently aphids respond to the appearance or touch of a coccinellid by performing rhythmical kicking movements, as recorded in *Aphis fabae* Scopoli (Ibbotson and Kennedy, 1951 : 77). This kicking does not appear to be directed accurately at the coccinellid, but often results in the aphid kicking a coccinellid larva and making it change direction. Aphids which made a coccinellid change direction by either of these methods, and which did so without withdrawing their stylets, were recorded as having avoided capture by kicking (fig. 3).

Irrespective of its instar, the tendency of an aphid to kick in response to the approach of larvae of the first three instars of *A. decempunctata* is strongest in response to relatively small coccinellids, and they show no kicking response to the presence of fourth instar or adult individuals of *A. decempunctata*, but drop or walk away instead.

Larvae of each successive instar of coccinellid are larger and capable of travelling at a greater speed. *M. evansi* will not avoid stationary coccinellid larvae or adults, and this aphid has frequently been seen walking over stationary coccinellids. Between the time of hatching and the first moult a coccinellid larva increases only slightly in size, but there is a considerable increase in the speed at which it walks. Its speed averages $1{\cdot}00 \pm 0{\cdot}53$ cm. ($n = 9$) per minute on the first day, and $9{\cdot}73 \pm 3{\cdot}19$ cm. ($n = 9$) per minute on the fourth day, respectively. The response of first instar aphids to one-day-old and four-day-old first instar coccinellids was noted, and the coccinellids were observed until they made a capture (Table III). Only encounters were recorded (p. 323).

TABLE III.—*The fate of first instar individuals of* Microlophium evansi *when encountered by one- and four-day-old first instar individuals of* Adalia decempunctata

Age of coccinellids	Number of coccinellids observed	Number of aphids eaten	Fate of first instar aphids encountered, but not eaten: Walked away	Dropped	Kicked	Escaped
1 day	31	31	97	9	18	7
4 days	28	28	19	8	0	0

Aphids which would have been categorised as having avoided capture by kicking, or which would have escaped when seized by a one-day-old first instar coccinellid, are more likely to be seized and overpowered by a faster moving four-day-old first instar coccinellid larva. Also, proportionately fewer aphids avoided capture by walking away than by dropping when encountered by four-day-old first instar coccinellid larvae. The ratio of the number of aphids which dropped off the plant to all the others (which walked away, or kicked, or escaped) when encountered by one-day-old first instar coccinellid larvae differs significantly from that when the aphids are encountered by four-day-old first instar coccinellid larvae ($P < 0{\cdot}01$). Hence aphids have a greater tendency to drop when encountered by a four-day-old larva than when encountered by a one-day-old first instar coccinellid larva. This change in the response of the aphid is probably due to an increase in the speed at which the coccinellid travels.

The increase in speed with each successive instar of coccinellid could partly account for the increase in the percentage of aphids of a particular instar which dropped when encountered by coccinellid larvae of each successive instar. Coccinellid larvae of different instars, however, apparently travelling at the same speed, will elicit different responses from individuals of a particular instar of aphid. Therefore, size may also have an effect on an aphid's response although, as already stated, a coccinellid will elicit no avoiding response if stationary, irrespective of its size.

(3) *Pulling and Waxing*

Since the legs of an aphid project from its body a coccinellid is likely to touch the aphid's legs before the body, and the tendency of an aphid to point its antennae towards an approaching coccinellid frequently enables the latter to seize an antenna and capture the aphid. If an aphid is relatively small compared with the coccinellid which encounters it (fig. 1), the aphid is quickly overpowered.

If an appendage of an adult aphid is seized by a first or second instar coccinellid larva, the aphid can often escape by pulling the appendage free (Table IV). Occasionally third and fourth instar aphids which have had a leg seized by a third or fourth instar coccinellid have lost the leg in the struggle which followed.

In a few instances, where the aphid was extremely large compared with the coccinellid, the latter walked between the legs and under the aphid's body, and then seized its proboscis. First instar coccinellids were twice observed to capture adult aphids by climbing up the aphids' hind legs and on to their backs.

