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Predacious behaviour of four species of Coccinellidae (Coleoptera) associated with the wheat aphid, *Schizaphis graminum* (Rondani), in South Africa

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With 4 text-figures

SYNOPSIS

An account is given of the predator efficiency of four species of Coccinellidae, *Lioadalia flavomaculata*, *Scymnus morelleti*, *Exochomus concavus* and *Cheilomenes lunata*, associated with the wheat aphid, *Schizaphis graminum*, in the Orange Free State province of South Africa. The method of attack employed by the predator and the way in which the aphid prey was overpowered by the different species and their respective instars are described and their influence on predator efficiency is assessed.

I INTRODUCTION

Modern methods of pest control involving the effective utilisation of entomophagous insects are still handicapped by lack of basic knowledge (van den Bosch & Stern, 1962). This is true even of such comparatively well-known insects as predacious Coccinellidae, where more precise information on the interaction between the predator and its prey is still required.

Although the prey preferences and feeding behaviour of Coccinellidae are fairly well documented, having formed the subject of several important reviews (e.g. Hagen, 1962; Hodek, 1967), little is known about their efficiency at capturing prey. Indeed published information on this aspect of coccinellid behaviour is limited. Fleschner (1950) studied the efficacy of three different predatory insects, one of them being the coccinellid *Stethorus picipes* Casey. Dixon (1959) investigated the predator efficiency of the different instars of *Adalia decempunctata* (L.) against the nettle aphid, *Microlophium evansi* (Theobald), and Blackman (1967) compared the efficiency of *Adalia bipunctata* (L.) and *Coccinella septempunctata* L., using four different aphid species as prey. More recently Dixon (1970) determined the efficiency of first instars of *A.bipunctata* in capturing selected instars of the sycamore aphid, *Drepanosiphum platanoides* (Schrank).

The present observations are concerned with the relative predator efficiency and tactics of four species of Coccinellidae, *Lioadalia flavomaculata* (DeGeer), *Scymnus morelleti* Mulsant, *Exochomus concavus* Fürsch and *Cheilomenes lunata* (F.), with a view to assessing their importance as predators of the wheat aphid, *Schizaphis graminum* (Rondani), in the Orange Free State province of South Africa. These four species of Coccinellidae were selected for investigation because they were the principal species occurring in fields infested with wheat aphid. Previous work on the relative abundance of these Coccinellidae (Brown, 1969) showed that *L.flavomaculata* was by far the most numerous species, *S.morelleti* ranked second in abundance and *E.concavus* third; *C.lunata* was the rarest of the four species.

A detailed account of the biologies of these coccinellid species has been provided by Brown (1969).

II EXPERIMENTAL PROCEDURE

Batches of from 20–30 aphids of a particular instar were selected from outdoor infestations and transferred to young shoots standing in corked vials of water in the laboratory. After about an hour, when the aphids had settled and distributed themselves over the preferred parts of the shoots, they were placed in a rotating device so as to keep both leaf surfaces under observation. Care was exercised not to disturb the aphids during the course of the experiments, and attacks by Coccinellids were confined, as in nature, to settled aphids only, i.e. stationary aphids with their mouthparts inserted into the leaf. Each successive aphid instar was examined in this way. Observations on adult aphids were limited to apterae; alatae, on account of their ability to fly, were not examined. Two aphid species, *Capitophorus elaeagni* (del Guercio), which colonises artichokes (*Cynara scolymnus*) and *S.graminum*, were used in these experiments; most of the observations were carried out on the latter species. *C.elaeagni* was examined for purposes of comparison and was selected because of its ready availability and greater size.

In order to stimulate feeding, coccinellid larvae and adults were kept without food for one day after eclosion or after moulting, depending on the instar examined. These unfed Coccinellids were then released individually against the settled aphids. At first, in order to accustom the Coccinellids to the plant surface, they were released on a similar uninfested shoot and, when searching normally, allowed to run on to the shoot with the aphids. Their subsequent movements on the infested shoot were then closely followed with the aid of a dissecting microscope at 16× magnification, each separate attack and its outcome being recorded. After successful capture of an aphid, the Coccinellid was removed from the shoot and the remaining aphids given time to resettle before release of the next test individual. In order to prevent habituation, aphids were frequently replaced with freshly collected batches.

