ABSTRACT

A study of the searching behaviour of certain insects feeding on aphids

The searching behaviour of insect predators in relation to the behaviour of their prey has received very little attention, with two notable exceptions. Fleschner (1950, *Hilgardia* **20** : 233-265) studied the searching capacity of the larvae of three predators of the citrus red mite. Banks (1954, *Brit. J. anim. Behav.*, **2** : 37-38; 1957, *Brit. J. anim. Behav.*, **5** : 12-24) studied the searching behaviour of individual coccinellid larvae on plants. No attempt, however, has been made to study the searching ability of all the instars of a particular insect predator.

The aim of the present laboratory study has been to determine the searching ability of all the larval instars and the adult, and the rate of increase, of the predatory coccinellid beetle, *Adalia decempunctata* (L.), when feeding upon the nettle aphid, *Microlophium evansi* (Theob.). The results have been used to test certain assumptions made by Volterra (1931, in Chapman, R.N., Animal ecology, New York) and Nicholson (1933, *J. Anim. Ecol.*, **2** : 132-178) in their mathematical formulations of the interaction of predator and prey populations.

Predispersal behaviour.

A. decempunctata lays its eggs in batches of from 3-30 eggs. Soon after hatching, first hatched larvae will attack and eat unhatched eggs of the same batch, but will not attack either dead or living newly emerged larvae. Just prior to dispersal

from the egg shells, 12-24 hours after emergence, the first hatched larvae will consume dead or freshly emerged larvae. Eggs which fail to hatch at the time when the majority of the batch do so do not normally hatch successfully. The delay in attack on freshly emerged or dead larvae allows for considerable variation in the time of hatching.

Orientation of larvae

Larvae are negatively geotactic, and positively phototactic. These responses guide the larvae to the apices of the plant stems, the area of the plant favoured by their prey. In searching the lower surface of a leaf, larvae tend to follow irregularities of the leaf surface such as the rim or veins, where most nettle aphids are also found.

Thoroughness with which larvae search an area

Well fed larvae tend to recross their tracks more frequently than starved individuals of the same instar, so that at high aphid population densities they turn more frequently, and so confine their search to a relatively small area. This maintains larvae in an area where prey is diffusely aggregated. Starved first instar larvae recross their tracks more frequently than starved larvae of succeeding instars, and therefore confine their search to a relatively smaller area and have less chance o finding aphid colonies.

Starved fourth instar larvae search an area which their responses to gravity and light lead them to occupy less thoroughly as the period of starvation increases, and consequently leave such an area more quickly than if prey were abundant.

Efficiency in capturing prey

On average, first instar A.decempunctata larvae are able to capture only one first instar aphid of every five encountered, but there is an increase in efficiency in capturing prey after the first capture is effected, and as the larvae increase in age. The coccinellid is most efficient in capturing young aphids. Efficiency of adults lies between that of second and third instar larvae.

M. evansi attempts to avoid capture by an approaching coccinellid by walking out of its path, dropping off the plant,o by rhythmical kicking. When approached by a relatively large coccinellid, it drops. If the coccinellid is small, and moving slowly, the aphid walks away from it or performs rhythmical kicking movements. This kicking occurs most frequently when an adult aphid is approached by a first instar coccinellid, and doe not appear to be directed at the coccinellid, although it often results in the aphid kicking the larva and causing it to change direction.

If seized by a coccinellid larva smaller than itself, the aphid is able to kick the larva away or pull the captured appendage free. Where both aphid and larva are similar in size, the aphid has less chance of pulling an appendage free. However, it may wax the coccinellid by means of an oily liquid exuded from the siphunculi. The oily liquid is placed on the head of the coccinellid, where it spreads and solidifies, becoming wax like. Waxing was first noted by Büsgen (1891, Jena. Z. Naturw., 25 : 339-428) who stated that it served to protect aphids against certain predators. More recent workers, however, doubt its protective function. The present observatior clearly support the opinion of Büsgen, as waxing results in a temporary immobilization of the coccinellid and often enables the aphid to escape.

M. evansi has less chance of avoiding capture when approached from the rear than from the front. Most individuals on nettle stems face downwards, and those on the leaves towards the petiole. As a coccinellid tends to move up the stem and moves on to a leaf from the petiole, this orientation enables the aphid to see approaching coccinellids.

The availability of other species of aphid to A. decempunctata larvae is also considered. Aphid species which do not react to the presence of an A. decempunctata larva by moving away, and appear helpless, are usually either attended by ants, distasteful to, or are capable of effectively waxing this predator. The fact that aphids which appear helpless are the most conspicuous, because they are highly coloured or tend to be gregarious, could very well have given rise to the general impression that aphids are helpless and sedentary.

Survival of larvae

The following observations were made on larvae placed with a fixed number of aphids in separate 7.5 cm. x 2.5 cm. specimen tubes, each containing a nettle leaf.

The chance of a first instar larva capturing its first aphid depends upon the number of aphids provided each day. Having once captured an aphid, a larva's chance of capturing a second is greater than was its chance of capturing the first, partly because of an increase in the efficiency in capturing prey.

For 50% survival, the larvae of successive instars of A. decempunctata require a greater number of aphids to be provided each day. Larvae also spend a greater length of time in each successive instar. The rate of development of larvae depends upon the number of aphids provided each day, and is greatest when a large number of aphids is provided.

When few aphids are provided each day, few or no larvae survive to become adults. However, even when a large number of aphids is provided some mortality occurs about the time of moulting.

Size and weight of the adults are greater when larvae are provided with a large number of aphids each day. Adults emerging from pupae taken in the field are of the same average size and weight as those reared from larvae provided with 20 third instar aphids each day.

An index of the relative aphid population densities required for 50% survival in each instar of coccinellid larva has been calculated, taking into consideration: 1) the age distribution of a nettle aphid population in the field attacked by A. decempunctata, 2) the efficiency of the larvae in capturing M. evansi, 3) the area which larvae of each instar can cover, 4) the number of aphids required for 50% survival by the larvae of each instar, and 5) the proportion of time spent feeding by larvae in each instar. First instar larvae require an aphid population density many times greater than that required by fourth instar larvae. The actual value of the index depends chiefly upon the age distribution of the aphid population being attacked. Therefore, for first instar larvae to survive, adult *A. decempunctata* must oviposit in young and relatively dense aphid populations.

Adult activity and oviposition

Egg batches of *A. decempunctata* on *Tilia x vulgaris* in the field are to be found either on leaves infested with aphids or close to infested ones. Since adult females are less active when well fed, they tend to remain in the close vicinity of aphids, and as the rate of maturation of eggs is greater when adults are well fed, the chance of eggs occurring close to aphids is further increased.

The searching behaviour of *A. decempunctata* larvae and adults would lead them to concentrate their attack in those areas most heavily infested with aphids. Therefore, at low overall prey population densities the number of encounters between *A. decempunctata* and its prey would be greater than expected by random search in the sense used by Nicholson (1933), or the probability relationship used by Volterra (1931). Therefore, theories based on the assumption of random search must be used with caution.

Rate of increase

An index of the rate of increase of *A. decempunctata* has been calculated, taking into consideration the number of eggs laid per unit time and the survival of the larvae at a particular aphid population density. Over the range of aphid population densities used there is a linear relationship between the rate of increase and the logarithm of the prey population density. Therefore, whilst Nicholson's and Volterra's assumption that survival and reproductive rate are a function of the prey population density is valid for A. decempunctata, the actual function is not the one they use in their calculations.

D. Phil

A STUDY OF THE SEARCHING BEHAVIOUR OF CERTAIN INSECTS FEEDING ON APHIDS

BY

A. F. G. DIXON
JESUS COLLEGE

SUPERVISOR:- PROFESSOR G.C.VARLEY

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A. INTRODUCTION

The problem of searching behaviour of insect predators in relation to the behaviour of their prey has received very little attention, with two notable exceptions. Fleschner (1950) compared the searching capacity of last instar larvae of three predators of the citrus red mite, _Paratetranychus citri_ (McGregor), one of the predators being the coccinellid beetle, _Stethorus picipes_ Casey. Banks (1954, 1957) studied the behaviour of first instar larvae of _Propylea quatuordecimpunctata_ (L.), and first and fourth instar larvae of _Adalia bipunctata_ (L.) and _Coccinella septempunctata_ L..

The aim of the present laboratory study of the predatory coccinellid beetle _Adalia decempunctata_ (L.) and its prey the nettle aphid _Microlophium evansi_ (Theob.) has been to estimate the effect of topography and feeding on the searching behaviour of the coccinellid larvae, the searching capacity of the different coccinellid instars and their survival, and the effect of prey population density on the rate of increase of the coccinellid.

Volterra (1931) and Nicholson (1933) have both given mathematical formulation to the interaction of predator and prey populations. It is of interest to know whether their assumptions are valid. To test these assumptions in the field is difficult, but in the laboratory conditions can be kept relatively constant. Their assumptions about the rate of increase and searching ability are considered in the present work.

B. CULTURING TECHNIQUES

1) Culturing of the nettle aphid Microlophium evansi (Theob.)

Rhizomes of nettles (Urtica dioica L.) were planted in boxes and placed either in a glasshouse, or in culture cages beside a window and under two 80 watt fluorescent tubes and four 100 watt tungsten bulbs to increase the light intensity. Stems were infested with M. evansi when approximately 25 cm. high.

2) Culturing of Adalia decempunctata (L.)

A. decempunctata adults collected from the field were kept in cages consisting of a wooden frame 45 cm. x 45 cm. x 45 cm., a wooden floor, two sides of muslin, and a top and two sides of glass. Nettle stems infested with M. evansi were placed in the cage as required. Copulating coccinellids were removed as found, and on completion of copulation, females were placed in separate vials.

The vials used throughout the work were 7.5 cm. x 2.5 cm. specimen tubes 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. The sides of the vials in which females were kept were lined with cambric to facilitate the removal of egg batches undamaged. In all feeding experiments aphids were placed on a nettle leaf in the vials, the leaf being replaced as necessary. First instar aphids were fed to first and second instar *A. decempunctata* larvae, but otherwise third instar aphids were used. Aphid instars were estimated according to size and general appearance.

Egg batches removed from the vials were isolated in celluloid pill boxes with moist filter paper until they hatched.

Vials and pill boxes were kept in an incubator at 21°C and 66% relative humidity. Fluorescent lighting mounted above a window in the roof of the incubator gave a light intensity at shelf level in the incubator of 1,398 metre candles, for 16 hours a day.

C. PREDISPERSAL BEHAVIOUR OF ADALIA DECEMPUNCTATA (L.)

In the field, egg batches of *A. decempunctata* contain from 3-30 eggs. Smee (1922) gives the smallest batch recorded as 6, and the average, as 18. In the larger batches larvae may hatch continuously over a period of a few hours. Banks (1956a) observed a hatching period of seven hours for a batch of 53 *Coccinella septempunctata* eggs. While its cuticle hardens and darkens, a freshly emerged larva remains on top of its egg shell and for about an hour is apparently incapable of defending itself against older larvae of the same batch. Palmer (1914), Hawkes (1920), Smee (1922), Jöhnssen (1930), and Banks (1956a) all found that cannibalism occurs in several species of coccinellid larvae before dispersal from the egg shells. However, it is not clear whether this cannibalism was the eating of eggs only or eggs and freshly emerged larvae. Banks states that in a batch of 53 *C. septempunctata* eggs, 4 infertile and one unhatched larva were destroyed by cannibals. He also states that larvae will attack even partly emerged larvae.

Predispersal larval mortality in batches of *A. decempunctata* eggs laid in the laboratory was estimated by noting the mortality due to cannibalism several hours after hatching. Of 8,029 eggs in 766 batches, 1,470 eggs were eaten but only 7 larvae: 6 of the larvae being partly emerged and one, totally emerged.

The following laboratory studies were made with eggs of A. decempunctata, to discover whether the larvae first hatched would attack freshly emerged individuals of the same batch; and whether they ate eggs with well developed embryos which would have hatched in due course.

Response of larvae to dead larvae and eggs placed on the batch

For this series of experiments batches of freshly emerged larvae were selected, in which there had been no mortality, and in which larvae hatched approximately together. The size of the batches varied from 7-16. Freshly emerged larvae, fresh eggs, and eggs containing well developed embryos, which were recognised by their dark colour, were killed by keeping them at a temperature of -7°C. for 12 hours.

Experiment 1. On each of 6 batches of living larvae were placed 2 larvae and 2 recently laid eggs, all freshly killed. Batches were then kept under observation until either both eggs or larvae had been eaten.

Of the 12 dead larvae and eggs used, no larvae but all the eggs were eaten before completion of the experiment.

Experiment 2. The above procedure was followed, using 5 batches of living larvae, except that eggs contained well developed embryos.

Of 10 dead larvae and eggs used, no larvae but all the eggs were eaten before completion of the experiment.

From the results it is concluded that just after hatching larvae will first suck out the contents of unhatched eggs but will reject and not eat dead freshly emerged larvae. If dead larvae are left on the batch they will, in most cases, eventually be eaten by the larvae just before they disperse from the egg shells. Therefore dead larvae are acceptable as food.

Response of larvae of different ages to living freshly emerged larvae placed on the batch

The total length of time spent on the egg shells before dispersal varies a great deal. Banks (1956a) records the interval as being 12-24 hours for *A.bipunctata*; it is the same for *A.decempunctata.* One may classify batches in which the larvae hatch approximately together into three categories according to the activity and general appearance of the larvae; first, *freshly emerged*, when the larvae have just hatched and are still pale in colour; second, *active*, when the larvae have darkened and begun to move about and palpate neighbouring larvae; third, *predispersal*, when the larvae move actively over the egg shells.

Batches in which there had been no mortality were selected and categorised. Two living freshly emerged larvae were placed on each, and the batches examined 24 hours later when any deaths due to cannibalism were recorded.

Of 16 and 12 freshly emerged larvae placed on batches of freshly emerged and active larvae respectively, none were eaten. However, of 10 placed on batches of predispersal larvae 6 were eaten. The difference in behaviour between active and predispersal larvae is significant (Exact test $P. < 0.01$).

Although freshly emerged larvae are apparently unable to defend themselves because their cuticle is unhardened, and they are incapable of walking, they are not attacked by active larvae, although these will consume eggs containing well developed embryos. Predispersal larvae will eat freshly emerged larvae.

Nature of eggs containing well developed embryos destroyed by cannibals

Batches were chosen for observation in which all the larvae had become active, but some undamaged unhatched eggs containing well developed embryos still remained. The larvae were removed, and 48 hours later the eggs were examined.

Of 31 eggs examined only 5 hatched within 48 hours. Of the 26 failing to hatch, 13 had a split chorion and in 5 a larval head was protruding.

Eggs which fail to hatch at the time when the majority of the batch do so are likely to be eaten. However, most of these, even though they may contain well developed embryos, would not normally hatch successfully. Eating of unhatched eggs by active larvae is therefore an adaptive behaviour pattern since if the larvae obtain some food before dispersal they are able to survive longer and stand a greater chance of finding their aphid prey (Banks 1954, 1956a). That freshly emerged larvae are not eaten by active larvae is also advantageous since it allows for variation in the time of hatching of eggs. Under normal conditions eating of freshly emerged larvae by predispersal larvae is adaptive, since dead or dying larvae would also provide surviving larvae with an increased chance of finding aphid prey.

D. ORIENTATION OF LARVAE

Larvae which consumed few aphids each day moved upwards when placed on a vertical surface, irrespective of the position of the light source. However, larvae placed on a horizontal surface moved towards a strong source of light: they are positively phototactic. Movement on a vertical surface may therefore be a result of negative geotaxis and positive phototaxis, in which the former is dominant. This behaviour pattern, also demonstrated in Stethorus picipes (Fleschner, 1950) and S. punctillum Weise (Putman, 1955), allows the larvae to reach the apices of plant stems: the region of the plant preferred by their prey.

The following experiment was carried out in order to determine the effect of leaf topography on the movement of third instar larvae which consumed few aphids each day. A triangular hastate leaf, 32.5 cm. long, of Typhonium giraldii (Baroni) Engl. (Araceae) was used.

The plant was placed on a bench beneath fluorescent lighting providing a light intensity of 269 metre candles at leaf level. Larvae were placed on the petiole of the leaf, and their position on reaching the lamina, whether on the area between veins, prominent veins, or rim, was noted every 10 seconds. The rim was taken to be a track running parallel to the edge of the leaf, extending the

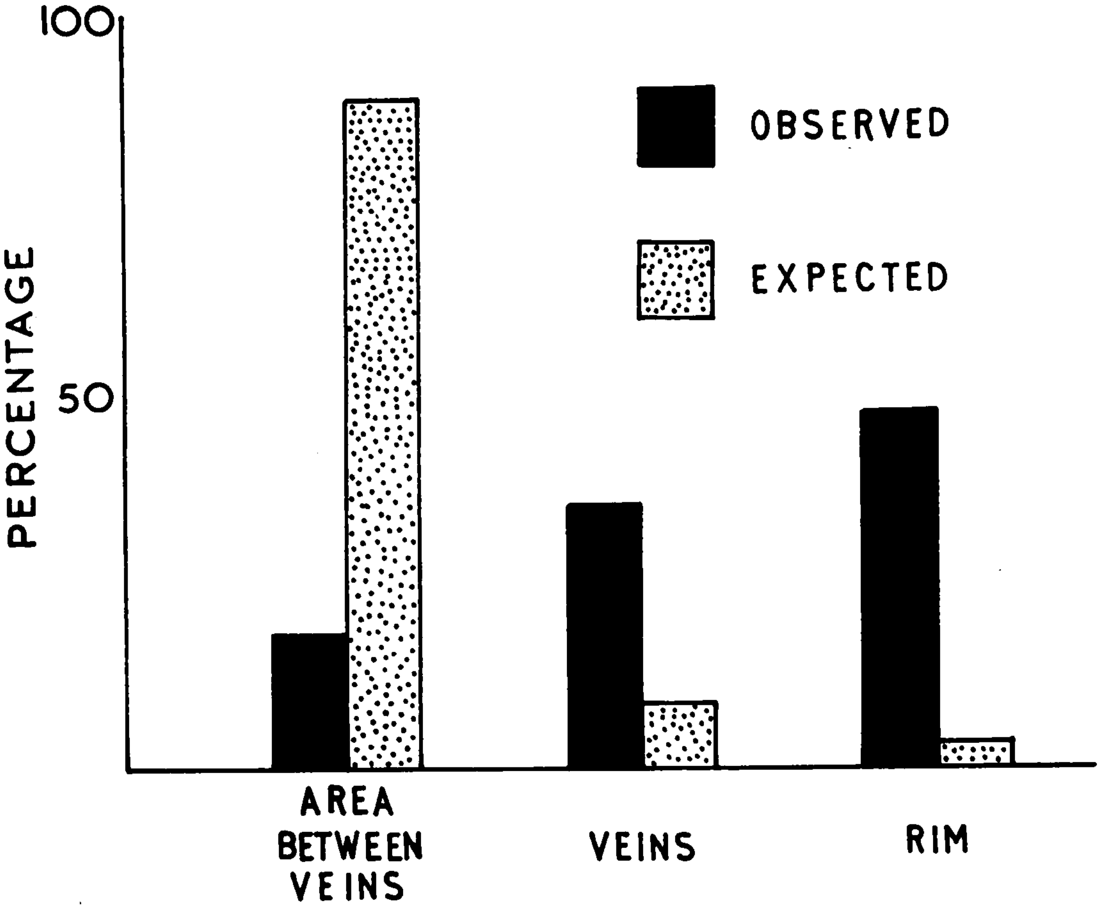

Fig. 1. Proportion of time spent by third instar <u>Adalia decempunctata</u> larvae on different parts of a <u>Typhonium giraldii</u> leaf: a) observed, b) expected if movement at random.