Where both aphid and coccinellid are similar in size, an aphid has less chance of pulling a seized appendage free, but escape may be facilitated by "waxing". A drop of oily liquid may appear at the tip of one or both siphunculi, and that nearest the point of contact swings over and touches the coccinellid, as described by Büsgen (1891). The drop of oily liquid often touches the head of the coccinellid, where it may spread over the mouthparts, solidifying rapidly and becoming wax like. *Waxing*, as it will be referred to here, may immobilise the coccinellid and allow the aphid to escape (Table IV).

Functions ascribed to the siphunculi by earlier workers include excretion (Réaumur, 1738; Linnaeus, 1758); respiration and excretion (Bonnet, 1745); levers for raising the hind part of the body during the squirting of excretory fluid from the anus (Kyber, 1815); and protection (Büsgen, 1891). Horvath (1905) supported Büsgen's view that they protected the aphid from certain predators by means of the wax-like substance they produced. However, Gillette (1908) and Hottes (1928) doubted their protective value, Hottes concluding that their function is secretory.

Table IV.—*The part of the body seized and the response of individuals of* Microlophium evansi *which escaped from* Adalia decempunctata

Coccinellid instar	Part of aphid seized		Response of aphid when seized	
	Appendage	Body	Pulled, did not wax	Pulled and waxed
	Number of first instar aphids			
First	10	0	4	6
Second	0	0	0	0
Third	0	0	0	0
Fourth	0	0	0	0
Adult	0	0	0	0
	Number of second instar aphids			
First	24	0	19	5
Second	7	1	3	5
Third	0	0	0	0
Fourth	0	0	0	0
Adult	1	0	1	0
	Number of third instar aphids			
First	18	0	18	0
Second	28	1	21	8
Third	2	0	2	0
Fourth	1	1	0	2
Adult	0	0	0	0
	Number of fourth instar aphids			
First	9	0	9	0
Second	36	0	34	2
Third	16	0	10	6
Fourth	6	0	4	2
Adult	0	5	0	5
	Number of adult aphids			
First	8	0	8	0
Second	13	0	13	0
Third	25	0	24	1
Fourth	6	0	4	2
Adult	0	1	0	1

V. The Effect of Experimental Waxing on Larvae of *A. decempunctata* and Upon the Ability of *M. evansi* to Escape

A first instar aphid was held by the legs with forceps and gently poked with a needle until a drop of liquid exuded from one or both of the siphunculi. The head of a first instar larva of *A. decempunctata* was touched with the drop and then watched under the microscope.

After it had been waxed the larva stopped walking, and at most only twitched its legs. After a period of 42–94 minutes, active movement began, and usually the wax began to flake off. Under laboratory conditions waxed larvae never released their hold on the plant. Later instar larvae cleaned off the siphuncular wax using the fore limbs and mandibles after a variable period of inactivity. Once the larva was free of the wax it was as efficient at capturing prey as an unwaxed larva.

First instar coccinellid larvae were allowed to seize a first instar aphid by a leg and were then experimentally waxed. They were then watched until the captured aphid escaped or was eaten. In a control experiment, a drop of water about the size of a drop of siphuncular wax was placed on the head of each of a number of larvae which had also seized an appendage of a first instar aphid. After experimental waxing, 16 out of 20 aphids escaped and 4 were eaten. When treated with a drop of water, only 3 aphids out of 20 escaped, but 17 were eaten. Waxing, therefore, facilitated escape ($P < 0{\cdot}01$). However, of six aphids seized by the body, only one escaped when the coccinellid larvae were waxed.

Hence, aphids which have had a leg seized by a coccinellid, and cannot pull the appendage free, can wax and immobilise the coccinellid and then have a considerable chance of escape. If, however, an aphid waxes the coccinellid after the latter has secured a body hold, it has little chance of escape.