In experiments aimed at comparing the relative efficiency of the four coccinellid species, 15 replications of each coccinellid instar were tested against each aphid instar. As there were five aphid instars in the species examined, a total of 75 individuals (15 Coccinellids × 5 aphids instars) were tested for determining the efficiency of each coccinellid instar. The method of scoring efficiency in these encounters was as follows. Each separate attack was recorded, and the efficiency of a particular instar assessed, by determining the number of attacks required to capture an aphid. An efficient predator readily captured every aphid it attacked, and the 15 replications tested therefore had a minimum total score of 15. An inefficient predator made a number of unsuccessful attacks and these added to the score. The total number of attacks and the proportion resulting in capture were then used to calculate the percentage efficiency of each coccinellid instar.

Each Coccinellid tested was allowed a maximum of ten chances in which to capture an aphid. If it failed, it forfeited any further opportunity and was recorded as unsuccessful. This seldom occurred against *S.graminum*, most of which were captured at the first attempt, but was more common against *C.elaeagni*, where many attacks were required before successful capture. Another complication that arose with this latter aphid species was that some of the predators, especially the early instars, became immobilised by the defensive secretion from the siphunculi of the aphid. Coccinellids that failed to capture an aphid after ten attempts were offered an aphid on the tip of a moistened paint brush as food in order to check that there was nothing wrong with their feeding behaviour.

In experiments designed to determine the method of attack and the part of the aphid seized by the predator, 10–20 replications of each coccinellid instar were tested against each aphid instar. Only *S.graminum* was examined in these later experiments.

All experiments were conducted in the laboratory at room temperatures ranging from 19–23° C., which favoured attack and capture of aphids.

III RELATIVE EFFICIENCY AT CAPTURING APHIDS

Some indication of the relative size of the four Coccinellids investigated and their aphid prey, *S.graminum*, is provided in figure 1, in which, to facilitate comparison, the different predators are arranged in order of increasing size beneath the prey, starting with the smallest species, *S.morelleti* and ending with the largest, *C.lunata*. The five different coccinellid instars are shown beneath the corresponding aphid instars. As can be seen, there was considerable difference in size between the four coccinellid species and between them and their prey.

The percentage successful attacks made by *L.flavomaculata* against each instar of *S.graminum* are given in Table 1. First and second instar Coccinellids were less successful than either third or fourth instars, and the former missed a number of aphids. Thus, the first instar showed an efficiency ranging from 88 to 94 per cent. against all prey instars, whereas the second instar was 100 per cent. efficient against first, second and third instar aphids but only 94 per cent. efficient against fourth instar and adult aphids. On the other hand, third and fourth instar Coccinellids were 100 per cent. efficient and captured all aphid instars successfully. The efficiency of the adult Coccinellid varied from 88 to 100