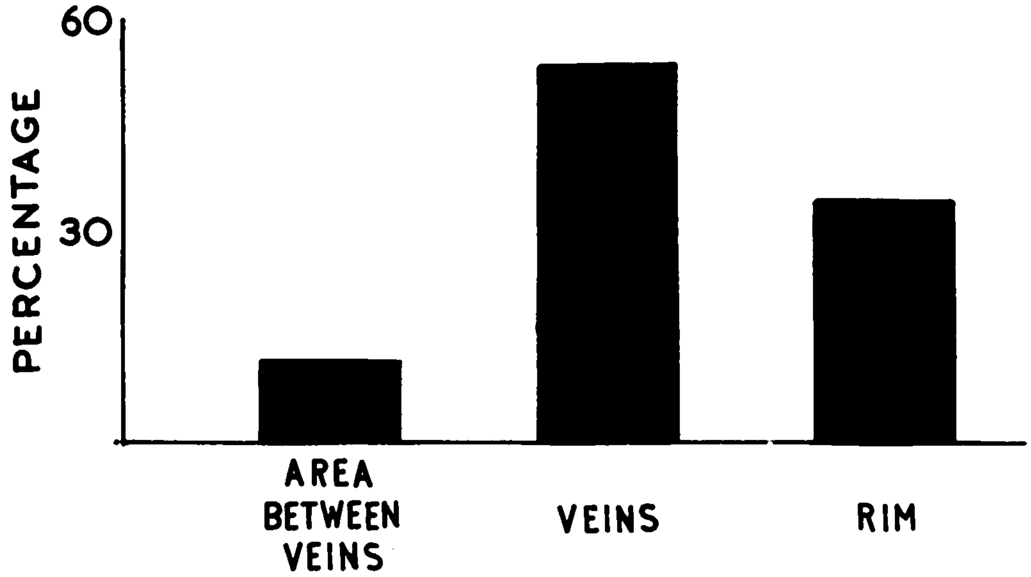

Fig. 2. Distribution of 600 <u>Microlophium evansi</u> on <u>Urtica dioica</u> leaves.

width of one third instar larva from the lamina edge towards the midrib. Preliminary experiments showed that larvae spent much less time on the upper than on the lower surface of the leaf. Records, therefore, refer only to movements of larvae on the lower surface (Table 1, Fig.1).

Most time was spent on the rim and veins. The expected percentages of time spent on the area between veins, veins, and rim, calculated by weighing the corresponding parts of a paper replica of the leaf, assuming that larvae move at random, are given in Table 1, Fig. 1. Larvae did not move at random over the lower surface of the leaf ($P < 0.001$), but tended to follow irregularities of the leaf surface, such as the veins or rim. This is in agreement with the observation of Banks (1957) for P. quatuordecimpunctata larvae.

The distribution of M.evansi on nettle leaves follows a similar pattern. Most aphids are found on the veins or very close to the edge of the leaf (Fig. 2). Therefore, in spending the greatest proportion of time walking on the veins and rim the chance of finding aphid prey is increased.

E. THOROUGHNESS WITH WHICH LARVAE SEARCH AN AREA

Trichogramma evanescens Westw. (Laing, 1937); *Chrysopa californica* Coq., *Conwentzia hageni* Banks, and *Stethorus picipes* Casey (Fleschner, 1950); and *A. bipunctata* (L.) (Banks , 1957) pursue a more tortuous path after parasitising or feeding upon their respective hosts or prey. In those cases where the hosts or prey are aggregated together it is advantageous to the parasite or predator to search an area more thoroughly after contacting host or prey, as by doing so its chance of contacting more is increased. Banks showed that 15 seconds after *A. bipunctata* larvae consume an aphid there is no significant difference between the rate of change of direction per unit time and that observed before the capture.

The experiments in this section were undertaken to determine the effect of different feeding rates upon the searching behaviour of *A. decempunctata* larvae and the ability of the larvae to leave an area where prey is absent.

Effect of feeding on thoroughness of search

Larvae were tested on a vertical wooden cylinder, 3.2 mm. in diameter, marked off at 2.54 cm. (1 in.) intervals, and mounted on a base. Two cylinders were used, one 78.7 cm. and the other 45.7 cm. long. A 100 watt bulb suspended 101.6 cm. above the base of the cylinder gave a light intensity of 129 metre candles at the base, and 6,450 and

430 metre candles, respectively, at the apices of the cylinders. The larger of the two cylinders was used only for third and fourth instar larvae.

Larvae were placed at the bottom of the pole, and their movements observed. Their position each time they changed direction and their final position were recorded. Observations extended over a period of five minutes, or until the larvae either reached the apex or returned to the base of the cylinder. Observations were made every 24 hours until the larva either moulted, pupated, or died. The sum of all results for an individual gives the total number of turns and the distance travelled.

Second instar larvae were fed first instar aphids; third and fourth instar larvae were fed third instar aphids. The number of aphids consumed each day by each larva was noted, and the average number of aphids it consumed each day calculated.

As there were three variates to be considered: the average number of aphids consumed each day, the number of turns, and the total distance travelled, the method of multiple regression analysis was used. The results are given in Table 2.

From the regression equations it is seen that for the second, third, and fourth instars, respectively, there is an increase of 2.6 ± 0.8, 4.3 ± 0.7, and 2.4 ± 0.6 turns for an increase in consumption of one aphid per day, if the distance travelled is constant.

In a similar experiment a flat horizontal surface was substituted for the vertical cylinder. The distance travelled and the number of times the larva recrossed its tracks were recorded. However, the results did not give the required level of significance, because of the large variation in the frequency of larvae recrossing their tracks. This variation is possibly due to the effect of uniform topography upon the larvae (Section D). However, the highest frequency of recrossing their tracks only occurred at the highest feeding rates.

Comparison (Discriminant analysis) of results obtained from the above experiment for starved first instar larvae with the sum of the results for starved second, third, and fourth instar larvae on the vertical cylinder (Table 3) shows that a first instar larva recrosses its tracks much more frequently than a second, third, or fourth instar larva. First instar larvae made an average of 3.1 turns in an average distance of 78.0 cm.; second, third and fourth instars, an average of 0.4 turns in an average distance of 164.9 cm.. The difference is highly significant.

The results show that larvae tend to recross their tracks more frequently at higher feeding rates. Different feeding rates simulate conditions of different population densities of prey. At high aphid population densities larvae turn frequently, and tend to confine their search to a small area; at low aphid population densities turning is rarer and thus the chance of arriving at more distant aphid colonies is increased. This behaviour pattern maintains larvae close to any aphid colonies they may find and, when these are exploited, enables them to find fresh colonies. Therefore, in addition to the change in behaviour seen immediately after feeding as described by Banks (1957) and Fleschner (1950), there is a change in A. decempunctata which extends over a greater period of time. This long term effect would serve to keep larvae in an area where prey is diffusely aggregated.

As starved first instar larvae cross their tracks more frequently than starved second, third, and fourth instar larvae they tend to confine their search to a small area and therefore stand less chance of finding aphid colonies.

Ability to leave an area not occupied by prey

This experiment was designed to test the ability of a starving larva to leave an area which its responses to gravity and light would normally lead it to occupy.

A 45.7 cm. cylinder was used as in the previous experiment. Recently moulted fourth instar larvae, fed a few aphids, were placed at the base of the pole, their movements observed, and the number of times each larva changed its

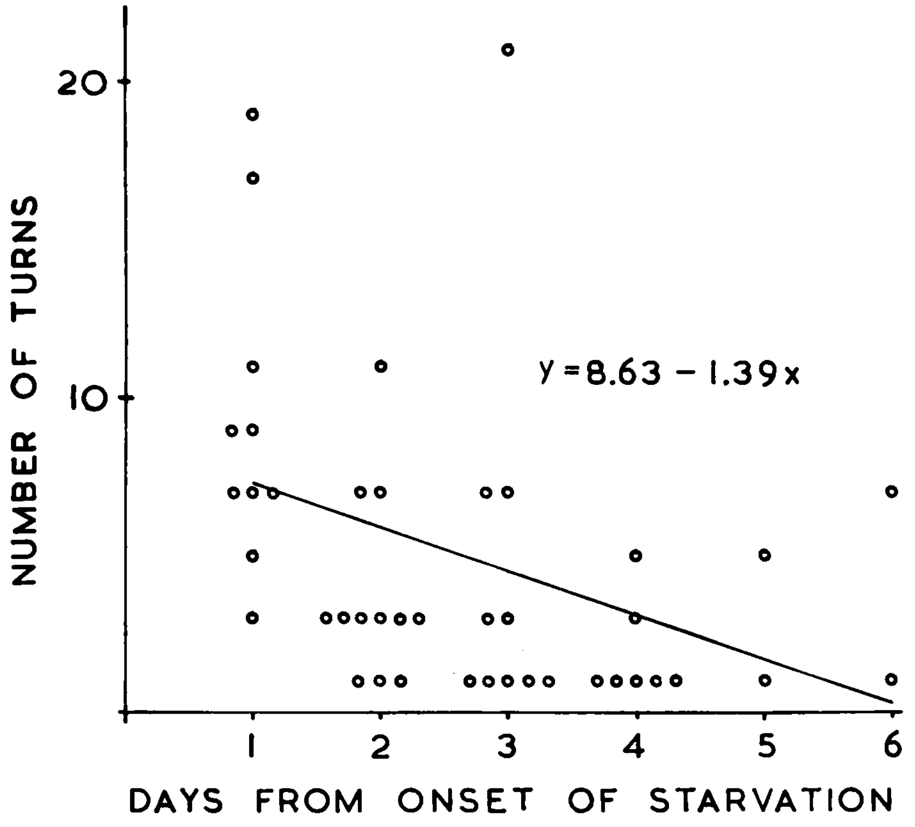

Fig.3. Number of turns on the vertical cylinder in relation to the number of days from onset of starvation for fourth instar Adalia decempunctata larvae.

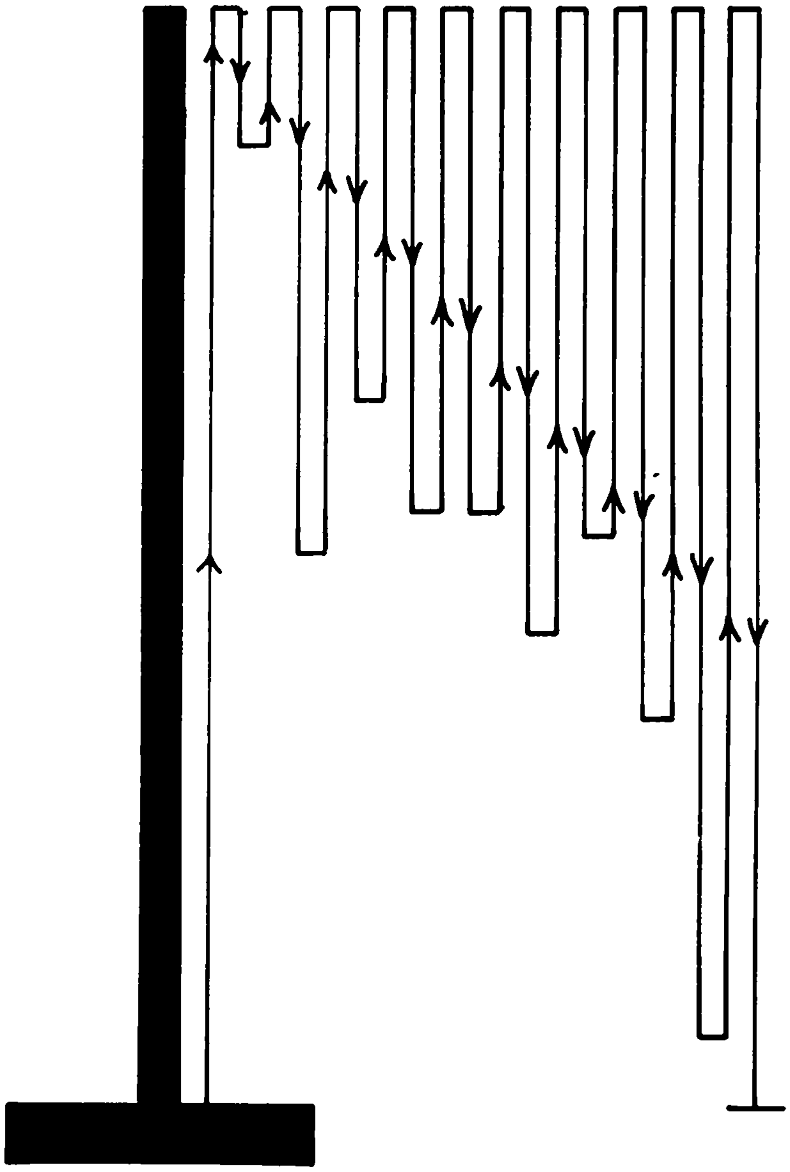

Fig.4. The track of a recently moulted fourth instar *Adalia decempunctata* larva on a vertical cylinder.

——←—— = Track

vertical direction was recorded (Fig. 3) until it left the cylinder. After the first day larvae were kept without food and tested every 24 hours until they died.

The tendency on the first day is to follow a pattern of movement similar to that illustrated in Fig. 4. Larvae climb to the apex of the cylinder, begin to descend but turn upwards again a short distance from the apex. This manoeuvre may be repeated several times, but there is a marked tendency to descend further down the cylinder on each successive occassion until finally they reach the base of the cylinder. It is concluded that the tendency to revisit the apex of a cylinder where there are no aphids decreases as the period of starvation increases (Fig. 3) ($P < 0.01$). This behaviour pattern would prevent larvae from becoming trapped at the apices of stems, and also allows them to leave such areas more quickly when starved. The experimental situation is very much simplified compared with a plant stem since there are no lateral projections. Nevertheless, observations suggest that the results apply to these more complicated situations.

Larvae placed on a similar, horizontal, cylinder did not behave in the same way: they returned to the base of the cylinder each time. Therefore, it appears the response to gravity is influenced by the degree of starvation.

F. AREA TRAVERSED BY LARVAE IN RELATION TO FOOD SUPPLY

Nicholson (1933, p.141) states that the area searched by animals can be measured in two ways. The total area searched by animals is what he terms the area traversed. As animals tend to recross areas that have already been searched, he calls the previously unsearched area the area covered. He assumes the area traversed is independent of prey population density.

It would be tedious to follow an animal throughout its life to determine the distance it travelled. However, an index of the distance it is capable of travelling can be obtained from the sum of the average speeds of locomotion of an individual on each successive day of its life. The results in this section were obtained in conjunction with those in Section E. In addition to the distance travelled on the vertical cylinder by a larva the time taken was noted, and from these results the average speed was calculated. The sum of the average speeds recorded each day for an individual larva gives a figure which will be referred to as the distance index. The distance index takes into account speed of locomotion and length of survival or duration of instar, at a particular feeding rate. The average results obtained for different feeding rates in each instar are summarised in Table 4

In each successive instar unfed larvae are capable of covering a greater distance before succumbing to starvation.

Larvae which consumed very few aphids each day were capable of travelling a greater distance than larvae of the same instar which consumed rather more. This is mainly because well fed larvae spend less time within an instar. A larva's range of perception of its prey is constant within an instar and, therefore, the area a larva is capable of traversing in any particular instar is much greater at the lower feeding rates. As different feeding rates are comparable with the number of captures made at different population densities of prey, it is concluded that the area traversed by _A. decempunctata_ larvae may vary with the population density of its prey. This point will be further considered in Section L.

G. EFFICIENCY IN CAPTURING PREY

The following behaviour study gives an estimate of the efficiency of A. decempunctata in capturing the aphid M. evansi and provides information on the latter's response to the presence of a coccinellid, and its efforts to escape capture.

Corked vials were filled with water and the petiole of a freshly cut nettle leaf was inserted through a hole in each cork. These leaves were left 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 during an experiment the aphids started to move about the leaf the experiment was rejected.