VI. The Effect of the Angle of Approach of the Coccinellid on an Aphid's Chance of Escape

As *M. evansi* can see a coccinellid approaching it from the front or side, an attempt was made to discover whether an aphid's chance of avoiding capture is affected by the direction from which the coccinellid approaches it. The number of aphids which avoided capture by walking away or dropping off the plant, and the number which were captured, when approached from the front and from the rear were recorded. The angle of approach included in front and rear is shown in figure 4. The results in Table V show that aphids have a

TABLE V.—*The effect of the angle of approach of* Adalia decempunctata *on the chance of* Microlophium evansi *avoiding capture*

	Number of aphids which avoided capture			Number of aphids which were captured		
Angle of approach	Number which walked away	Number which dropped	Total	Number which escaped	Number which were eaten	Total
		Second instar aphid : adult coccinellid				
Front .	11	12	23	1	2	3
Rear .	1	4	5	0	7	7
		Third instar aphid : third instar coccinellid				
Front .	64	8	72	0	10	10
Rear .	40	11	51	4	15	19
		Third instar aphid : adult coccinellid				
Front .	18	31	49	0	0	0
Rear .	1	5	6	0	6	6

significantly greater chance of avoiding capture when approached from the front, probably because they have more warning of the presence of the predator. When approached from the front by third instar larvae or adult coccinellids, aphids of all instars tested have a greater tendency to avoid capture by walking away instead of dropping off the plant than when approached from the rear. However, as too few observations were made there was not a significant difference in behaviour.

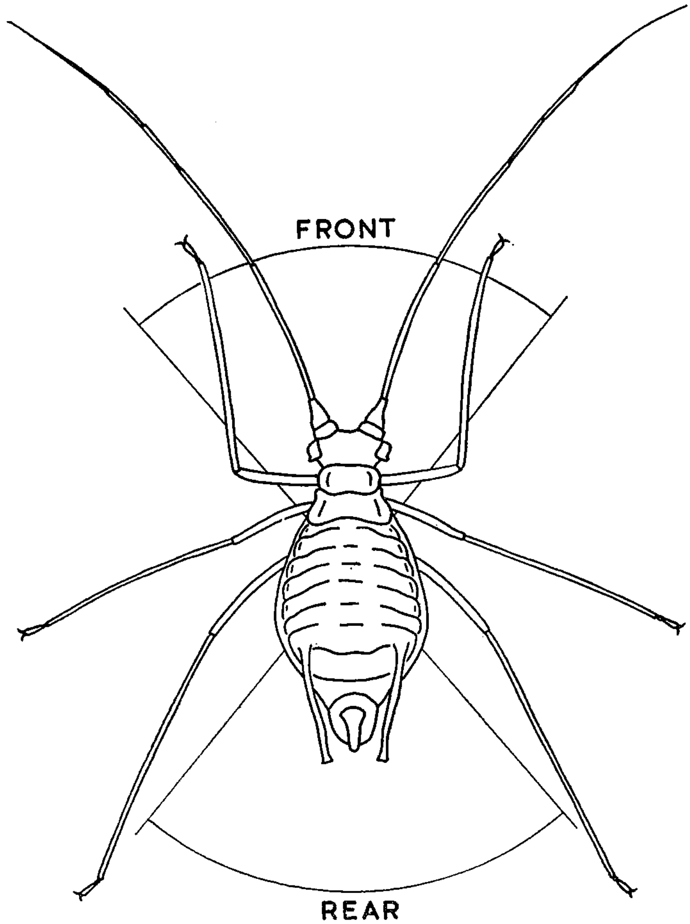

FIG. 4.—*Microlophium evansi* adult showing angles of approach of a coccinellid included in front and rear.

VII. APHID ORIENTATION ON THE PLANT AND THE DIRECTION OF APPROACH OF THE COCCINELLID

For these observations nettles supporting a relatively low population of *M. evansi* were selected and only aphids with their stylets inserted were considered. Those on the stem were noted as facing up or down, and those on the leaves as facing towards or away from the petiole of the leaf (Table VI).

TABLE VI.—*Orientation of* Microlophium evansi *on* Urtica dioica

Aphid instar	Orientation on stem: Down		Orientation on stem: Up		Orientation on leaf: Towards the petiole		Orientation on leaf: Away from the petiole	
	Number	%	Number	%	Number	%	Number	%
First	50	50	50	50	66	60·5	43	39·5
Second	65	65	35	35	99	90·8	10	9·2
Third	111	85·5	19	14·5	96	88·8	12	11·2
Fourth	83	79	22	21	96	96	4	4
Adult	92	80	23	20	101	94·5	6	5·5

Most aphids on the stems faced downwards, and those on the leaves towards the petiole. As a coccinellid tends to move up a stem, and outwards on to a leaf *via* the petiole, this behaviour pattern is advantageous to the aphid since it will see a coccinellid approaching.