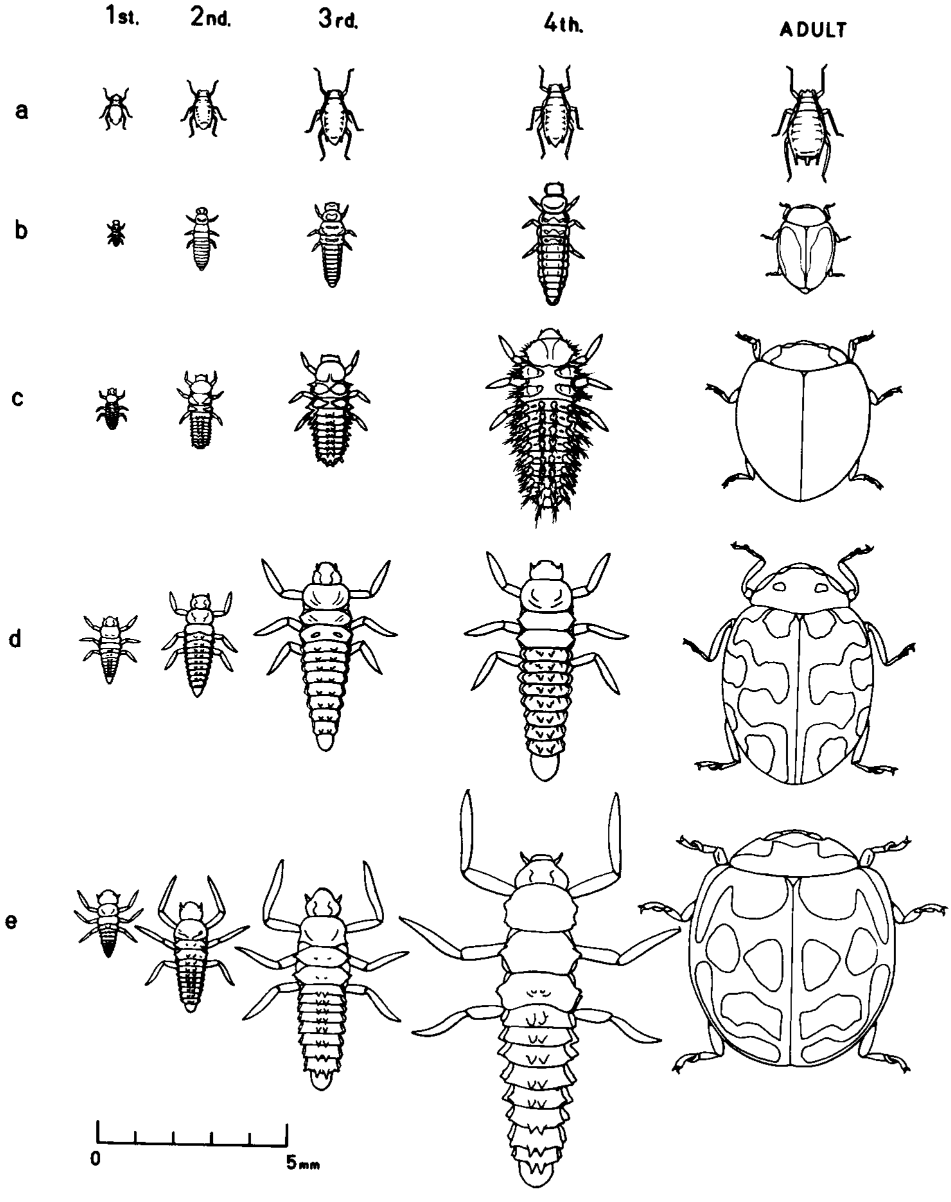

Fig. 1. Relative sizes of wheat aphid and principal coccinellid predators: (a) *S.graminum*; (b) *S.morelleti*; (c) *E.concavus*; (d) *L.flavomaculata*; (e) *C.lunata*.

per cent. against all aphid instars and was therefore below that shown by the older larval instars.

The results of similar attacks made by the different instars of *S.morelleti* are shown in Table 2. First instar Coccinellids failed to capture many aphids and were only 12 to 79 per cent. successful, depending on the aphid instar. Although the second instar was more efficient, it still only captured from 20 to 100 per cent. of the different aphid instars.

Table 1. The percentage *S.graminum* captured by the different instars of *L.flavomaculata* (15 replicates per instar).

Coccinellid instar	Percentage of each aphid instar captured				
	1st	2nd	3rd	4th	Apterae
First	88	88	94	88	94
Second	100	100	100	94	94
Third	100	100	100	100	100
Fourth	100	100	100	100	100
Adult	94	100	100	88	94

Both these instars experienced difficulty in capturing certain older aphid instars and were least efficient against apterae. However, on reaching the third instar, their efficiency improved, and from 68 to 100 per cent. of all aphid instars were captured. There was a further increase in the efficiency of the fourth instar coccinellid, which was 100 per cent. efficient against the first four aphid instars and 94 per cent. against apterae. Efficiency declined in the adult Coccinellid, which was only 44 per cent. successful against apterae and 94 per cent. against second, third and fourth instar aphids, although it was 100 per cent. efficient against the small first instar aphid.