A. decempunctata larvae of a selected instar, which had recently hatched or moulted and were actively moving about their vials, were placed one on each leaf and continuous observations of coccinellid and aphid began. If an aphid avoided a coccinellid larva the method of avoidance was noted. However, 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 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 20th encounter were offered an aphid held with a pair of

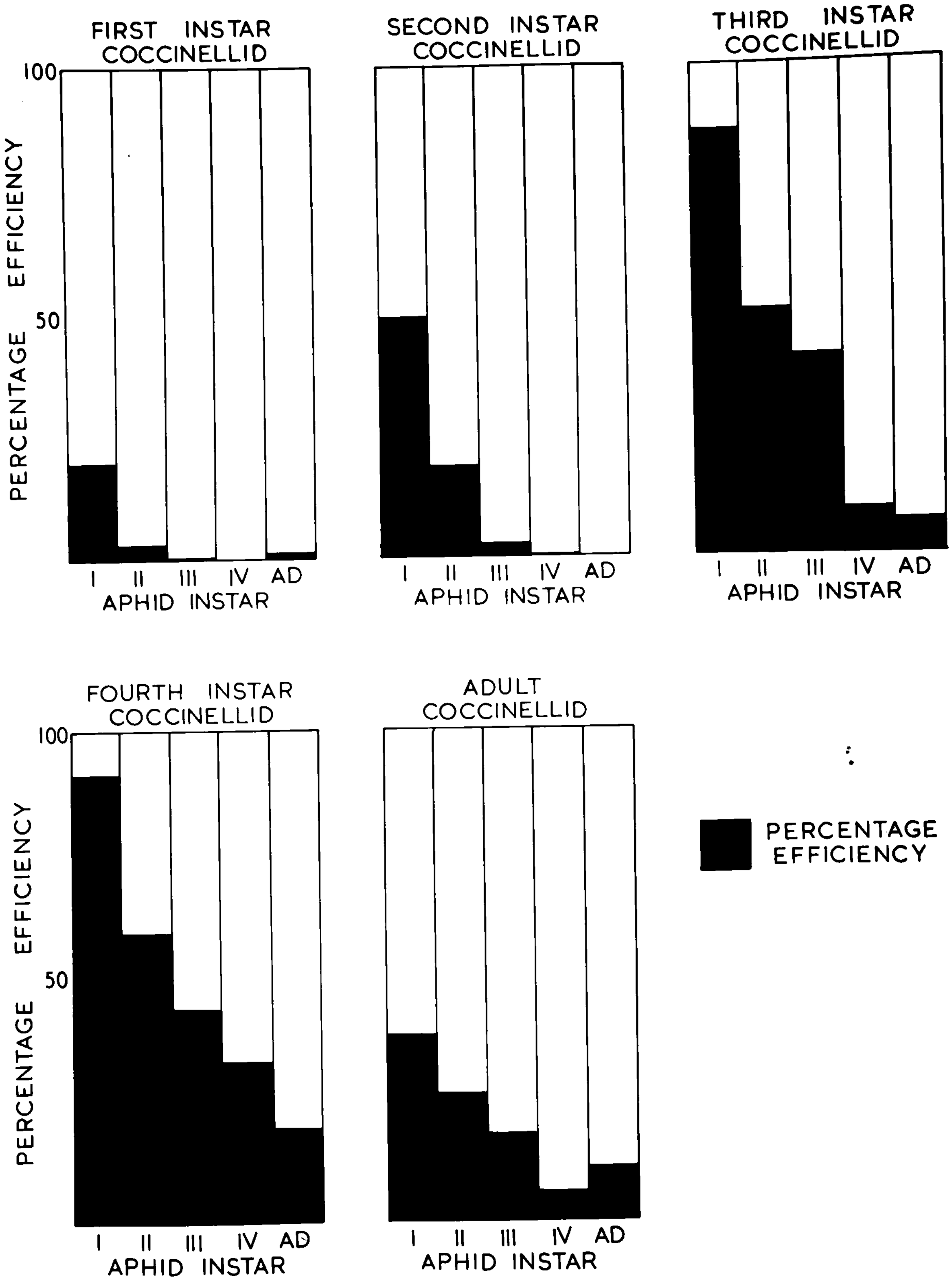

Fig.5. Percentage efficiency of <u>Adalia decempunctata</u> in capturing <u>Microlophium evansi</u> (percentage of encounters resulting in capture).

forceps. 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 24 hours without food before testing.

Efficiency of *A. decempunctata* in capturing *M. evansi*.

Larvae of *A. decempunctata* apparently only respond to an aphid after touching it with the head or fore limbs. The same has been observed in *Stethorus picipes* (Fleschner, 1950) and *A. bipunctata* (Banks, 1957). Adults appear to require actual palpal contact with prey before showing a response, although other species respond to form (Tischler, 1936) and movement (Gaffron, 1934).

Table 5 and Fig. 5 show that first instar *A. decempunctata* larvae are able to capture on average only one first instar aphid of every five encountered, but there is a definite increase in efficiency in capturing prey as the larvae increase in age. A coccinellid is most efficient in capturing young aphids. Efficiency of the adults lies between that of the second and third instar larvae. This point will be returned to in Section N.

Responses of *M. evansi* to *A. decempunctata*

Walking and dropping

At the approach of a coccinellid *M. evansi* may first

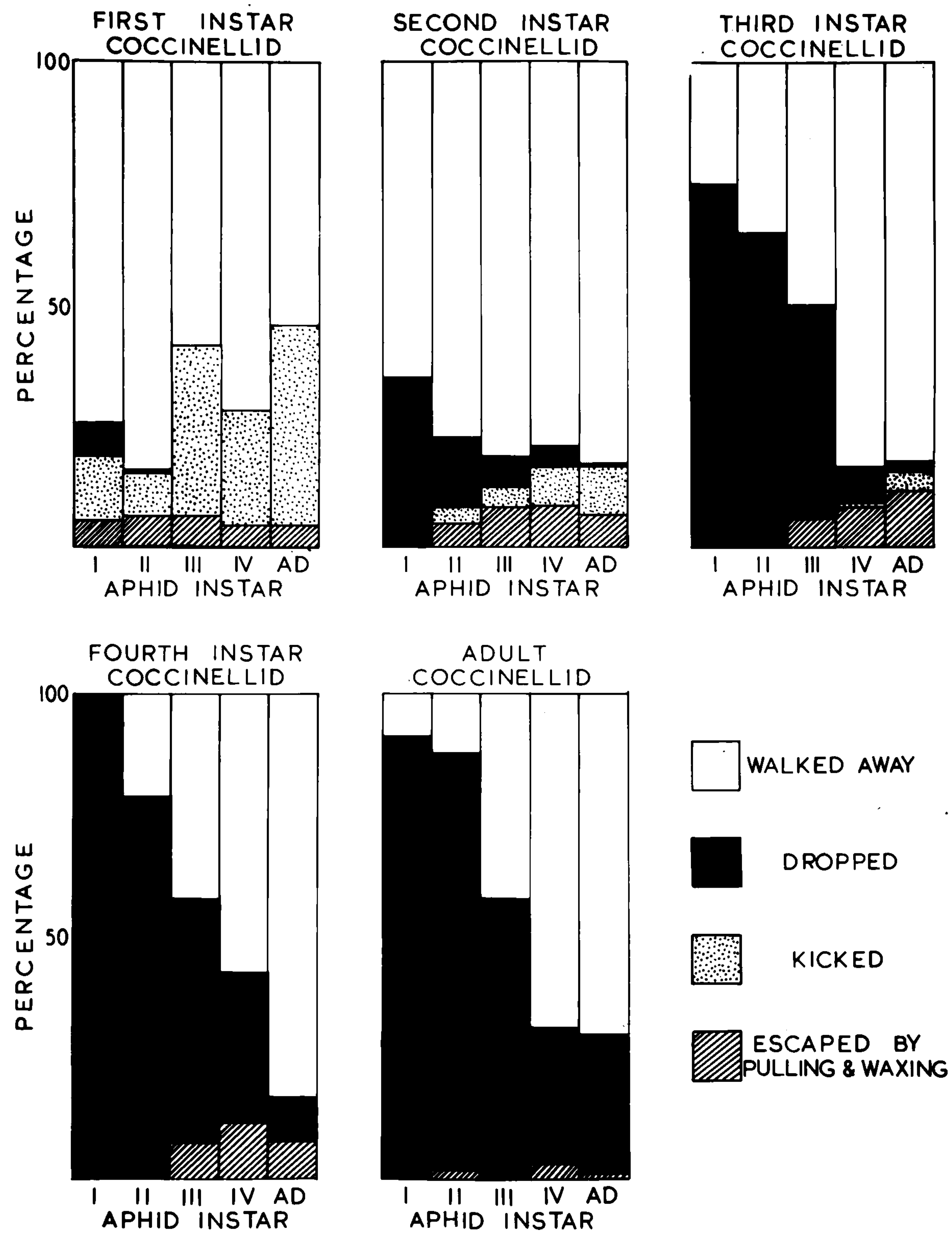

Fig.6. Response of Microlophium evansi to the presence of Adalia decempunctata larvae and adults.

make exploratory movements of the antennae towards the intruder. When the coccinellid is close it often withdraws the stylets, and either walks out of the path of the coccinellid, or drops off the plant. Table 5 and Fig. 6 show that when an aphid sees a relatively big coccinellid it drops; if the coccinellid is small and moving slowly, the aphid walks.

The decrease in dropping and increase in walking with each successive aphid instar in response to a particular coccinellid instar (Fig. 6), could be due to the earlier instars being less able to evade the coccinellids path, should they try to avoid capture by walking. By increasing the number of walking responses by the number of captures observed an approximate correction is applied, and the difference is still significant.

Kicking

Should a first instar coccinellid larva touch the leg of an adult aphid the latter may kick the larva off the plant with the leg that has been touched.

More frequently aphids respond to the appearance or touch of a coccinellid by rhythmical kicking movements, as recorded in Aphis fabae Scop. (Ibbotson and Kennedy, 1951: p. 77). This kicking does not appear to be directed accurately at the coccinellid, but often results in the aphid kicking the coccinellid larva and making it change direction. Aphids making a coccinellid change direction by either of these means, and which did so without withdrawing the stylets, were recorded as having avoided capture by kicking (Table 5 and Fig. 6).

The incidence of kicking in response to the approach of larvae of the first three instars of A. decempunctata increases with age of the aphid. Aphids showed no kicking response to the presence of fourth instar or adult coccinellids.

Pulling and Waxing

If an appendage of an adult aphid is seized by a first or second instar coccinellid larva, then the aphid can often escape by pulling the appendage free (Table 6). Where both aphid and coccinellid are similar in size the aphid stands less chance of pulling the captured appendage free. Under these conditions a drop of oily liquid may appear at the tip of one or both siphunculi. If the aphid is in a suitable position the siphunculus nearest the point of contact swings over and touches the coccinellid, as described by Busgen (1891). This often results in placing the drop of oily liquid on the head of the coccinellid, where it may spread over the mouth parts, and rapidly solidifies and becomes wax like. Waxing, as it will be referred to here, may immobilize the coccinellid and allow the escape of the aphid (Table 6)

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 Busgen'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 excretory.

Effect of waxing on larvae

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 A. decempunctata larva was touched with the drop. The larva was then watched under a binocular microscope.

After it had been waxed the larva ceased walking, and at most only twitched its legs. After a period of 42 to 94 minutes, active movement began and usually the wax began to flake off. In later instars the wax was cleaned off by the fore limbs and mandibles, after a variable period of inactivity. Once the coccinellid was free of the wax it was as efficient at capturing prey as an unwaxed animal.

Effect of waxing upon escape

First instar coccinellid larvae were allowed to capture

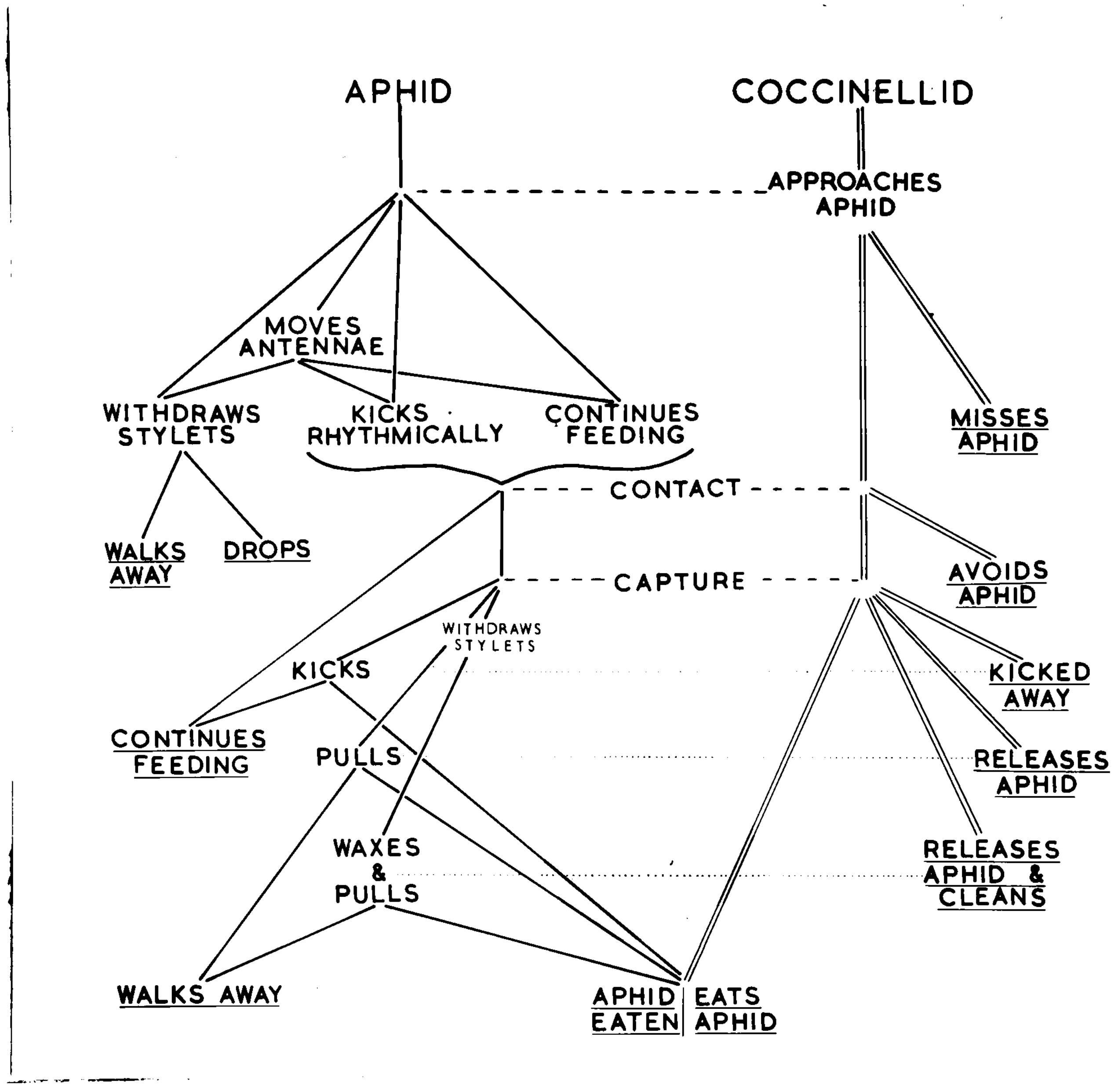

Fig.7. Diagrammatic representation of the possible interactions between the behaviour patterns of Microlophium evansi and Adalia decempunctata during an encounter.

a first instar aphid by a leg and were then experimentally waxed with a second aphid. They were then observed until the captured aphid either escaped or was eaten. As a control, a drop of water about the size of the drop of wax was placed on the head of a number of larvae which had similarly captured an aphid. After experimental waxing, 16 aphids escaped and 4 were eaten; when treated with a water drop, 3 escaped and 17 were eaten. Therefore, waxing facilitated escape ($P < 0.01$). Of 6 larvae which had captured an aphid by the body, and were then experimentally waxed, only one allowed the aphid to escape.

Aphids which have had a leg seized by a coccinellid and cannot pull it free may wax and immobilize the coccinellid, and then escape by pulling. If the aphid waxes the coccinellid after the latter has secured a body hold then it stands less chance of escape.

Responses shown by both aphids and coccinellids to the other's presence vary, and depend mainly upon the instar of aphid and coccinellid. The possible interactions of the aphid and coccinellid behaviour patterns are summarised diagrammatically in Fig. 7.

Effect of the angle of approach of the coccinellid on the aphids chance of escape

As *M. evansi* sees coccinellids when they approach from the front or side, an attempt was made to find if the

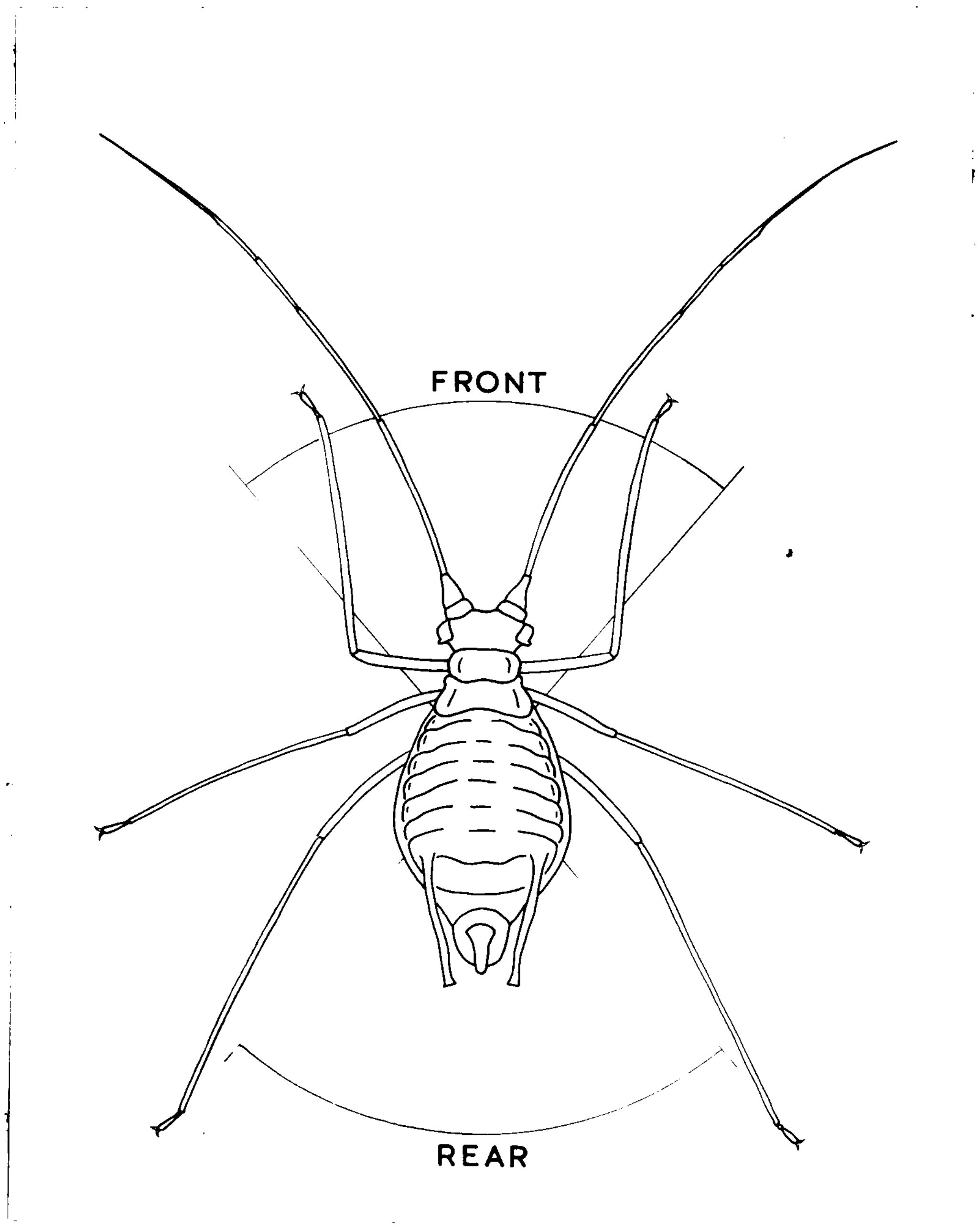

Fig.8. Microlophium evansi adult showing angles of approach of a coccinellid included in front and rear.

coccinellid's approach from the front or from the rear affected the aphid's avoidance of capture. The angle of approach included in front or rear is shown in Fig. 8. The results are given in Table 7.