VIII. Responses of Other Species of Aphid to *A. decempunctata*

Many other species of aphid try to avoid coccinellids which approach them. Quednau (1954) states that many members of the Callaphididae show modifications of their legs which can be correlated with their ability to jump. This ability, as already commented upon, has led certain observers to suggest that it renders the species immune from predaceous and parasitic enemies.

The response shown by members of the Callaphididae to fourth instar larvae of *A. decempunctata* varies. Of 100 adult and fourth instar individuals of *Eucallipterus tiliae* (L.) which were observed, 70 avoided capture by jumping when the coccinellid had almost touched them, and only two avoided capture by walking away. Of 50 adult individuals of *Drepanosiphum platanoides* (Schrk.) observed only two avoided capture by jumping, and 46 responded by walking away. Fourth instar individuals of *Euceraphis punctipennis* (Zett.) were never seen jumping, and avoided capture mainly by walking out of the path of the coccinellid and occasionally by dropping off the plant.

As already described, when individuals of *M. evansi* are captured by *A. decempunctata* they may wax the latter and then escape. Unlike *M. evansi*, *Dactynotus jaceicola* H. R. L. does not try to avoid *A. decempunctata* larvae which approach it, although it may perform rhythmical kicking movements. When the coccinellid is close but not actually touching the aphid, the latter will swing over and wax the larva. If an aphid is captured, then very large quantities of the wax are placed on the coccinellid larva. Several third instar larvae were unable to free themselves from this wax and finally died.

(1) *Unpalatable Aphids*

Johnson (1907) and Hawkes (1922) have both commented on the fact that highly coloured and " woolly " aphids are often not readily acceptable as food to coccinellids. *Adalia bipunctata* (L.) and *Coccinella septempunctata* L. both increase their consumption of aphids when the species they are provided with is changed from *Aphis sambuci* Kalt. to *A. hederae* L. (Jöhnssen, 1930). Hodek (1956, 1957) has shown that, although mature adults of *C. septempunctata* will lay eggs when feeding on *A. sambuci*, young adults do not survive and larvae never complete their development. He also states that Radzievskaja (1939) has recorded that *C. septempunctata* avoids eating the aphid *Brevicoryne brassicae* (L.).

Hyalopterus pruni (Geoffr.) is rejected immediately a larva of *A. decempunctata* pierces the body wall. In subsequent attacks on this aphid the body is not pierced and it is rejected as soon as the coccinellid touches it with its palps. Not only are some aphids distasteful, but some are even poisonous. *Aphis fabae* Scop. and *Megoura viciae* Bckt. are both attacked, and eaten, by larvae of *A. decempunctata*, but after about two minutes the larvae frequently release their prey and regurgitate their gut contents. Six out of 12 fourth instar larvae provided with *M. viciae* died a few days after feeding on this species, although offered other species of aphid as food.

Because of their relatively small size, adults of *Aphis fabae* are invariably killed when attacked. However, as adult individuals of *M. viciae* are relatively large compared with the coccinellid larvae attacking them, the wounds sustained are only slight, and as a result three of seven individuals observed were able to survive and reproduce. Heinze (1955) also observed that *Acyrthosiphon pisum* (Harris) could survive even severe wounding, and continue to feed and reproduce in the normal way.

(2) *Myrmecophiles*

Both *Aphis fabae* and *M. viciae* produce a honey dew which is acceptable to the ant *Lasius niger* (L.). When aphids of these two species are approached by a coccinellid larva they perform rhythmical kicking movements and, if repeatedly disturbed, move away. However, *A. fabae* does not respond in this manner to ants, remaining quite still (Ibbotson and Kennedy, 1951 : 77). On the other hand, *M. viciae* responds to an ant in the same way in which it responds to a coccinellid ; when ants touch an individual of this species they react by cleaning their antennae immediately afterwards, possibly because of the presence of a repellent substance on the body of the aphid. *M. evansi* also responds to an ant in the same way as it does to a coccinellid, and twice in a hundred encounters between *Lasius niger* and *M. evansi* the aphid even waxed the ant.