Table 2. The percentage *S.graminum* captured by the different instars of *S.morelleti* (15 replicates per instar)

Coccinellid instar	Percentage of each aphid instar captured				
	1st	2nd	3rd	4th	Apterae
First	71	68	79	65	12
Second	94	100	94	75	20
Third	94	100	100	88	68
Fourth	100	100	100	100	94
Adult	100	94	94	94	44

To facilitate comparison between *L.flavomaculata* and *S.morelleti*, the two most numerous species in the field, the results are presented in the form of a histogram in figure 2, in which the total number of attacks and percentage efficiency are given for each coccinellid instar. Comparison between the two sets of histograms clearly shows the greater efficiency of *L.flavomaculata*, its superiority being particularly noticeable in the first two instars. Thus, first instar *L.flavomaculata* captured 94 per cent. of all apterae they attacked, whereas first instar *S.morelleti* captured only 12 per cent. Similarly, second instar *L.flavomaculata* captured 94 per cent. of all apterae in comparison with only 20 per cent. taken by the corresponding instar of *S.morelleti*. However, there was little difference in efficiency between the fourth instar of both coccinellid species, as *S.morelleti* captured all but one aptera. There was again disparity between the efficiency of the adults of both species, *S.morelleti* being for instance only 44 per cent. efficient against apterae as compared with 94 per cent. by *L.flavomaculata*. Because of their initial low efficiency, the increase in ability to capture aphids with each successive moult up to the fourth instar is more strikingly illustrated by the different instars of *S.morelleti* than by *L.flavomaculata*.

Similar assessment of the predator efficiency of *E.concavus*, using the same prey, showed that its efficiency was well below that of *L.flavomaculata* and more comparable with that of *S.morelleti*, although this varied from instar to instar (Table 3). First instars of *E.concavus* were only 21 per cent. efficient against apterae, whereas second and third instars were 46 and 79 per cent., respectively, efficient against this aphid instar. These percentages are higher than those recorded above for first, second and third instars of *S.morelleti* attacking apterae. However, fourth instars of *E.concavus* were slightly less efficient than the corresponding instar of *S.morelleti*, the former being 83 per cent. efficient and the latter 94 per cent. efficient against apterae. In the adult Coccinellid the position was again slightly reversed, *E.concavus* being 48 per cent. efficient against apterae as compared with 44 per cent. for *S.morelleti*.