For the purpose of analysis the total number of captures and the sum of the number of avoidances by walking away and dropping were used. It is concluded that an aphid has less chance of avoiding capture when approached from the rear. Aphids approached from the rear have little warning of the presence of the predator and avoid capture more often by dropping from the plant than by walking. However, the differences do not reach the required level of significance because of the small number of observations.

Aphid orientation on the plant and the direction of approach of the coccinellid

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 8).

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

H. AVAILABILITY OF OTHER SPECIES OF APHID TO A. DECEMPUNCTATA LARVAE

Many other aphid species try to avoid coccinellids that approach them. Quednau (1954) states that all members of the Callaphididae show modifications of their legs which can be correlated with their ability to jump. Davis (1914, p.26) found that in Callipterus trifolii Mon. (Callaphididae) the least disturbance caused it to jump from its host plant and concluded that, "This habit is much to its advantage, for it seems to render the species immune from predaceous and parasitic enemies".

Response shown by members of the Callaphididae to fourth instar A. decempunctata larvae is variable. Of 100 adult and fourth instar Eucallipterus tiliae (L.) observed, 70 avoided capture by jumping when the coccinellid had almost touched them; only 2 avoided capture by walking away. Adult Drepanosiphum platanoides (Schrk.) were observed to avoid capture by jumping on only 2 occasions in 50 encounters; 46 adults responded by walking away. Fourth instar Euceraphis punctipennis (Zett.) were never seen to jump, avoiding capture mainly by walking out of the path of the coccinellid and occasionally by dropping.

Johnson (1907) and Hawkes (1922) have both commented on the fact that highly coloured and woolly aphids are often not readily acceptable to coccinellids. The following observations pertain to aphids which are rejected by A. decempunctat larvae.

Hyalopterus pruni (Geoffr.) is rejected immediately the larva pierces the aphid's body wall. In subsequent attacks the body is not pierced and the aphid is rejected as soon as the coccinellid touches the aphid with its palps. *Aphis fabae* Scop. and *Megoura viciae* Bckt. are attacked and eaten by *Adalia decempunctata* larvae, but after 2 minutes larvae frequently release the aphid and regurgitate the gut contents. *M. viciae* is toxic, as 6 of 12 fourth instar larvae tested died a few days after feeding on this species although offered alternative food. Because of their relatively small size, adult *Aphis fabae* are invariably killed when attacked. However, as adult *M. viciae* are relatively large compared with the coccinellid larvae attacking them, the wounds inflicted are slight, and as a result 3 of 7 were able to survive and reproduce young.

Aphis fabae and *M. viciae* produce a honeydew which is acceptable to the ant *Lasius niger* L.. When *A. fabae* and *M. viciae* 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: p.77). *M. viciae* responds to an ant in the same way as it responds to a coccinellid. When ants touch *M. viciae* they immediately clean their antennae, possibly because of a repellant substance on the body of the aphid. *M. evansi* reacts to an aphid in the same way as it does to a coccinellid; on 2 occasions in 100 encounters they were even seen to wax an ant.

A. fabae is attractive to ants, and does not avoid them in contrast to *M. viciae* which, although its honeydew 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 honeydew is acceptable to them.

Aphids that allow ants to attend them are protected against certain predators. El Ziady and Kennedy (1956) and Banks (1957) showed that *Lasius niger* attending *Aphis fabae* attacks and removes approaching larvae of *Adalia bipunctata* and *C. septempunctata.*

M. evansi when captured by *Adalia decempunctata* may wax the latter and escape. Unlike *M. evansi*, *Dactynotus jaceicola* H.R.L. does not try to avoid *Adalia decempunctata* larvae approaching 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. Should an aphid be captured then large quantities of the wax are placed on the coccinellid larva; several third instar larvae were unable to free themselves from this wax and eventually died although provided with alternative food.

Therefore it may be concluded that certain aphids may avoid an approaching _Adalia decempunctata_ larva and escape being captured in this way, whereas others do not avoid an approaching larva, unless repeatedly disturbed, as their distastefulness or ability to effectively wax the larva, or their normally being attended by ants, affords them some protection.

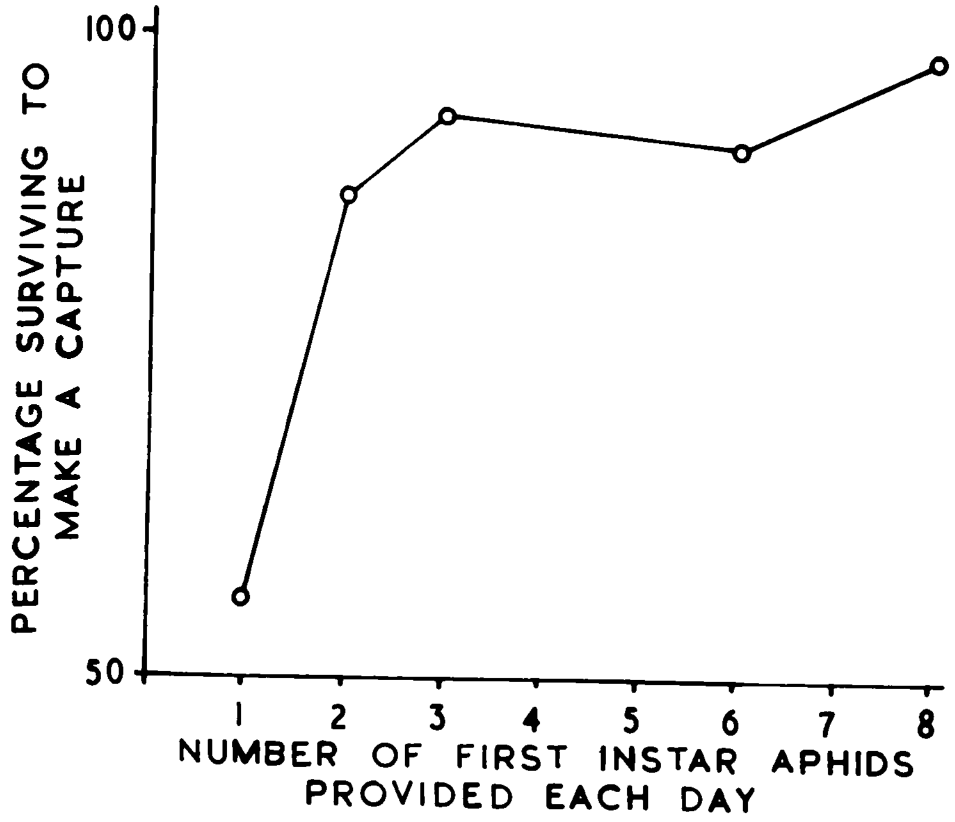

Fig.9. Effect of the number of aphids provided each day on the percentage of first instar Adalia decempunctata larvae surviving to capture an aphid.

I. EFFECT OF THE NUMBER OF APHIDS PROVIDED EACH DAY ON:

1) SURVIVAL OF FIRST INSTAR LARVAE

Effect of the number of aphids provided each day on the proportion of newly hatched larvae capturing their first aphids

First instar larvae from batches in which no mortality had occurred were taken just after dispersal from the egg shells and placed with a fixed number of aphids in separate vials, each containing a nettle leaf 1.5 cm. long and 1.5 cm. broad. Every 24 hours the aphids eaten by each larva were replaced and the number recorded. The results are shown in Table 9 and Fig. 9.

Of 50 larvae each provided with a first instar aphid each day, only 28 captured an aphid; of 65 each provided with three first instar aphids each day, 61 captured aphids. First instar larvae have a much greater chance of capturing their first aphid when provided with three first instar aphids than when provided with one ($P < 0.01$).

Of 28 larvae which captured their first aphid when provided with one aphid each day, 23 survived to make a second capture. First instar larvae have a better chance, therefore, of capturing their second aphid than they do of capturing their first when the same number of aphids is provided each day ($P < 0.05$).

Efficiency incapturing prey

To determine the efficiency of first instar coccinellid

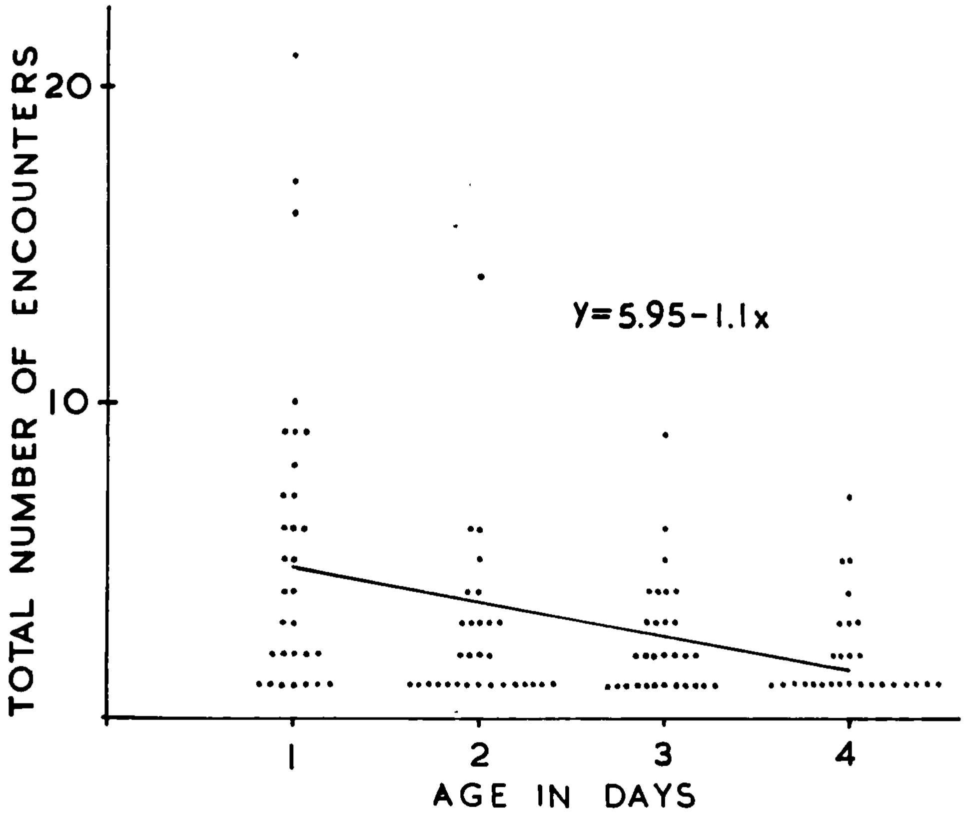

Fig.10. Effect of age on first instar *Adalia decempunctata* larvae, fed one first instar aphid each day, on the average number of encounters required to capture a first instar *Microlophium evansi*.

larvae in capturing first instar aphids on consecutive days, the following experiment was undertaken. Encounters between coccinellid larvae and aphids were observed, (see also p. 19), and the number of encounters required to capture a first instar aphid was recorded. Larvae were tested every 24 hours for four days, so that they captured and consumed one first instar aphid every 24 hours. The experiment was discontinued after four days in order to avoid complications arising as a result of premoulting behaviour. The results are illustrated in Fig. 10.

The efficiency of first instar larvae of A. decempunctata in capturing first instar M. evansi increases from an average of 1 capture in 4.8 encounters on the first day, to 1 capture in 1.5 encounters on the fourth day ($P < 0.01$).

As the numbers of aphids provided each day simulate conditions of different prey population densities, the likelihood of a first instar larva capturing its first aphid would depend upon the aphid population density. Having once captured an aphid, a larva's chance of capturing a second is greater than was its chance of capturing the first. This, in part, is due to an increase in the efficiency in capturing prey.

2) DURATION OF EACH INSTAR AND SURVIVAL OF LARVAE

In the following experiment the number of aphids provided each day to larvae of each instar was varied, and deaths and moults were recorded. From observations, the feeding rate for 50% survival and the time spent in each instar when that number of aphids is provided each day was calculated.

First instar larvae were placed in separate vials with a fixed number of aphids. Every 24 hours consumed aphids were replaced. Larvae failing to make a capture were rejected. Once the number of aphids required to be provided each day for 50% survival in the first instar had been determined approximately, first instar larvae were provided with this number of aphids each day. Those larvae reaching the second instar were split up into batches. Larvae of each batch were provided with a fixed number of aphids each day, the number differing from batch to batch, and the approximate number of aphids required to be provided for 50% survival in this instar was found. Similarly, the number of aphids provided each day required for 50% survival in the third and fourth instars were found. To reduce mortality amongst newly hatched or moulted larvae, these were offered suitable aphids held with forceps. In the instar in which observations were made larvae were never offered aphids, but left to capture their prey.

Even at the highest feeding rates (Table 10) some larvae died. This mortality may be due to the process or after affects of moulting. For probit analysis of the results this mortality was taken as 7%, 6%, and 10%, respectively, for the first, second, and fourth instars. These figures correspond to the mortality observed at the highest feeding rates in each instar; as only three alternative numbers of aphids were provided each day to third instar larvae, no accurate estimate of natural mortality in that instar could be made. Duration of the instar, the total number of aphids eaten, and the average number of aphids eaten each day were recorded (Table 10) for larvae which survived.

The number of aphids required to be provided each day for 50% survival in the different coccinellid instars was calculated (probit analysis) to be: 0.95 ± 0.14 first instar aphids, 2.66 ± 0.22 first instar aphids, 1.07 ± 0.11 third instar aphids, and 1.93 ± 0.15 third instar aphids, for the first, second, third, and fourth instar coccinellid larvae, respectively.

As several first instar aphids are equivalent to the mass of one third instar aphid, larvae of successive instars of A. decempunctata require a greater number of aphids to be provided each day for 50% survival. They also spend a greater length of time in each successive instar.

3) DURATION OF LARVAL DEVELOPMENT AND SURVIVAL, AND ADULT SIZE

Larvae from batches in which no mortality had occurred were taken just after dispersal from the egg shells and placed in separate vials, and provided with a fixed number of first instar aphids. Every 24 hours the vials were examined, consumed aphids replaced, and the occurrence of moulting and

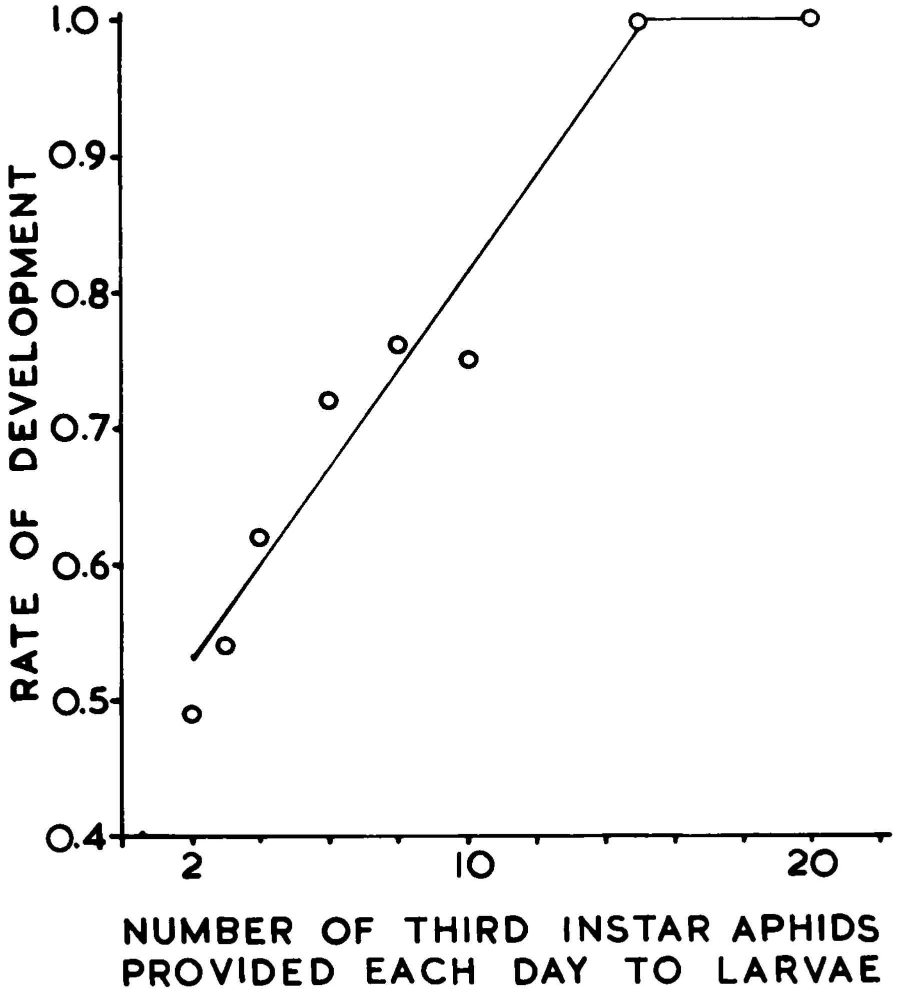

Fig.11. Effect of the number of third instar aphids provided each day to larvae on the average rate of development from eclosion to pupation in Adalia decempunctata.