A. fabae is attractive to ants and does not avoid them, in contrast to *M. viciae* which, although its honey dew is acceptable to ants, does not allow them to attend it and may even be repellent to them. *M. evansi* also does not tolerate attendant ants although its honey dew is acceptable to them.

Aphids which do allow ants to attend them are protected against certain predators. El Ziady and Kennedy (1956) and Banks (1957) showed that when *Aphis fabae* is attended by *Lasius niger*, these ants attack and remove larvae of *Adalia bipunctata* and *Coccinella septempunctata* from the aphid colony. However, both adults and larvae of *Coccinella divaricata* Olivier habitually feed on aphid colonies attended by *Formica rufa* L. (Donisthorpe, 1927).

IX. Discussion

The nettle aphid *M. evansi* avoids capture by the coccinellid *A. decempunctata* by kicking, walking away, or dropping off the plant. Each method of escape is most effective in different circumstances. While it is advantageous to an aphid to be able to repel a coccinellid and continue feeding meanwhile, if it is unable to deter a young coccinellid by kicking and the latter continues to approach, the most effective means of escape is by withdrawing the stylets and walking away. As older and larger coccinellid larvae are capable of walking faster than even adult aphids, it is then most expedient to drop off the plant, although this may expose the aphid to death by starvation before it is able to find a host ; where plants such as nettles grow in fairly pure stands this may, in fact, rarely occur. Nevertheless the aphid is unable to feed for a prolonged period. The orientation of aphids on nettle plants is of survival value since they are able to see an approaching coccinellid and can therefore avoid capture by walking instead of dropping.

The posterior position of the siphunculi is advantageous as an aphid has less chance of avoiding capture when a coccinellid approaches it from the rear. An aphid which has had one of its hind legs seized by a coccinellid is more likely to wax the predator effectively than one which has had an antenna or fore limb seized.

Lüstner (1904) pointed out that aphids living on exposed parts of plants have long siphunculi, whereas those protected in galls, or on roots, or which tend to be hirsute or covered with flocculent wax, have short or rudimentary siphunculi which are not as valuable as protective devices. In many aphid families the degree of development of the siphunculi varies, and those with short or rudimentary siphunculi usually have other means of protection. In the Callaphididae, long siphunculi are found only in the genus *Drepanosiphum* and other species in this family protect themselves mainly in three ways. For example, *Euceraphis punctipennis*, *Eucallipterus tiliae* and *Tuberculoides annulatus* (Htg.) tend to form diffuse colonies and individuals all actively avoid certain predators as they approach. *Symydobius oblongus* (v. Heyd.), *Calaphis callipterus* (Koch) and *Callaphis juglandis* (Goetze), since they are adapted to tolerate the presence of attendant ants, are afforded some protection from enemies. *Phyllaphis fagi* (L.) is concealed in leaf curls which develop as a result of the aphid feeding on the leaves.

However, although *Drepanosiphum platanoides* has long siphunculi, it tends to walk away or jump from the plant and was never seen waxing a coccinellid, although it may wax other predators. The subfamily Dactynotinae includes species all with very long siphunculi, but their importance as protective devices also varies. *Dactynotus jaceicola* can wax certain predators as they approach, but *Microlophium evansi* tends to avoid predators by kicking or moving away, and waxes the predator once it has been captured only if it cannot pull itself free. *Macrosiphum rosae* (L.) is frequently attended by ants which will drive off certain predators approaching the colony. *Megoura viciae* is toxic, and because it is a large aphid and quickly released by the predator, it is often able to survive the wounds it sustains. In fact the importance of the siphunculi as protective devices cannot be correlated with their size.