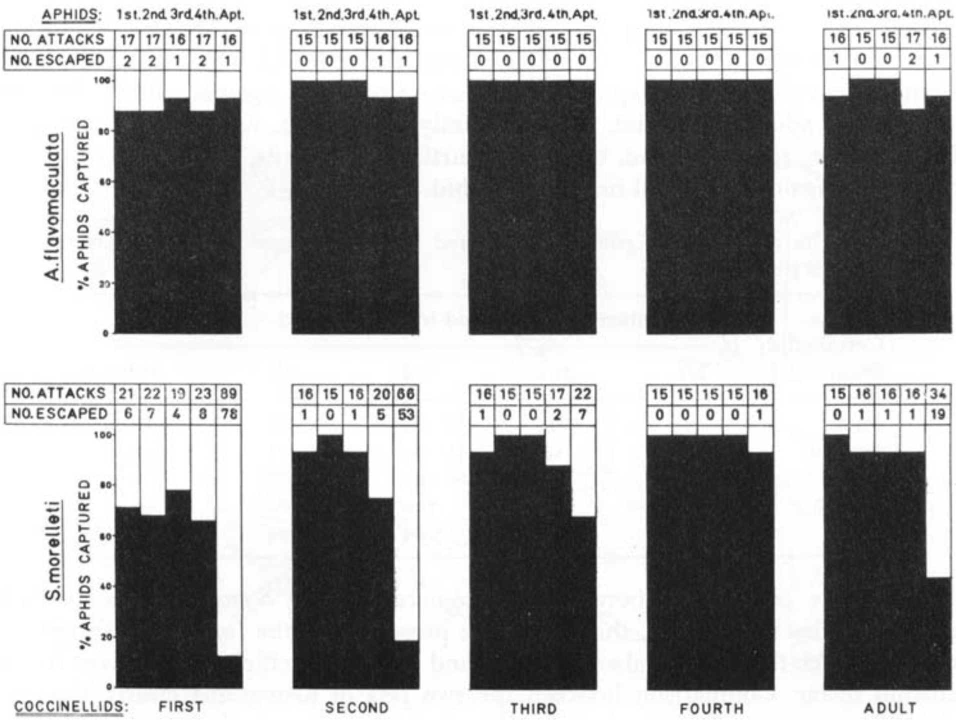

Fig. 2. Relative efficiency of two Coccinellids, *L.flavomaculata* (above) and *S.morelleti* (below), at capturing the different instars of *S.graminum*. Blocks denote coccinellid instars; columns denote aphid instars; number of attacks observed and number of aphid escaped shown above each block; 15 coccinellids tested against each aphid instar.

On the other hand the efficiency of certain instars of *C.lunata*, as shown in Table 4, was higher than either *E.concavus* or *S. morelleti*; the adult of *C.lunata* was not investigated. First instars of *C.lunata* captured from 83 to 100 per cent. of the different aphid instars, being 83 per cent. successful against apterae. Second instars were more efficient and captured 88 per cent. of all apterae encountered, and third and fourth instars were 100 per cent. efficient against all aphid instars.

Table 3. The percentage *S.graminum* captured by the different instars of *E.concavus* (15 replicates per instar)

Coccinellid instar	Percentage of each aphid instar captured				
	1st	2nd	3rd	4th	Apterae
First	75	71	56	68	21
Second	94	94	83	83	46
Third	100	94	94	88	79
Fourth	94	100	94	83	83
Adult	94	83	71	75	48

The four coccinellid species therefore display considerable variation in their ability to capture the same aphid prey. Efficiency varied not only with the species of Coccinellid but also with its stage of development, older larvae being more efficient than younger larvae. The efficiency of a particular Coccinellid was also influenced by the age of the aphid prey, late instar aphids being generally more difficult to capture than the earlier instars. Under these experimental conditions, the ability of most instars of *L.flavomaculata* and *C.lunata* to capture *S.graminum* was superior to that of either *S.morelleti* or *E.concavus*.

Table 4. The percentage *S.graminum* captured by the larval instars of *C.lunata* (15 replicates per instar).

Coccinellid instar	Percentage of each aphid instar captured				
	1st	2nd	3rd	4th	Apterae
First	94	94	100	88	83
Second	100	100	94	94	88
Third	100	100	100	100	100
Fourth	100	100	100	100	100

The most important conclusion emerging from these observations is that the most abundant species in the field, *L.flavomaculata*, is also one of the most efficient at capturing aphid prey. That the reverse premise, that the rarest species in the field is the least efficient predator, is not necessarily true is illustrated by the results obtained for *C.lunata*. Although this Coccinellid ranked equally well with *L.flavomaculata* in ability to capture prey, it never achieved the same degree of abundance in the field. Brown (1969) has shown that *C.lunata* is the least common species in the field, unknown factors in the environment appearing to determine its numbers.

IV EFFECTS OF PREY SPECIES ON PREDATOR EFFICIENCY

The ability to capture aphids rests not only with the species of Coccinellid and its stage of development but also with the species of aphid that is attacked. This can be clearly seen from the following experiment, in which the efficiency of *C.lunata* against each of the aphid species, *S.graminum* and *C.elaeagni*, is compared.