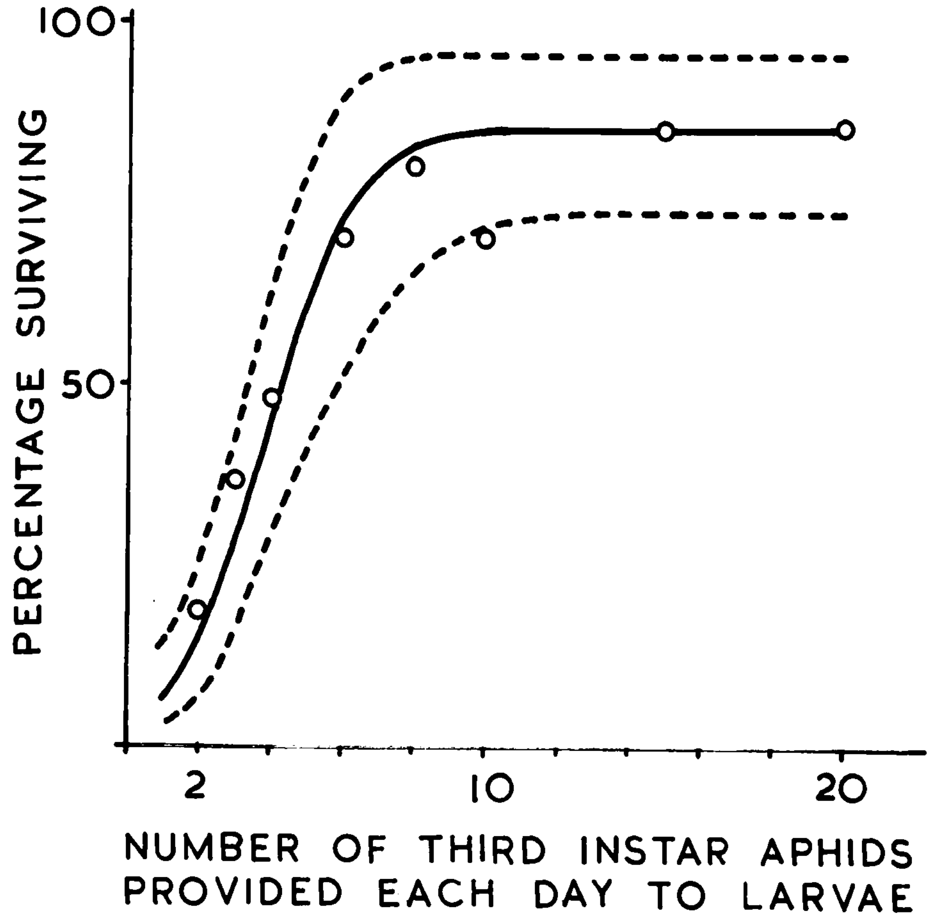

Fig.12. Effect of the number of third instar aphids provided each day to larvae on the average percentage of Adalia decempunctata larvae surviving to become adults, based upon a probit analysis of the results shown in Table 11.

——— = Mean

- - - - = 95% upper and lower fiducial limits

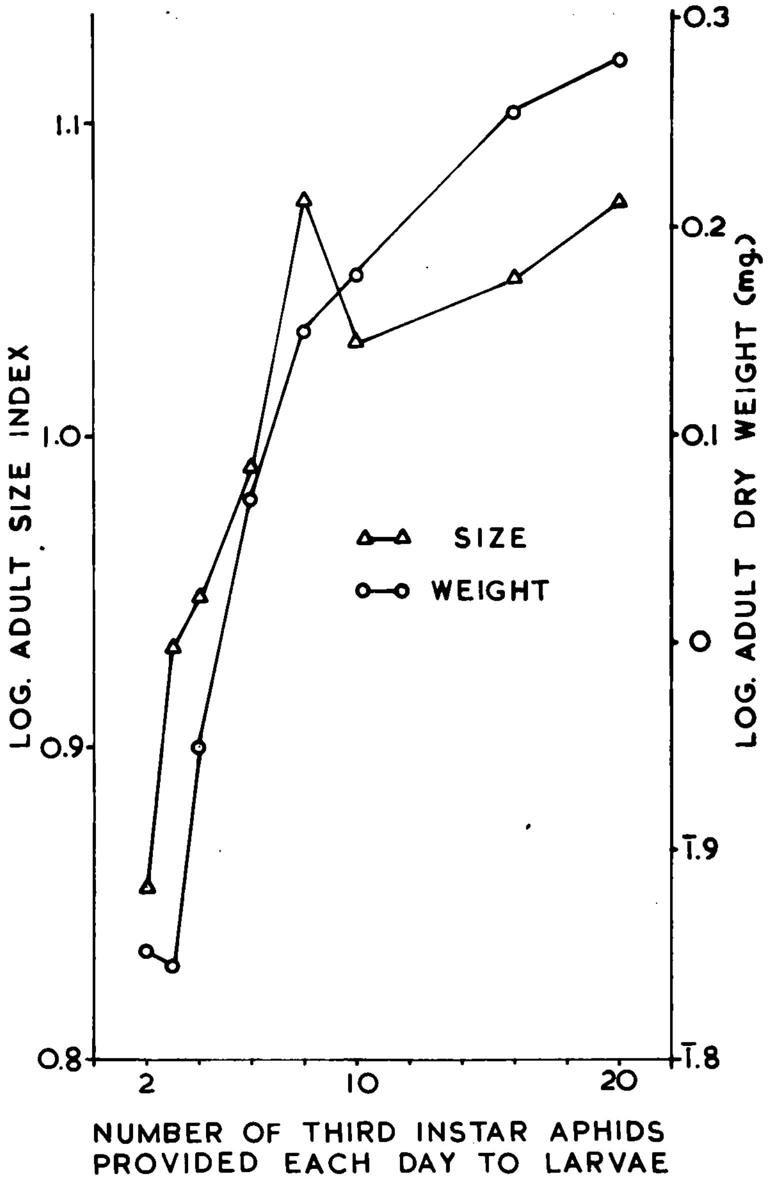

Fig.13. Effect of the number of third instar aphids provided each day to larvae on the average size and dry weight of adult Adalia decempunctata.

pupation noted. On reaching the second instar, larvae were fed third instar aphids. The duration of development, survival, and size of adults were recorded (Table 11).

As the number of aphids provided each day increases from batch to batch (Fig. 11), there is an increase in the rate of development until satiety is reached at approximately 15 aphids each day. The pupal stage lasts 5 days irrespective of the number of aphids consumed by the larvae. The minimum time required for development from eclosion to adult is 15 days at 21°C.

As the number of aphids provided each day increases from batch to batch, there is an increase in the percentage of larvae surviving to become adults (Fig. 12). However, even when a large number of aphids is provided, some mortality occurs just before, or after, moulting.

Adults from the pupae obtained in this experiment were allowed to harden, and then their breadth and length were measured. The product of the measurements of each individual was used as an index of its size. Adults were killed, desiccated, and then weighed. From Table 11 and Fig. 13 it is seen that the size and weight of the adults are greater when the larvae are provided with a large number of aphids each day. Comparison of size and weight, which is achieved by plotting size on a logarithmic scale 1.5 times greater than that for weight, suggests that at the higher feeding rates adults are relatively heavier, possibly due to deposition of fat.

Adults that emerged from 44 pupae of A. decempunctata taken in the field on Malus sp., Tilia x vulgaris Hayne, and Urtica dioica L., feeding on Sappaphis plantaginea (Pass.), Eucallipterus tiliae (L.), and Microlophium evansi, respectively, have an average size index of 11.99 ± 0.30, and an average weight of 2.14 ± 0.07 mg.. Adults reared in the laboratory from larvae provided with 20 aphids per day, the highest feeding rate, have an average size index of 12.0 ± 0.13, and an average weight of 1.924 ± 0.038 mg.. The difference between the average weight of adults obtained from pupae taken in the field and those reared in the laboratory is not significant ($P > 0.05$). However, larger adults have been obtained from pupae taken in the field, the largest size index being 16.63, and the greatest weight, 3.4 mg.. The absence of smaller adults in the field could be due to death at an earlier stage in their development. This appears unlikely and will be discussed more fully in Section N.

J. TIME TAKEN TO CONSUME PREY

As the amount of time available for searching varies with the instar of the coccinellid larva, the following study was undertaken to determine the time taken by A. decempunctata larvae of each instar to consume their aphid prey.

Observations were made in conjunction with those in Section G. On capturing an aphid the coccinellid was removed from the leaf, placed in its vial and the time taken to consume the aphid noted (Table 12).

Within a given instar in A. decempunctata, there is a tendency to take longer to consume successive instars of aphid. The time taken to consume a particular instar of aphid decreases with each successive instar of the coccinellid larva; for example, a first instar larva takes about 30 times as long as a fourth instar to consume a first instar aphid. The actual proportion of time spent feeding in any particular coccinellid instar is considered in the next section.

K. LARVAL POWERS OF SURVIVAL

In order to complete an instar in a certain time, unfed A. decempunctata larvae need to eat a certain weight of aphids. Survival depends upon the efficiency of the larvae in capturing aphids and the area larvae can search. From the following calculations an estimate of the relative aphid population density required for 50% survival in each instar of coccinellid can be made.

The age distribution in a population of M. evansi attacked by A. decempunctata larvae in the field was determined (Table 13). In 100 encounters, in a population of the age distribution shown in Table 13, the number of aphids (N) of an instar which would be captured by an A. decempunctata larva is given by:

$$N = A E \quad .. \quad .. \quad .. \quad \text{(Table 14)}$$

where A is the relative abundance (Table 13), and E the efficiency of a coccinellid larva in capturing that aphid instar (Table 5).

The average size and weight of individuals of each aphid instar were found, and the number of aphids of each aphid instar equivalent to a third instar aphid (one aphid unit) was calculated (Table 15). Where C equals the number of aphid units equivalent to an average individual of a particular aphid instar, the total number of aphid units (U) captured by a coccinellid instar in 100 encounters, all aphid instars considered, is given by:

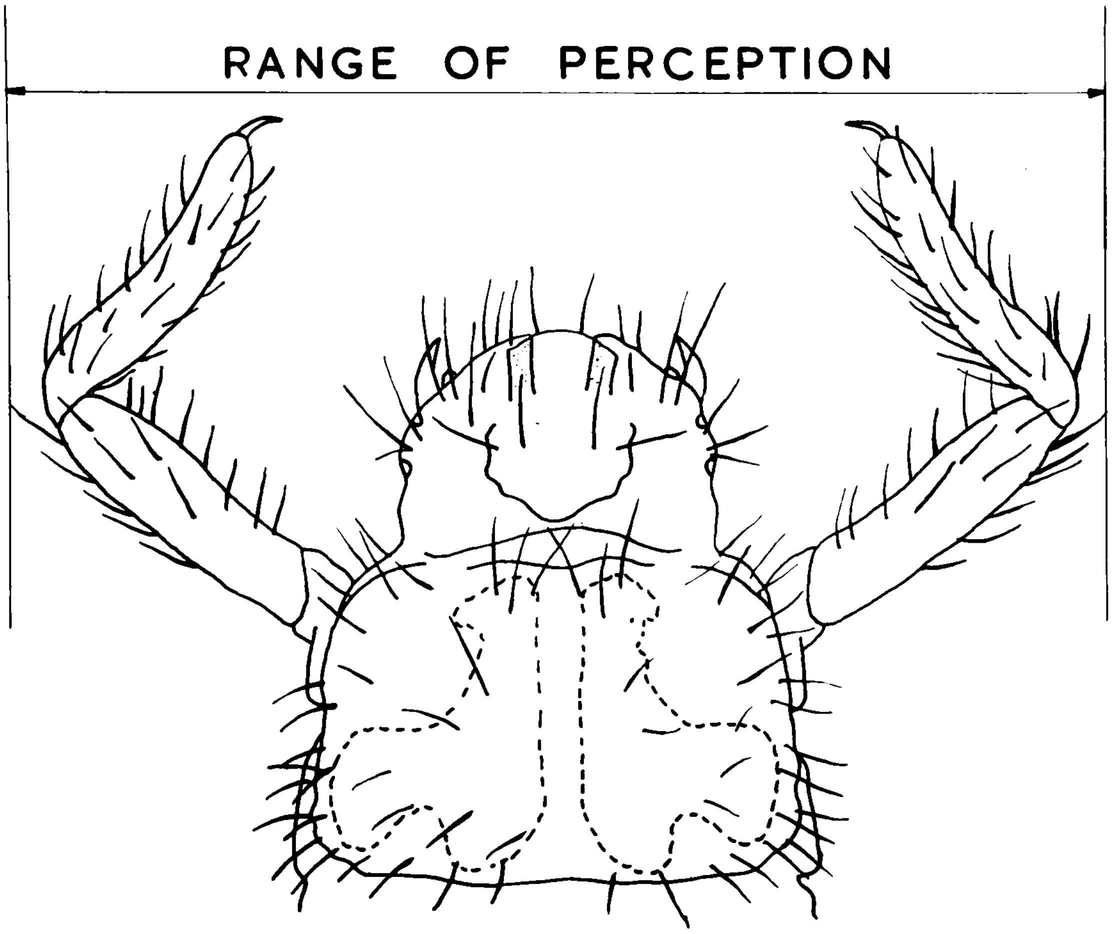

Fig.14. Range of perception of an Adalia decempunctata larva.

$$U = \sum (N C) \quad .. \quad .. \quad \text{(Table 16)}$$

From the number of aphids required for 50% survival in a particular coccinellid instar (Table 10, and p. 33), the number of aphid units required for 50% survival (S) can likewise be calculated (Table 18).

The time (t) taken to consume an aphid of a particular instar is given in Table 12. The time (T_1) taken by a coccinellid instar to consume the aphids of all instars (ΣN) captured in 100 encounters is given by:

$$T_1 = \sum (N \; t) \quad .. \quad .. \quad \text{(Table 17)}$$

Only S aphid units are required for 50% survival; therefore the time (T_2) spent feeding in an instar is given by:

$$T_2 = \frac{T_1 S}{U} \quad .. \quad .. \quad \text{(Table 18)}$$

The time spent in an instar when 50% survived (D) is given in Table 18 (from Table 10). Assuming larvae search 24 hours a day, the percentage time spent consuming sufficient aphid units for 50% survival (L) is given by:

$$L = \left(\frac{T_2}{D}\right) 100 \quad .. \quad .. \quad \text{(Table 18)}$$

Since larvae do not appear to see their prey, touch with the head or forelimbs being required for recognition, a larva's range of perception is taken to be that shown in Fig. 14. The average range of perception (R) of 20 individuals of each instar was calculated (Table 19).

The distance index (D.I.) at the number of aphids eaten

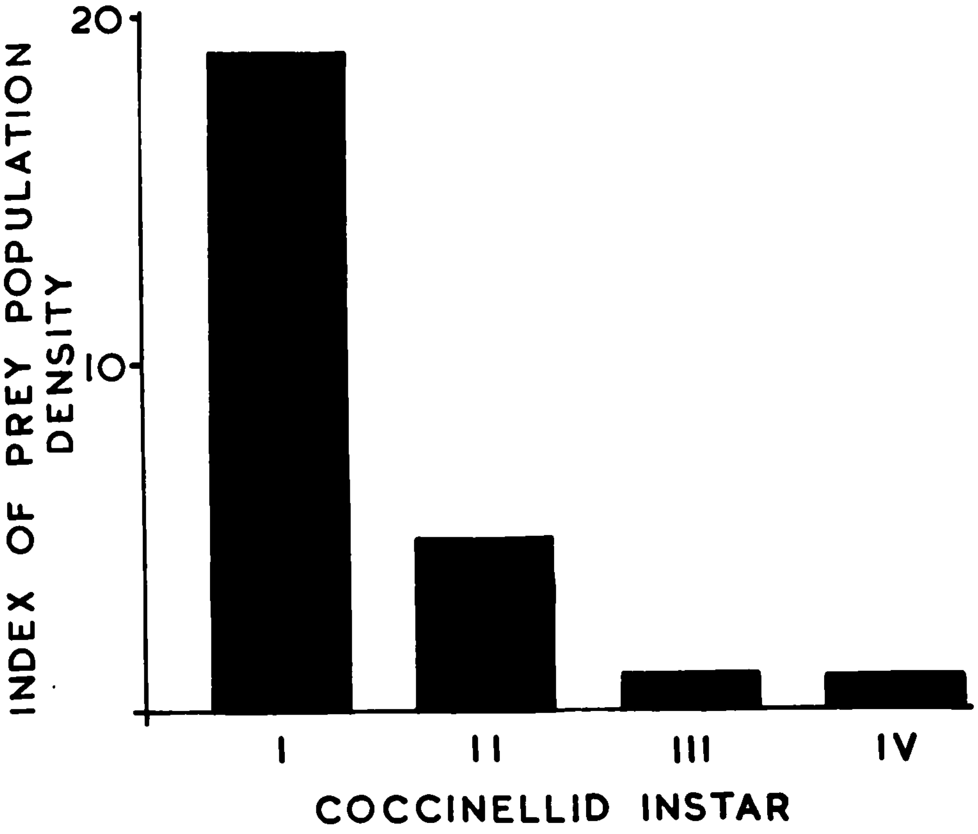

Fig.15. Index of prey population density required for 50% survival in each instar of Adalia decempunctata.

each day when 50% of each instar survived was found from Table 4 (Table 19). An index of the area traversed by larvae when 50% survived ($A.I_1$) is given by:

$$A.I_1 = (D.I.)\ R \quad .. \quad .. \qquad \text{(Table 19)}$$

As some of the time spent in an instar is required for feeding upon the prey captured, the area index has to be corrected to take this into account:

$$A.I._2 = A.I._1 \left(\frac{100 - L}{100}\right) .. \qquad \text{(Table 19)}$$

An index of the prey population density required for 50% survival in each instar ($P.I._1$) is given by:

$$P.I._1 = S/(A.I._2) \quad .. \quad .. \qquad \text{(Table 19)}$$

This assumes that all aphids are equally available. The number of aphid units captured in 100 encounters (U), (Table 16), gives a measure of the availability of the aphid to each coccinellid instar. The prey population index is corrected for availability of prey:

$$P.I._2 = (P.I._1)/U \quad .. \quad .. \qquad \text{(Table 19)}$$

This gives a prey population index (prey population index 2, Table 19, Fig. 15) for 50% survival in each instar.