The present work concerns the responses of certain aphids to larvae and adults of only one species of coccinellid, but parasites and other predators may elicit different responses. *Drepanosiphum platanoides* can jump (Quednau, 1954; Rietschel, 1952), but rarely does so in response to an approaching coccinellid. However, vibration or large shadows passing across the leaf on which the aphids are feeding frequently elicit an immediate jumping response. Other aphids such as *Microlophium evansi* and species of *Dactynotus* respond to similar stimuli by dropping. Both these responses would allow them to avoid large predators such as birds.

Evidence from the present study of the responses of *M. evansi* to *A. decempunctata* contradicts the widely held view expressed by Imms (1947) that aphids are " helpless sedentary creatures ", nor is it in agreement with the views of Hottes (1928 : 79) on the Aphididae : " It has been my experience, however, that aphids are not easily frightened, and that they remain unconcerned even while being walked over by those who are in the habit of feeding upon them . . . . Droplets may, however, be brought to the surface of the cornicles (siphunculi) by the pressure applied to the body of the aphid. In nature, this pressure naturally is produced by the aphid's enemy at the moment of grasping the aphid between its mandibles. The droplet must, therefore, be looked upon as a result of pressure, and not as a result of the desire of the aphid to defend itself." That *Dactynotus jaceicola* waxes a coccinellid before it is seized by the predator, however, indicates that waxing is not the direct result of external pressure.

Aphids exhibit two main trends in the evolution of their behaviour in relation to enemies. Certain species such as *M. evansi* and some members of the Callaphididae depend chiefly upon their activity to avoid an approaching predator. Most of these aphids are also characterized by cryptic coloration and the tendency to form diffuse colonies only. In contrast, inactive species do not avoid approaching predators or parasites and are myrmecophilous and often conspicuous as the result of their coloration and tendency to form large dense colonies. Some inactive species may be either unpalatable, or even toxic, or they effectively wax certain insect predators. The fact that some aphids of economic importance are myrmecophilous and also conspicuous has unfortunately led to false generalisation.

X. Summary

The nettle aphid *Microlophium evansi*, (Theobald), frequently avoids an approaching coccinellid by walking out of its path, dropping off the plant, or by kicking. If the coccinellid seizes an appendage of the aphid, the latter will attempt to kick the coccinellid away, or pull the appendage free. If pulling fails, the secretion from the siphunculi may be daubed on to the predator's head, after which pulling is frequently effective, and the predator is temporarily paralysed. The response depends upon the instar of aphid and coccinellid involved.

Waxing and then pulling occur most frequently when both aphid and coccinellid are approximately equal in size. In these circumstances the aphid is frequently unable to pull itself free, but after waxing the coccinellid its chances of doing so are greatly increased. If the aphid is the larger it has a considerable chance of pulling itself free without first waxing the coccinellid. Aphids smaller than the coccinellid are usually quickly overpowered and eaten.

M. evansi has less chance of avoiding capture when approached from the rear. However, on nettle stems in the field the aphid normally faces downwards, and on the leaves, towards the petiole, and therefore stands a greater chance of seeing the coccinellid approach.

Other species of aphid are also able to avoid an approaching coccinellid, but many conspicuous and gregarious species do not attempt to do so, and are afforded some protection by their unpalatability, their ability to wax the coccinellid effectively, or by attendant ants.

XI. Acknowledgments

It is a pleasure to thank Professor G. C. Varley for supervising this work and for his helpful criticisms of the manuscript. I also wish to thank Mr. H. L. G. Stroyan for identifying aphid material, and Dr. A. R. Hill for reading the manuscript. The work was carried out while I was in receipt of an Agricultural Research Studentship.

XII. References

BANKS, C. J., 1957, The behaviour of individual coccinellid larvae on plants. *Brit. J. anim. Behav.* **5** : 12–24.

BONNET, C., 1745, *Traité d'insectologie.* Paris.

BÜSGEN, M., 1891, Der Honigtau. Biologische Studie an Pflanzen und Pflanzenläusen. *Jena Z. Naturw.* **25** : 339–428.

DAVIS, J. J., 1914, The yellow clover aphis (*Callipterus trifolii* Monell.). *Tech. Ser. U.S. Bur. Ent.* **25** : 17–40.

DONISTHORPE, H. ST. J. K., 1927, *The guests of British ants.* London.