The results of attacks by the different instars of *C.lunata* on both aphid species are summarised, for ease of comparison, in the histograms in figure 3. Comparison between the efficiency of the adult Coccinellid is unfortunately not possible, as this instar was only tested against the one aphid species. From figure 3 it will be seen that the percentage aphids captured varied with the species of aphid, *C.lunata* being more efficient at capturing *S.graminum* than *C.elaeagni*, especially in its first two instars. Thus first instar Coccinellids captured from 83 to 94 per cent. of all instars of *S.graminum*, compared with 10 to 88 per cent. of all instars of *C.elaeagni*. Second instar Coccinellids were also more efficient at capturing *S.graminum* and captured from 83 to 100 per cent. of all aphid instars; against the different instars of *C.elaeagni* the second instar was only 23 to 94 per cent. efficient. Both instars found apterae of *C.elaeagni* the most difficult to capture, and many of their attacks against this prey proved abortive. First instar Coccinellids were only 10 per cent. efficient against apterae, and second instar Coccinellids 23 per cent. efficient, compared with 83 and 88 per cent. efficiency against the apterae of *S.graminum* by these respective coccinellid instars. Although third and fourth instar Coccinellids were more efficient than the earlier instars at capturing *C.elaeagni*, they still missed many of the older aphid instars and were only 68 and 79 per cent. successful against apterae. On the other hand these instars were 100 per cent. successful against apterae of *S.graminum*. Efficiency of the adult Coccinellid against certain instars of *C.elaeagni* was again below the level recorded for either the third or fourth instars.

The results indicate that certain species of aphids are more difficult to capture than others, and that this is likely to influence the efficiency of a predator in nature. By com-

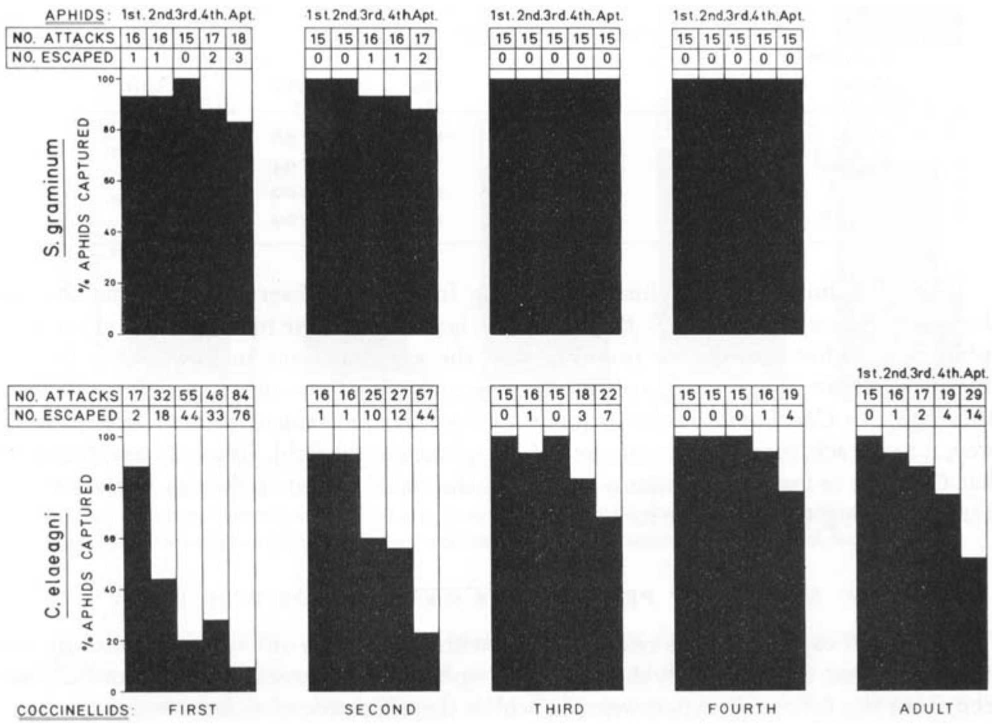

Fig. 3. Efficiency of the coccinellid *C.lunata* at capturing the different instars of the two aphid species, *S.graminum* (above) and *C.elaeagni* (below). 15 Coccinellids tested against each aphid instar; other representation as in figure 2.

parison with *C.elaeagni*, the wheat aphid is shown to be particularly susceptible to predation by the Coccinellids under investigation.

V METHOD OF ATTACK

Valid differences in efficiency between the four coccinellid species and their various instars have been found even when the same aphid species was used. More detailed observations on the actual method of attack were therefore undertaken to determine the possible causes of this variable efficiency.