For 50% survival, first instar larvae require an aphid population density 18.8 times greater than fourth instar larvae. This difference would be greater if the pronounced tendency of first instar larvae to recross their tracks (Section E) were taken into consideration. The increase in the area index of successive instars of coccinellid is partly offset by the increase in the number of aphid units required for 50% survival.

A decrease in the proportion of young aphids would greatly increase the aphid population density required for survival in the first instar. If the aphid age distribution in Table 13 were reversed, a condition which could occur in an older population, the aphid population density required for 50% survival in first instar larvae would be 50 times greater than for fourth instar larvae. Oviposition near or in young aphid colonies of very high density is therefore necessary for the survival of first instar larvae; and a larger proportion of successive instars would survive.

The efficiency in capturing prey used in the above calculation is based upon observations of newly hatched or moulted larvae (p. 19). As first instar larvae increase in age their efficiency in capturing prey also increases. On the fourth day they are as efficient as newly emerged second instar larvae in capturing first instar _M. evansi_ (Figs. 5, 10). Therefore, even within the first instar the aphid population density required for 50% survival will decrease as the coccinellid increases in age. This may also be true for the later instars, but may not be as marked. Eating of unhatched eggs and dead or dying larvae by active and predispersal larvae, respectively, (p. 9), would also decrease the aphid population density required for 50%

survival in the first instar.

In the field, Kuenen (1945) and Putman (1955) have shown that larval survival in *Scymnus minimus* and *Stethorus punctillum*, respectively, feeding on *Metatetranychus ulmi* Koch, is dependent upon abundance of prey. Banks (1956b) could find no evidence of a correlation between survival rate in coccinellid larvae (considering 5 species collectively) and population density of *Aphis fabae*. He suggests that larger quantities of honeydew on heavily infested plants hindered feeding of young larvae. However, he estimates that a greater percentage of older larvae survives than of younger larvae.

L. AREA OF DISCOVERY OF LARVAE

Nicholson (1933, pp. 144, 165) assumes that the area traversed by an average individual during its life time is a constant. The area effectively traversed is referred to as the area of discovery of the species. If the average individual captured only half the prey that it met, then the area of discovery would be half the area traversed. He assumes that the efficiency of capture of an average individual when searching is constant, and therefore the area of discovery is constant.

A. decempunctata must move almost continuously to capture M. evansi even in relatively dense populations of the aphid, as the latter tends to avoid the larvae and be diffusely distributed over the host plant. Use of the distance index as a measure of the distance travelled (p. 18) is therefore justifiable, until satiation comes into effect. The distance index when a large number of aphids is eaten each day is possibly an overestimate as the animals are tested under conditions in which they are more likely to walk. Therefore, the distance travelled at the higher feeding rates is probably less than the distance index indicates. However, the suggestion (p. 18) that the area traversed by A. decempunctata larvae is greater at the lower prey population densities is valid. Therefore, assuming even that efficiency of capture is independent of prey population density, which is unlikely, the area of discovery decreases with increasing prey population density for A. decempunctata.

M. ADULT ACTIVITY AND OVIPOSITION

Gilliat (1935) noticed that well fed adults of *Stethorus punctorum* Lec. tend to remain at rest on leaves for periods of half to one hour. Putman (1955) noticed that if food is scarce activity is prolonged in *S. punctillum*, and fewer eggs are laid. To determine the effect of feeding rate on activity and oviposition in *A. decempunctata* adults the following experiments were undertaken.

Activity

A. decempunctata females placed in separate vials were each provided with a fixed number of third instar aphids. Every 24 hours consumed aphids were replaced. The females were allowed five days to accommodate to the conditions, and were then placed in celluloid tubes 21.6 cm. long and 1.5 cm. in diameter, closed at each end by a rounded celluloid cap. The tubes were laid on a bench beneath fluorescent lighting which gave a light intensity of 376 metre candles at bench level, the tubes being screened from one another. After 15 minutes, the females were observed every 10 minutes and any activity (walking) was recorded. Observations were made over a period of 2½ hours, and repeated every five days until each adult had been tested four times. The temperature was maintained at 21°C..

Not all aphids provided were eaten, even when only 4 were provided each day. For purposes of analysis the average number of aphids eaten each day when provided with 4, 8, 16,

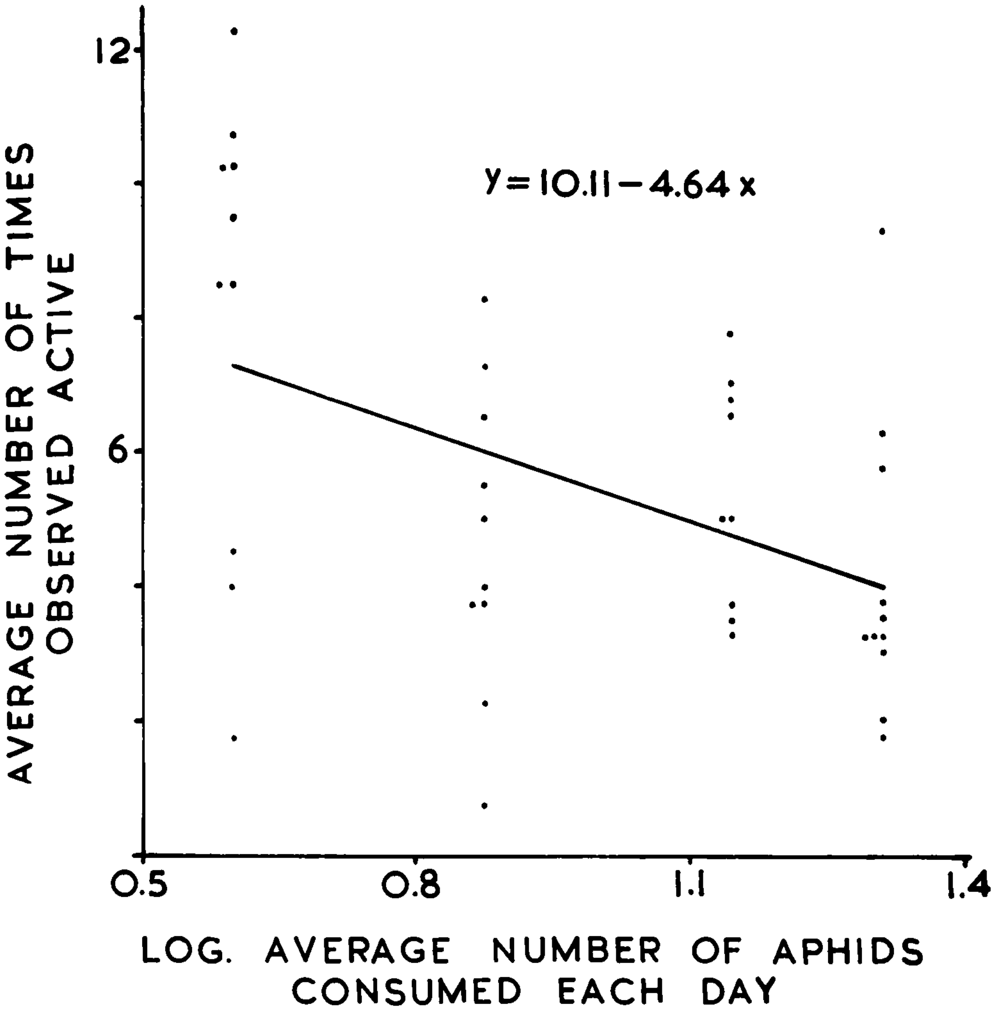

Fig. 16. Effect of the number of third instar aphids consumed each day on the activity of adult female *Adalia decempunctata*.

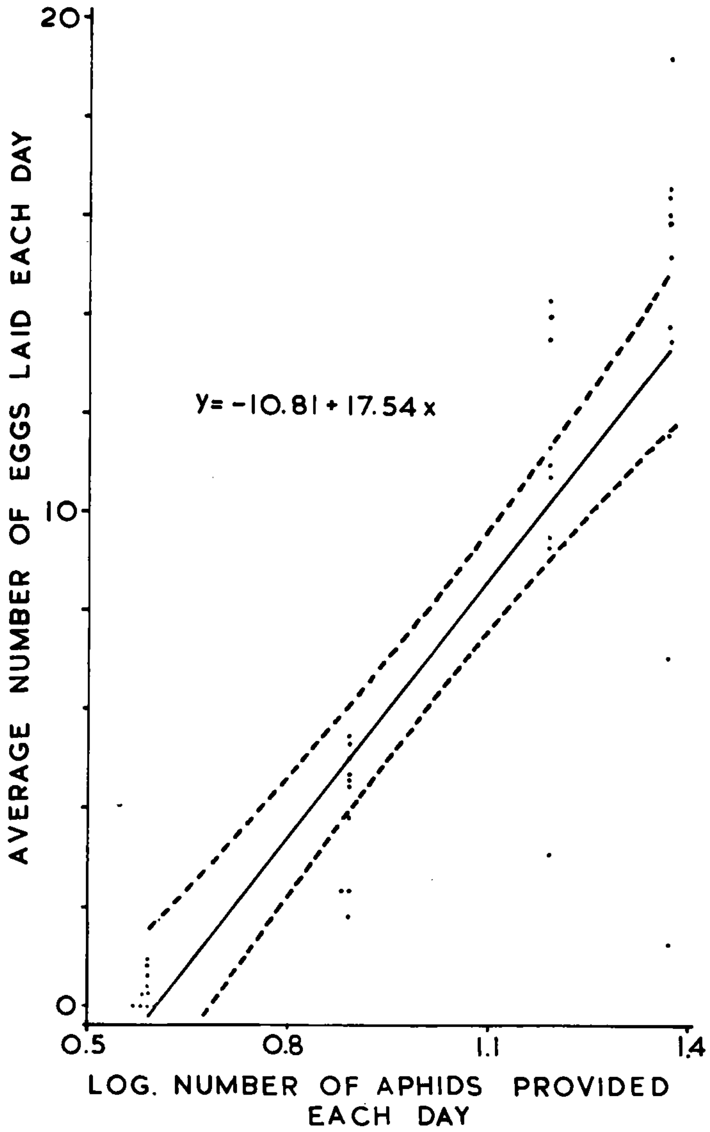

Fig.17. Effect of the number of third instar aphids provided each day on the number of eggs laid each day by Adalia decempunctata.

------ = 95% upper and lower fiducial limits and 24 third instar aphids, respectively, each day, and the average number of times activity was observed, for each individual was used.

Activity of A. decempunctata decreases as the average number of aphids consumed each day increases (Fig. 16). This behaviour would tend to keep adults in the close vicinity of dense aphid populations.

Oviposition

These results were obtained in conjunction with those of the above experiment. Females were allowed to mate before the start of the experiment and again two weeks later. After the first five days eggs were removed from the vials and counted. As adults will eat their eggs when aphids are scarce, eggs were removed three times a day. There was no evidence to show that females ate any eggs during the experiment.

After 20 days adults were killed, their ovaries removed and stained in acetocarmine. The numbers of mature eggs, and of immature eggs at least three quarters the size of mature eggs, were noted (Table 20).

The number of eggs laid by A. decempunctata increases as the number of aphids eaten each day increases, the rate of increase falling off at the higher feeding rates. Fig. 17 shows a linear relationship between the number of eggs laid each day by each female and the logarithm of the number of aphids provided each day. The increase in the number of mature and nearly mature eggs in the ovaries also falls off at higher feeding rates.

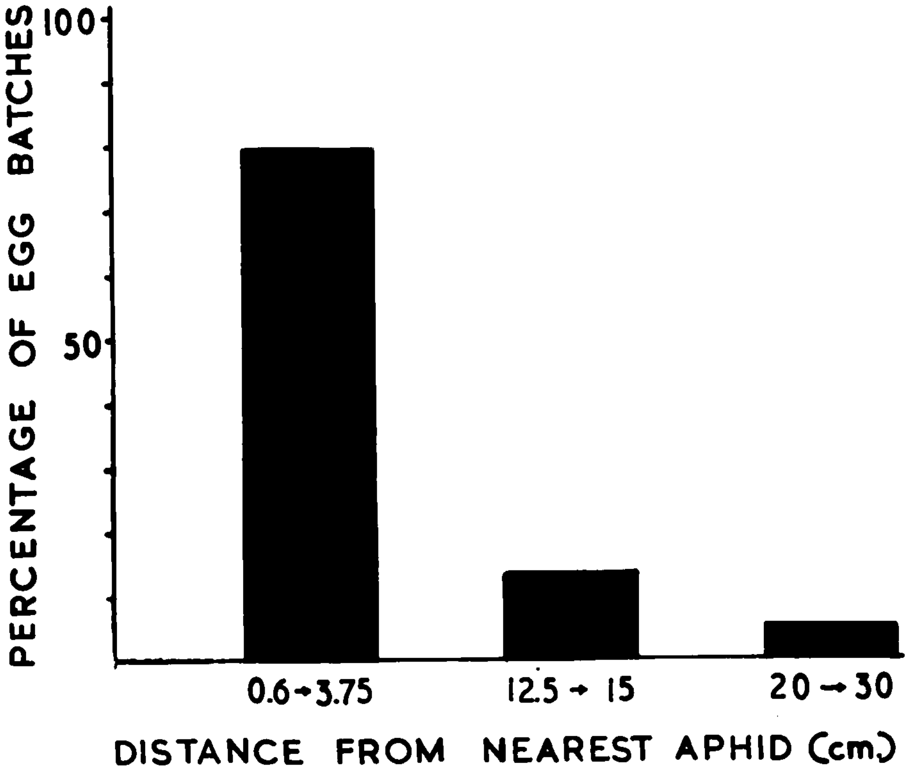

Fig. 18. Distance of Adalia decempunctata egg batches from the nearest aphid on Tilia x vulgaris.

N. OVIPOSITION SITES OF *A. DECEMPUNCTATA* IN THE FIELD

Egg batches of *A. decempunctata* were collected from a lime tree, *Tilia x vulgaris*, infested with *Eucallipterus tiliae* in the University Parks, Oxford, in 1956. This aphid does not aggregate, but is diffusely distributed over its host. Of 319 leaves from the periphery of the tree, 61 were infested with aphids. The most abundant coccinellid adult attacking *E. tiliae* was *A. decempunctata*. However, a few *A. bipunctata*, *Coccinella septempunctata* and *Propylea quatuordecimpunctata* were seen. Batches of large eggs (*C. septempunctata*) and orange eggs (*A. bipunctata*) were not recorded. The distance between the egg batch and the nearest aphid was noted.

Of 37 egg batches, comprising a total of 526 eggs, 81% were laid within 3.75 cm. of an aphid (Fig. 18). Eggs were either on leaves infested with aphids or close to infested ones.

The proximity of coccinellid eggs to larval food has been noted in *Hyperaspis binotata* Say (Simanton, 1916), *A. bipunctata* (Jöhnssen, 1930), *C. septempunctata* (Bodenheimer, 1943), *Scymnus minimus* Payk. (Kuenen, 1945), *Stethorus punctillum* (Putman, 1955), and *Chilocoris stigma* Say (Muma, 1955). Eggs laid some distance from larval food, or on plants bearing little or no larval food, are probably laid soon after the adults have left a locality where aphids are present. For example, *A. bipunctata* feeds upon nettle aphids and oviposits on beans (Banks, 1956b). However, in this case, since Aphis fabae does not avoid coccinellids (p. 27), the lowest average population density per stem he recorded may have been sufficient for the coccinellids to have matured eggs.

Adults of Adalia decempunctata appear to oviposit close to aphids because they are less active when well fed and consequently remain in the vicinity of aphids. The chance of eggs occurring close to aphids is further increased because the oviposition rate increases with food supply.

As first instar A. decempunctata larvae require a prey population density 18 times greater than the fourth instar for 50% survival (p. 39), the relative inefficiency of adults compared with third and fourth instar larvae (Fig. 5) in capturing M. evansi may be of adaptive significance. If the adult can capture sufficient aphids in unit time to bring about an appreciable decrease in its activity and increase in the rate of maturation of its eggs, then the larvae have a greater chance of surviving. If larvae can survive the first instar then the chance of their survival in the later instars will be great and they will give rise to large adults. This probably accounts for the absence of small adults in the field (p. 35).

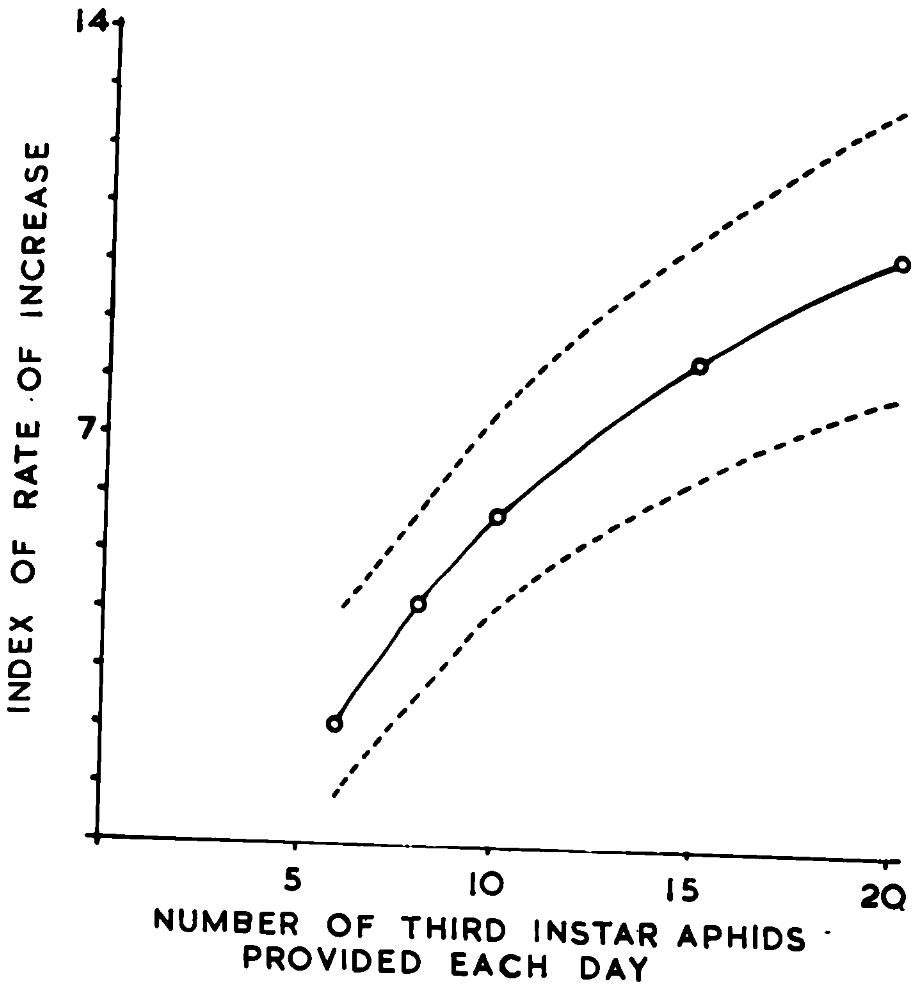

Fig.19. Effect of the number of third instar aphids provided each day on the index of rate of increase of <u>Adalia decempunctata</u>.