EL ZIADY, S. and KENNEDY, J. S., 1956, Beneficial effects of the common garden ant, *Lasius niger* L., on the black bean aphid, *Aphis fabae* Scopoli. *Proc. R. ent. Soc. Lond.* (A) **31** : 61–65.

FLESCHNER, C. A., 1950, Studies on searching capacity of the larvae of three predators of the citrus red mite. *Hilgardia* **20** : 233–65.

GAFFRON, M., 1934, Untersuchungen über das bewegungssehen bei Libellenlarven, Fliegen und Fischen. *Z. vergl. Physiol.* **20** : 299–337.

GILLETTE, C. P., 1908, Honeydew and the cornicles of the Aphididae. *Canad. Ent.* **40** : 235–6.

HAINE, E., 1955, The flight activity of the sycamore aphid, *Drepanosiphum platanoides* Schr. (Hemiptera, Aphididae). *J. Anim. Ecol.* **24** : 388–94.

HAWKES, O. A. M., 1922, The cannibal ladybird. *Conquest* **3** : 399.

HEINZE, K., 1955, Survival of aphids after injection. *J. econ. Ent.* **48** : 751.

HODEK, I., 1956, The influence of *Aphis sambuci* L. as prey of the ladybird beetle *Coccinella septempunctata* L. *Mém. Soc. zool. tchécosl.* **20** (1) : 62–74.

—— 1957, The influence of *Aphis sambuci* L. as food for *Coccinella 7-punctata* L. II. *Acta Soc. ent. Bohem.* (*Csl.*) **54** (1) : 1–8.

HORVATH, G., 1905, Sur les cornicules ou nectaires des Aphidiens. *C.R. 6me int. Congr. Zool., Berne* **1904** : 421–4.

HOTTES, F. C., 1928, Concerning the structure, function, and origin of the cornicles of the family Aphididae. *Proc. biol. Soc. Wash.* **41** : 71–84.

IBBOTSON, A. and KENNEDY, J. S., 1951, Aggregation in *Aphis fabae* Scop. I. Aggregation on plants. *Ann. appl. Biol.* **38** : 65–78.

IMMS, A. D., 1947, *Insect natural history.* London.

JOHNSON, R. H., 1907, Economic notes on aphids and coccinellids. *Ent. News* **118** : 17–4.

JÖHNSSEN, A., 1930, Beiträge zur Entwicklungs- und Ernährungsbiologie einheimischer Coccinelliden unter besonderer Berücksichtigung von *Coccinella septempunctata* L. *Z. angew. Ent.* **16** : 87–158.

KYBER, J. F., 1815, Einige Erfahrungen und Bemerkungen über die Blattlause. [In] *Mag. Ent.* (Germar) **1** (2) : 1–39.

LINNAEUS, C., 1758, *Systema Naturae per Regna tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis.* 1, Ed. X, reformata, Holmiae.

LÜSTNER, G., 1904, Über die Bedeutung der Rükenröhren der Aphiden. *Ber. Lehranst. Weinb. Geisenheim* **1903** : 175–84.

QUEDNAU, W., 1954, Monographie der mitteleuropäischen Callaphididae [Zierläuse (Homoptera, Aphidina)] unter besonderer Berücksichtigung des ersten Jugenstadiums. I. Die Junglarven des ersten Stadiums der mitteleuropäischen Callaphididae. *Mitt. biol. Zent. Anst. Berl.* Heft **78.**

*RADZIEVSKAJA, S. B., 1939, Concerning the hibernation of the ladybird and the struggle with the aphis. *Probl. Ecol. Biocen., Moscow.* **4** : 268–75.

RÉAUMUR, R. A. F. DE,1738, *Mémoires pour servir a l'histoire des insectes* **3** (2). Paris.

RIETSCHEL, P., 1952, Vergleichende Untersuchungen über Bau und Funktion des Sprungbeines der Blattlaus *Drepanosiphum.* *Z. vergl. Physiol.* **34** : 142–58.

TISCHLER, W., 1936, Ein Beitrag zum Formensehen der Insekten. *Zool. Jb.* (Abt. 3) **57** : 157–202.

*** Original not consulted.**