-------- = 95% upper and lower fiducial limits

O. RATE OF INCREASE

The rate of increase of a species is equal to the total number of births minus the total number of deaths in unit time. Thompson (1922) used a generation as a unit of time. Lotka (1923) criticised this on the basis that the delimitations of a generation are ill-defined. Nicholson (1933) also uses a generation as a unit of time. For insects which have only one generation a year this is acceptable. A. decempunctata, like A. bipunctata (Jöhnssen, 1930; and Banks, 1955), may have more than one generation in more favourable years, but for simplicity it is assumed that A. decempunctata has only one.

Assuming that irrespective of the number of aphids eaten each day, adults of A. decempunctata live the same length of time, then the number of eggs laid each day per female (Fig. 17) multiplied by the percentage survival of larvae when the same number of aphids is provided (Fig. 12), gives an index of the rate of increase in relation to the number of aphids provided each day (Fig. 19). Different numbers of aphids provided each day simulate the conditions of different aphid population densities. Therefore the rate of increase of A. decempunctata depends upon aphid population density. At higher prey population densities the rate of oviposition tends to become constant and there is no further rise in the percentage survival.

Volterra (1931, p. 415) considers that the coefficient

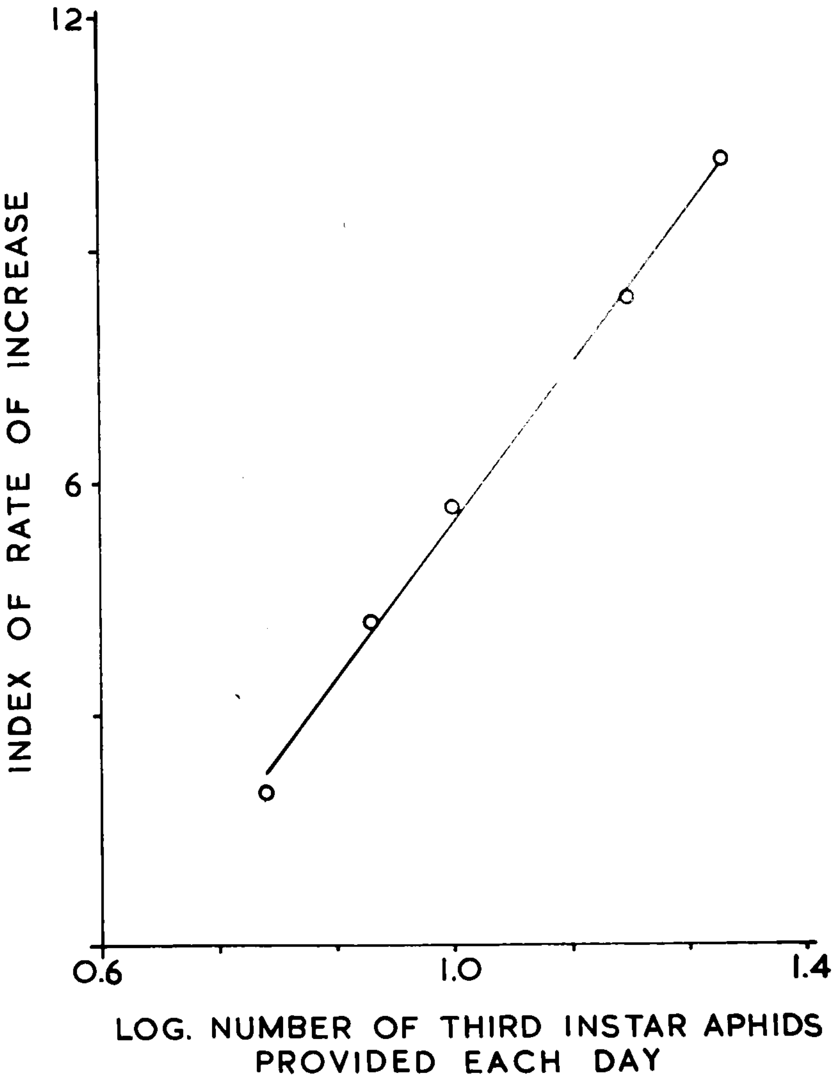

Fig.20. Index of rate of increase of Adalia decempunctata in relation to the logarithm of the number of third instar aphids provided each day.

of decrease of a predator is linear in relation to prey population density or some function of prey population density. For simplicity in his calculations he considers it is linear in relation to prey population density. However, over the range of aphid population densities used, Fig. 20 shows a linear relation between the rate of increase, or the coefficient of decrease of A. decempunctata, and the logarithm of prey population density. Volterra states that even if the rate of increase is non linear in relation to prey population density the mode of integration used in his calculations would still work out the same.

Nicholson (1933) also assumes that the rate of increase of a predator population is limited by the population density of its prey. However, Nicholson (l.c., pp. 148, 166) states that, "the number of offspring produced, though it may be influenced, is clearly not proportional to the number of prey eaten by the predator." and, "All mature predators tend to produce a surplus of offspring, so it is clear that in the steady state this surplus must in some way be destroyed." Thus with increasing prey population density there would be a corresponding increase in the survival of predator offspring, for then fewer would die as a result of difficulty in finding prey.

Although Nicholson's assumption that the number of eggs produced by a predator is not proportional to the number of prey eaten is not valid for A. decempunctata, except at the very highest feeding rates used, the assumption that the rate of increase of a predator is limited by the prey population density is valid.

P. DISCUSSION

Imms (1947, p. 129) in considering the prey of ladybirds 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." The results in Section G show that the aphid M. evansi is neither helpless nor sedentary.

Members of the Callaphididae also try to avoid A. decempunctata larvae that approach them (p.26). The Callaphididae maintain a diffuse distribution over their host plant, as is also typical of some Aphididae, for example, Acyrthosiphon spartii (Koch) and M. evansi. The combination of diffuse distribution over the host plant and the ability to avoid capture by a predator is of survival value, since A. decempunctata will usually remain in the area and oviposit only when the aphid population density is relatively high.

Aphids which do not react to the presence of A. decempunctata larvae by moving away, and appear helpless, are usually either attended by ants, distasteful to, or are capable of effectively waxing this predator (pp. 26-29). The fact that aphids which appear helpless are the most conspicuous, because they are highly coloured or tend to be gregarious, could very well have given rise to the general impression that aphids are helpless and sedentary.

Varley (1941, p. 48), quoting Laing (1937), states that an animal moves at random when it finds the things it seeks, "by movements which, until they are influenced by the qualities of the object sought, are random with respect to it. When the qualities are perceived they direct the movement, which thereupon ceases to be random." As touch is necessary before A. decempunctata larvae or adults respond to the presence of an aphid (p. 20), they can be said to move at random with respect to their prey.

Individuals of A. decempunctata search independently of one another as they will cross each other's tracks. Therefore, "the searching within the population is unorganized, and therefore random" (Nicholson 1933, p. 141). Varley (1941, p. 48) in considering "random search" as used by Nicholson (l.c.), and Nicholson and Bailey (1935) states that, "Their use of the term shows that in random search the number of encounters between predator and prey, or parasite and host, is proportional to the product of the population densities of the two species". Volterra (1931, p. 425) also assumes this to be the case for the number of encounters between individuals of two species one of which feeds upon the other. Nicholson (1954, p. 62) states that he uses random search as a convenient term for the underlying mechanism of the probability relation, as used by Volterra in his equations.

Bodenheimer (1932) states that *Novius cardinalis* Muls. adults leave old infestations of *Icerya purchasi* Mask. when these are reduced to a minimum, and attack recently established colonies of *I. purchasi* in other parts of the orchard. Increasing activity in *A. decempunctata* adults with decreasing prey population density would also lead them to occupy and lay most of their eggs in those areas where the prey population density is high, and to leave an area as soon as the prey population density fell to a certain critical level. The larvae also tend to concentrate their attack in those areas which are most heavily infested (p. 15). Therefore, at low overall prey population densities the number of encounters between *A. decempunctata* and its prey would be greater than expected by random search in the sense used by Nicholson (1933, 1954) and Nicholson and Bailey (1935), or the probability relationship used by Volterra (1931).

Nicholson (1933, p. 171) also considered the case of a polyphagous predator that concentrates its attack in those areas where a species of prey is abundant. He concludes that this would tend to damp any fluctuations in the density of the prey, and also allows a single species of predator to control simultaneously the densities of a number of different species of prey.

Nicholson (1933) and Nicholson and Bailey (1935) assume that the area traversed by an average individual and the efficiency of the individual in obtaining objects of the required kind it meets, are constant. The area effectively traversed, or the area of discovery of the species, incorporates these two assumptions. Andrewartha and Birch (1954, p. 438) conclude on very slender evidence that the area traversed by a predator depends upon the prey population density. The results obtained in the present study are in agreement with this conclusion, and show that the area traversed by A. decempunctata larvae is dependent upon the prey population density. Since the activity of adult female A. decempunctata also depends upon the number of aphids eaten (Fig. 16, p. 44), and therefore on prey population density, the area traversed by adults is not a constant.

The assumption that the rate of increase of a predator population increases with prey population density (Volterra, 1931; Nicholson, 1933) is valid for A. decempunctata. However, the assumption (Nicholson, 1933) that it is brought about solely by increasing survival of surplus offspring produced, is not valid for A. decempunctata. Other predators, such as Syrphids, where the adults do not feed on the same food as their larvae, may however, respond in the way suggested by Nicholson.

The present laboratory study has shown that the area effectively traversed by A. decempunctata is not constant, as assumed by Nicholson, nor is the number of encounters between A. decempunctata and its prey at low overall prey population densities likely to be as low as one expects from the theories of Nicholson and Volterra. Therefore, theories based on the assumption that the area effectively traversed is constant and, or, that random search occurs must be used with caution. However, the claim (Thompson, 1939, p. 358) that any theory based on the idea that animals search at random is untenable, and the rejection (l.c., p. 359) of the assumptions of Nicholson and Volterra, that survival and reproductive rate are a function of the prey population density, cannot be accepted here.

Q. SUMMARY

1) A study has been made of the behaviour of the predatory coccinellid beetle, Adalia decempunctata (L.), and its prey, the nettle aphid Microlophium evansi (Theob.).

2) Just after hatching, larvae of A. decempunctata will not eat dead or living newly emerged larvae, but will consume eggs. Prior to dispersal from the egg shells larvae will consume dead or freshly emerged larvae.

3) Of eggs containing well developed embryos which fail to hatch at the time when the majority of the batch do so, most are eaten, but few are capable of hatching successfully.

4) Larvae are negatively geotactic and positively phototactic.

5) In searching a leaf larvae spend most time on the rim and veins. Most nettle aphids on leaves are found either on the veins or very close to the edge of the leaf.

6) Well fed larvae tend to search an area much more thoroughly than starved ones. Starved first instar larvae search an area much more thoroughly than starved second, third, and fourth instar larvae.

7) The tendency of starving fourth instar larvae to revisit the apex of a cylinder where there are no aphids decreases as the period of starvation increases.

8) In each successive instar unfed larvae are capable of

covering a greater distance before succumbing to starvation. Larvae which consumed very few aphids each day traversed a greater area than those that received rather more.

9) As larvae increase in age their efficiency in capturing the aphid M. evansi increases. Larvae are more efficient in capturing young aphids. Efficiency of adults lies between that of the second and third instar larvae.

10) M. evansi tries to avoid capture by a coccinellid that approaches it by walking out of its path, dropping off of the plant, or by rhythmical kicking. If captured the aphid tries to kick the coccinellid away, pull the appendage free, or wax the coccinellid and then pull the appendage free. The response depends upon the instar of aphid and coccinellid involved.

11) M. evansi has less chance of avoiding capture when approached from the rear. On nettle stems the aphid normally faces downwards, and on leaves towards the petiole

12) The availability of other species of aphid to A. decempunctata larvae is also considered.

13) Having once captured an aphid, a first instar larva's chance of capturing a second is greater than was its chance of capturing the first. As a first instar

larva increases in age its efficiency in capturing its aphid prey increases.

14) For 50% survival the number of aphids necessary per vial each day is 0.95 ± 0.14 first instar aphids, 2.66 ± 0.22 first instar aphids, 1.07 ± 0.11 third instar aphids, and 1.93 ± 0.15 third instar aphids, for first, second, third, and fourth instar coccinellid larvae, respectively. The time spent in the instar at such a feeding rate that 50% survived increases with each successive instar.

15) With increasing aphid population density there is an increase in the rate of development and percentage survival of larvae until satiety is reached when approximately 15 third instar aphids are provided per day. The size and weight of adults are greater when larvae are provided with a large number of aphids each day.

16) Adults emerging from pupae taken in the field were of the same average size and weight as those reared from larvae provided with 20 third instar aphids each day.

17) In each successive instar the time taken to consume a particular aphid instar decreases. Fourth instar larvae take 12 times longer to consume an adult aphid than they do a first instar aphid.

18) For 50% survival first instar larvae require a prey population density many times greater than that required by fourth instar larvae. The actual value is mainly dependent upon the age distribution of the aphid population being attacked.

19) The area of discovery of *A. decempunctata* larvae depends upon the prey population density.

20) Adult females lay a greater number of eggs per unit time and are less active when well fed.

21) Egg batches of *A. decempunctata* in the field are usually found either on leaves infested with aphids or close to infested ones.

22) Over the range of aphid population densities used experimentally the rate of increase of *A. decempunctata* is proportional to the logarithm of the aphid population density.

23) The behaviour of aphids and its bearing on the general impression of aphids is discussed. The searching ability and rate of increase of *A. decempunctata* are also considered in relation to the assumptions of Nicholson and Volterra.

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REFERENCES

Andrewartha, H.G., & Birch, L.C., 1954. The distribution and abundance of animals. Chicago.

Banks, C.J., 1954. The searching behaviour of coccinellid larvae. *Brit. J. anim. Behav.*, **2** : 37-38.

--- 1955. An ecological study of Coccinellidae (Col.) associated with *Aphis fabae* Scop. on *Vicia faba*. *Bull. ent. Res.*, **46** : 561-587.

--- 1956a. Observations on the behaviour and mortality in Coccinellidae before dispersal from the egg shells. *Proc. R. ent. Soc. Lond.*,(A) **31** : 56-60.

--- 1956b. The distributions of coccinellid egg batches and larvae in relation to numbers of *Aphis fabae* Scop. on *Vicia faba*. *Bull. ent. Res.*, **47** : 47-56.

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

Bodenheimer, F.S., 1932. *Icerya purchasi* Mask., und *Novius cardinalis* Muls.. Eine bevölkerungswissenschaftliche Studie über die Grundlagen der biologischen Bekampfung. *Z. angew. Ent.*, **19** : 514-543.

--- 1943. Studies on the life history and ecology of Coccinellidae: 1. Life history of *Coccinella septempunctata* L. in four different zoogeographical regions. *Bull. Soc. Fouad Ent.*, **27** : 1-28.

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 trifollii* Monell.), *Tech. Ser. U.S. Bur. Ent.*, **25** : 17-40.

El-Ziady, S., & 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** : 233-265.

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 : 235-236.

Gilliat, F.C., 1935. Some predators of the European red mite Paratetranychus pilosus C. & F. in Nova Scotia. Canad. J. Res., (D) 13 : 19-38.

Hawkes, O.A.M., 1920. Observations on the life-history, biology and genetics of the lady-bird beetle Adalia bipunctata (Mulsant). Proc. zool. Soc. Lond., 1920 : 475-490.

--- 1922. The cannibal ladybird. Conquest 3 : 399.

Horvath, G., 1905. Sur les cornicules ou nectaires des Aphidiens. C.R. 6me Congr. int. Zool. Berne 1904 : 421-424.

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., & Kennedy, J.S., 1951. Aggregation in Aphis fabae Scop. 1. Aggregation on plant. 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 18 : 171-174.

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

Kuenen, D.J., 1945. On the ecological significance of two predators of Metatetranychus ulmi C.L.Koch (Acari, Tetranychidae). Tijdschr. Ent., 88 : 303-312.

Kyber, J.F., 1815. Einige Erfahrungen und Bemerkungen über die Blattläuse. [In] Germar, Magazin der Entomologie, 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.

Laing, J., 1937. Host finding by insect parasites. 1. Observations on the finding of hosts by Alysia manducator, Mormoniella vitripennis and Trichogramma evanescens. J. Anim. Ecol., 6 : 298-317.

Lotka, A.J., 1923. Contribution to quantitative parasitology. *J. Wash. Acad. Sci.*, **13** : 152-158.

Muma, M.H., 1955. Some ecological studies on the twice stabbed lady beetle, *Chilocorus stigma* (Say). *Ann. ent. Soc. Amer.*, **48** : 493-498.

Nicholson, A.J., 1933. The balance of animal populations. *J. Anim. Ecol.*, **2** : 132-178.

--- 1954. An outline of the dynamics of animal populations. *Aust. J. Zool.*, **2** : 9-65.

Nicholson, A.J., & Bailey, V.A., 1935. The balance of animal populations.- Part 1. *Proc. zool. Soc. Lond.*, **1935** : 551-598.

Palmer, M.A., 1914. Some notes on life history of ladybeetles. *Ann. ent. Soc. Amer.*, **7** : 213-238.

Putman, W.L., 1955. Bionomics of *Stethorus punctillum* Weise (Coleoptera: Coccinellidae) in Ontario. *Canad. Ent.*, **87** : 9-33.

Quednau, W., 1954. Monographie der mitteleuropäischen Callaphididae [Zierlause (Homoptera, Aphidina)] unter besonderer Berücksichtigung des ersten Jugendstadiums. 1. Die Junglarven des ersten Stadiums der mitteleuropäischen Callaphididae. *Mitt. biol. Zent. Anst. Berl.*, Heft **78**.

Réaumur, R.A.F. de, 1738. Memoires pour servir de l'histoire des insectes, **3** (2). Paris.

Simanton, F.L., 1916. *Hyperaspis binotata*, a predatory enemy of the terrapin scale. *J. agric. Res.*, **6** : 197-203.

Smee, C., 1922. British ladybird beetles. Their control of aphids. *Fruit. Gr.*, **53** : 675-676, 717-718, 759-760.

Thompson, W.R., 1922. Théorie de l'action des parasites entomophages. Les formules mathématiques du parasitisme cyclique. *C.R. Acad. Sci. Paris* **174** : 1201-1204.

--- 1939. Biological control and the theories of the interactions of populations. *Parasitology* **31** : 299-388.

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

Varley, G.C., 1941. On the search for hosts and the egg distribution of some chalcid parasites of the knapweed gall-fly. Parasitology 33 : 47-66.

Volterra, V., 1931. Variations and fluctuations of the number of individuals in animal species living together. [In] Chapman, R.N., Animal ecology. New York.

Table 1.

The number of times third instar *Adalia decempunctata* larvae were observed on different parts of a *Typhonium giraldii* leaf.

No. of larvae tested	Total no. of observations	Area between veins				Veins				Rim			
		Observed		Expected		Observed		Expected		Observed		Expected	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
10	832	149	17.9	736	88.5	288	34.6	70	8.4	395	47.5	26	3.1

Table 2.

Results of multiple regression analysis of the average number of aphids consumed each day (y), the number of turns executed (x), and the distance travelled (z) by *Adalia decempunctata* larvae.

Correlation Coefficients				Regression Equation	Multiple Correlation Coefficient
Second Instar (n = 81)					
	y	x	z		
y	-	0.29**	-0.20		
x	0.29**	-	0.25*	$y = 4.38 + 0.39x - 0.012z$ $(\pm 0.12)\ (\pm 0.004)$	0.40 **
z	-0.20	0.25*	-		
Third Instar (n = 87)					
y	-	0.48**	-0.21		
x	0.48**	-	0.07	$y = 2.20 + 0.23x - 0.0032$ $(\pm 0.04)\ (\pm 0.001)$	0.54 **
z	-0.21	0.07	-		
Fourth Instar (n = 69)					
y	-	0.34**	-0.36**		
x	0.34**	-	0.11	$y = 8.09 + 0.41x - 0.011z$ $(\pm 0.11)\ (\pm 0.003)$	0.53 **
z	-0.36**	0.11	-		

n = number of larvae tested

* = $P < 0.05$

** = $P < 0.01$

Table 3.

Results of discriminant analysis of the number of turns executed (x), and the distance travelled (z) by starved *Adalia decempunctata* larvae.

	No. of larvae tested	x	z	Best function	Means given by best function	Difference between means
First Instar	17	3.1	78.0	x - 0.03z	0.94	5.21 ± 0.67**
Second, Third & Fourth Instar	57	0.4	164.9		-4.27	

** $P < 0.01$

Table 4.

Effect of the average number of aphids consumed per day on the distance index of *Adalia decempunctata* larvae.

Average number of aphids consumed per day	Number of coccinellid larvae tested	Average distance index
First instar larvae		
0 First instar aphids	17	16.15 ± 2.36
0.75 - 1.0 "	9	39.27 ± 5.26
1.0 - 2.0 "	9	23.95 ± 2.97
Second instar larvae		
0 "	19	42.11 ± 5.33
1 - 2 "	2	88.65 ± 37.77
2 - 3 "	12	79.20 ± 10.95
3 - 5 "	24	37.77 ± 3.25
5 - 8 "	19	47.63 ± 4.17
Third instar larvae		
0 Third instar aphids	25	63.96 ± 7.77
1 - 2 "	19	219.91 ± 19.81
2 - 4 "	21	70.03 ± 6.17
4 - 7 "	19	64.49 ± 4.90
Fourth instar larvae		
0 "	13	120.65 ± 14.07
2 - 3 "	21	282.04 ± 21.31
4 - 8 "	12	142.42 ± 17.22
8 - 12 "	7	125.20 ± 25.25
12 - 16 "	11	114.94 ± 17.73

TABLE 5.

Percentage of encounters between *Adalia decempunctata* and *Microlophium evansi* resulting in capture, and response of those aphids which avoided capture.

Aphid instar	Number of coccinellids tested	Number of encounters observed	Number of aphids captured	Percentage captured (E)	Number of coccinellids tested	Number of aphids observed avoiding capture	Walked away		Dropped		Kicked		Escaped by waxing and pulling	
							No.	%	No.	%	No.	%	No.	%
					First instar coccinellid									
First	48	240	48	20	31	131	97	74.04	9	6.87	18	13.7	7	5.3
Second	20	335	10	2.98	12	299	250	83.6	3	1.0	28	9.4	18	6.0
Third	15	300	1	0.33	15	299	175	58.5	0	0	106	35.5	18	6.0
Fourth	10	200	0	0.0	10	200	143	71.5	0	0	48	24.0	9	4.5
Adult	10	179	2	1.11	10	177	96	54.23	0	0	73	41.2	8	4.5
					Second instar coccinellid									
First	26	54	26	48.14	16	20	13	65	7	35	0	0	0	0
Second	42	207	39	18.84	20	101	78	77.2	15	14.9	3	3.0	5	5.0
Third	22	369	9	2.43	17	324	263	81.2	21	6.5	14	4.3	26	8.0
Fourth	22	439	1	0.22	22	438	348	79.5	17	3.9	37	8.4	36	8.2
Adult	10	203	0	0.0	10	203	168	82.8	1	0.49	21	10.3	13	6.4
					Third instar coccinellid									
First	20	24	20	83.3	20	4	1	25	3	75	0	0	0	0
Second	20	40	20	50.0	20	20	7	35	13	65	0	0	0	0
Third	20	49	20	40.81	15	18	9	50	8	44.4	0	0	1	5.6
Fourth	20	206	19	9.22	18	178	149	83.7	13	7.3	1	0.56	15	8.4
Adult	20	229	15	6.55	20	214	176	82.2	5	2.3	8	3.7	25	11.7
					Fourth instar coccinellid									
First	20	22	20	90.9	20	2	0	0	2	100	0	0	0	0
Second	20	34	20	58.8	20	14	3	21.4	11	78.6	0	0	0	0
Third	20	46	20	43.48	20	26	11	42.3	13	50	0	0	2	7.7
Fourth	20	62	20	32.26	20	42	24	57.1	13	31	0	0	5	11.9
Adult	20	105	20	19.05	20	85	71	83.5	8	9.4	0	0	6	7.1
					Adult coccinellid									
First	20	53	20	37.70	20	33	3	9	30	91	0	0	0	0
Second	20	74	19	25.7	20	55	7	12.7	47	85.5	0	0	1	1.8
Third	20	103	18	17.5	20	85	36	42.4	49	57.6	0	0	0	0
Fourth	20	217	13	6.0	20	204	141	69.1	58	28.4	0	0	5	2.5
Adult	20	148	16	10.8	20	132	93	70.5	38	28.8	0	0	1	0.7

Table 6.

Number of *Microlophium evansi* escaping from *Adalia decempunctata* according to the part of the body seized, and occurrence of waxing.

Aphid instar	Total no. of encounters observed	Aphid successfully captured			Aphid escapes			
		No.	Part of aphid seized		Part of aphid seized		Response of aphid	
			Appendage	Body	Appendage	Body	Waxes	Does not wax
First instar coccinellid								
First	240	48	38	10	10	0	6	4
Second	335	10	7	3	24	0	5	19
Third	300	1	0	1	18	0	0	18
Fourth	200	0	0	0	9	0	0	9
Adult	179	2	1	1	8	0	0	8
Second instar coccinellid								
First	54	26	4	22	0	0	0	0
Second	207	39	26	13	7	1	5	3
Third	369	9	8	1	28	1	8	21
Fourth	439	1	1	0	36	0	2	34
Adult	203	0	0	0	13	0	0	13
Third instar coccinellid								
First	24	20	0	20	0	0	0	0
Second	40	20	9	11	0	0	0	0
Third	49	20	9	11	2	0	0	2
Fourth	206	19	16	3	16	0	6	10
Adult	229	15	9	6	25	0	1	24
Fourth instar coccinellid								
First	22	20	0	20	0	0	0	0
Second	34	20	0	20	0	0	0	0
Third	46	20	4	16	1	1	2	0
Fourth	62	20	13	7	5	0	2	3
Adult	105	20	14	6	6	0	2	4
Adult coccinellid								
First	53	20	0	20	0	0	0	0
Second	74	19	0	19	1	0	0	1
Third	103	18	0	18	0	0	0	0
Fourth	217	13	1	12	0	5	5	0
Adult	148	16	2	14	0	1	1	0

Table 7.

Effect of the angle of approach of *Adalia decempunctata* on the chance of *Microlophium evansi* avoiding capture.

Angle of approach	Avoided capture		Captured	
	Walked away	Dropped	Aphid escaped	Aphid failed to escape
Second instar aphid: Adult coccinellid				
Front	11	12	1	2
Rear	1	4	0	7
Third instar aphid: Adult coccinellid				
Front	18	31	0	0
Rear	1	5	0	6
Third instar aphid: Third instar coccinellid				
Front	64	8	0	10
Rear	40	11	4	15

Table 8.

Orientation of *Microlophium evansi* on *Urtica dioica*.

Direction faced	Stem				Leaf			
	Down		Up		Towards the petiole		Away from the petiole	
	No.	%	No.	%	No.	%	No.	%
First instar aphid	50	50	50	50	66	60.5	43	39.5
Second instar aphid	65	65	35	35	99	90.8	10	9.2
Third instar aphid	111	85.5	19	14.5	96	88.8	12	11.2
Fourth instar aphid	83	79	22	21	96	96	4	4
Adult aphid	92	80	23	20	101	94.5	6	5.5

Table 9.

Effect of aphid population density on the survival of first instar <u>Adalia decempunctata</u> larvae.

Number of aphids provided each day per vial	Number of coccinellids tested	Number surviving to make a capture	Percentage surviving to make a capture
1	50	28	56
2	16	14	87.5
3	65	61	93.8
6	46	42	91.3
8	115	113	98.3

Table 10.

Effect of the number of aphids provided per day upon percentage survival in, and duration of, each instar in Adalia decempunctata.

No. of aphids provided per day	No. of larvae tested	No. of larvae surviving	Percentage survival	Total no. of aphids eaten	Average duration of instar	Average no. of aphids eaten per day
First instar larvae						
1 First instar aphid	28	15	54	4.47±0.38	5.67±0.48	0.79±0.04
2	13	12	92	6.08±0.36	4.25±0.22	1.46±0.1
3	60	56	93	7.16±0.23	3.68±0.13	2.02±0.06
6	42	39	93	8.51±0.40	3.03±0.06	2.82±0.13
8	113	105	93	10.75±0.31	3.05±0.04	3.55±0.1
Second instar larvae						
1	21	0	0	-	-	-
2	17	2	12	10.5±1.5	6.0±1.0	1.75±0.05
3	15	13	87	10.92±0.87	4.08±0.26	2.68±0.10
4	23	17	74	16.29±1.29	4.47±0.32	3.65±0.13
5	18	17	94	13.59±0.58	3.24±0.14	4.26±0.17
Third instar larvae						
0.5 Third instar aphid	13	0	0	-	-	-
1	20	11	55	7.36±0.56	8.0±0.63	0.92±0.03
2	15	14	93	7.64±0.48	4.36±0.20	1.74±0.05
Fourth instar larvae						
1	10	0	0	-	-	-
2	10	6	60	15.50±0.67	9.50±0.56	1.64±0.004
3	10	9	90	17.0 ± 1.05	8.33±0.44	2.06±0.12
4	10	8	80	23.25±1.13	7.13±0.40	3.28±0.08
10	10	9	90	39.33±1.18	5.44±0.18	7.25±0.35

Table 11.

Effect of the number of aphids provided each day per larva on the rate of development, survival, and adult size in Adalia decempunctata.

No. of aphids provided each day per larva	No. of larvae tested	No. of larvae surviving	Percentage survival	Duration of development in days (D.)	Rate of development = 10.18/D	Average adult size index	Average adult dry weight (mg.)
1	39	0	0	-	-	-	-
2	42	8	19.05	20.88±0.87	0.49	7.22±0.32	0.71±0.04
3	30	11	36.66	18.73±0.54	0.54	8.56±0.29	0.70±0.03
4	25	12	48	16.5±0.48	0.62	8.89±0.31	0.89±0.02
6	20	14	70	14.21±0.28	0.72	9.75±0.19	1.19±0.03
8	20	16	80	13.31±0.29	0.76	11.91±0.17	1.42±0.03
10	30	21	70	13.57±0.22	0.75	10.74±0.31	1.51±0.06
15	20	17	85	10.24±0.20	0.99	11.24±0.19	1.81±0.06
20	20	17	85	10.18±0.13	1.0	12.0±0.13	1.92±0.04

Table 12.

Average time taken by <u>Adalia decempunctata</u> larvae to consume <u>Microlophium evansi</u>.

Aphid instar	Coccinellid instar							
	First		Second		Third		Fourth	
	No.	Average time taken (min.)	No.	Average time taken (min.)	No.	Average time taken (min.)	No.	Average time taken (min.)
First	47	118.5 ± 11.38	24	38.33 ± 5.65	20	14.25 ± 1.17	20	4.3 ± 0.38
Second	7	256.4 ± 41.63	30	84.97 ± 8.54	20	26.5 ± 2.82	20	10.15 ± 0.86
Third	1	920 (not finished)	8	181.88 ± 24.51	20	56.0 ± 5.77	19	32.63 ± 4.44
Fourth	-	-	1	215.0	16	136.4 ± 15.41	17	54.7 ± 5.64
Adult	-	-	-	-	15	96.66 ± 9.9	20	62.1 ± 10.96

Table 13.

Age distribution of a population of the nettle aphid *Microlophium evansi*, being attacked by *Adalia decempunctata* larvae, in the field.

Aphid instar	Number	Percentage (A)
First	429	39.6
Second	410	37.8
Third	118	10.9
Fourth	34	3.1
Adult	93	8.6

Table 14.

Number of Microlophium evansi of each instar (N) captured by Adalia decempunctata larvae in a 100 encounters in the population sampled.(estimated).

Coccinellid instar	Aphid instar				
	First	Second	Third	Fourth	Adult
First	7.92	1.13	0.04	0.0	0.10
Second	19.06	7.12	0.26	0.01	0.00
Third	32.99	18.9	4.45	0.29	0.56
Fourth	36.00	22.23	4.74	1.00	1.64

Table 15.

Length and weight of *Microlophium evansi*.

Aphid instar	Number measured	Average length (l)	Number weighed	Weight per 100 (W)	$\frac{\text{Weight per 100 aphids}}{\text{Average length}} = W/l$	Equivalent no. of aphid units (C)
First	200	0.87 ± 0.01mm.	200	0.00205gms.	0.0024 gms/mm.	0.32
Second	100	1.35 ± 0.02 "	100	0.0069 "	0.0051 "	0.69
Third	102	1.71 ± 0.02 "	100	0.0127 "	0.0074 "	1.0
Fourth	100	2.26 ± 0.02 "	100	0.0250 "	0.0111 "	1.5
Adult	100	2.45 ± 0.02 "	100	0.0285 "	0.0116 "	1.57

Table 16.

Number of aphid units captured by _Adalia decempunctata_ larvae in a 100 encounters in the population sampled. (estimated).

Coccinellid instar	Number of aphid units available from the total capture of each instar of aphid					Total number of aphid units captured per 100 encounters (U)	Ratio of number of aphid units
	First	Second	Third	Fourth	Adult		
First	2.57	0.78	0.04	0.0	0.16	3.55	1
Second	6.19	4.91	0.26	0.02	0.00	11.38	3.21
Third	10.56	13.03	4.45	0.44	0.88	29.36	8.27
Fourth	11.69	15.33	4.74	1.50	2.57	35.83	10.09

Table 17.

Time spent feeding by *Adalia decempunctata* larvae for every 100 encounters with *Microlophium evansi* in the population sampled.(estimated).

Coccinellid instar	Time (min.) spent feeding on					Total time spent feeding T_1
	First instar aphids	Second instar aphids	Third instar aphids	Fourth instar aphids	Adult aphids	
First	939.31	289.73	36.80	-	?	1,265.84 mins.
Second	730.57	604.99	47.29	2.15	-	1,385.00 "
Third	470.11	500.85	249.20	39.56	54.13	1,313.85 "
Fourth	154.80	225.63	154.67	54.70	101.84	691.64 "

Table 18.

Percentage of time spent feeding by surviving *Adalia decempunctata* larvae, when 50% survived. (estimated).

Coccinellid instar	Number of aphid units required for 50% survival (S)	Time taken to consume aphid units (T_2)	Time spent in the instar (D)	Percentage of time spent feeding (L)
First	1.45	517.03 mins.	8,164.8 mins.	6.33
Second	3.50	425.95 "	6,811.2 "	6.25
Third	7.36	329.36 "	11,520.0 "	2.85
Fourth	15.50	299.15 "	13,680.0 "	2.19

Table 19.

Index of prey population density required for 50% survival in *Adalia decempunctata* larvae (estimated).

Coccinellid instar	Distance index (D.I.)	Range of perception (R.)	Area index (A.I.= D.I.xR.)	Area index corrected for time spent feeding (A.I.2)	Prey population index 1. ($P.I_1$)	Prey population index 2. ($P.I_2$)	Prey population index 2. ratio
First	39.27	0.94±0.03	36.91	34.57	0.04194	0.04194	18.81
Second	79.20	1.28±0.04	101.38	95.04	0.03683	0.01147	5.14
Third	219.91	1.67±0.05	367.25	356.78	0.02063	0.00249	1.12
Fourth	282.04	2.5±0.04	705.1	689.66	0.02247	0.00223	1.0

Table 20.

The effect of the number of third instar *Microlophium evansi* provided each day on the number of mature and almost mature eggs present in the ovaries of *Adalia decempunctata*.

Average number of third instar aphids provided per day	Average number of mature and almost mature eggs present in the ovaries
4	3 ± 1.14
8	12.78 ± 2.31
16	18.25 ± 1.75
24	15.36 ± 2.44