The Coccinellids under investigation crawled preferably along the margins of the leaves of wheat plants in search of aphids. Besides facilitating movement on the plant, the leaf margin also provided an important foothold from which to launch attacks on nearby aphids. During attack larvae generally anchored themselves to the leaf margin by means of the adhesive sucker at the end of the abdomen, and adults invariably supported themselves by hooking their legs over the leaf margin. During the ensuing struggle, the leaf margin also provided good purchase and prevented the aphid from dislodging the predator and escaping. Even disproportionately large aphids were successfully captured by small Coccinellids anchored to the leaf margin.

Observations on Coccinellids attacking aphids suggest that two factors could influence predator efficiency. Firstly there is the part of the aphid that is seized by the predator: aphids seized by an appendage, for example, might possibly stand a better chance of escaping than those captured by some more vulnerable part of the body. Secondly, the way in which the aphid is overpowered following seizure is possibly important. Unless this is rapidly accomplished, the aphid may struggle free and escape. These problems are considered in further detail below.

(1) *The part of the aphid seized*

In order to investigate the part of the aphid that is seized by the predator, different instars of the four species under discussion were tested against each instar of *S.graminum*, and the precise method of attack was recorded

From Table 5 it will be seen that, although most larvae of *L.flavomaculata* seized aphids by the head, thorax and especially the abdomen, a small number of first instar larvae also caught their prey by the antenna and legs. However, even in the instances where aphids were caught by the appendages, a subsequent preference was shown for the body. Immediately after capture these larvae transferred their grip to the body, where feeding commenced. Instances where aphids had been seized by the appendages by first instar larvae were limited to encounters with relatively large aphids attempting to escape. Subsequent instars, however, easily overpowered these large aphids and capture by means of the appendages was not observed.

Table 6 shows the method of attack employed by the larval instars of *C.lunata*. The body of the aphid was the main target, and prey was seized chiefly by the abdomen. Only in one instance was an aphid captured by an appendage; immediately after subduing the aphid with the fore legs, this Coccinellid transferred its jaws to the abdomen and fed there. Only incidental observations were carried out on the method employed by the adult, and these indicate a preference also for the body of the prey.

Table 5. Part of the aphid seized by the different instars of *L.flavomaculata* (19–20 replicates per instar).

Coccinellid instar	No. of aphids captured	Percentage aphids caught by				
		Antenna	Leg	Head	Thorax	Abdomen
First	99	8	15	19	13	45
Second	100	0	0	12	33	55
Third	100	0	0	10	40	50
Fourth	100	0	0	5	36	59
Adult	100	0	0	12	31	57

As shown by Table 7, the method of attack employed by *S.morelleti* varied with the age of the predator. Larval instars captured their prey mainly by the appendages, especially the legs (fig. 4), whereas adults captured them mainly by the body, especially the abdomen. The 12 per cent. listed under the heading of abdomen caught by the third instar in Table 7 refers to aphids seized by the siphunculi, and strictly speaking, for present purposes, the siphunculi should have been listed as appendages of the abdomen. The marked increase in the percentage aphids seized by the antennae by the second, third and fourth instars may be partly explained by size. Aphids appeared to pay scant attention to first instar larvae, possibly on account of their small size and slower movements, but responded to older larvae by pointing their antennae at them. The antennae of the aphid were hence placed within more convenient reach of these older instars, which promptly responded by seizing them.

Table 6. Part of the aphid seized by the larval instars of *C.lunata* (20 replicates per instar).

Coccinellid instar	No. of aphids captured	Percentage aphids caught by				
		Antenna	Leg	Head	Thorax	Abdomen
First	100	0	1	15	30	54
Second	100	0	0	10	24	66
Third	100	0	0	4	33	63
Fourth	100	0	0	8	20	72

According to Table 8, the method of attack employed by *E.concavus* was also shown to vary with the age of the predator. First instar larvae captured prey mainly by the appendages, especially the legs, whereas second instar larvae favoured the body, especially the abdomen, and to a lesser extent the legs. Third and fourth instar larvae showed an increasing preference for the body of the prey, especially the abdomen; very few seized their prey by the legs, and none were captured by the antennae. Adult Coccinellids seized their prey only by the body.

The results obtained show that the part of the aphid that is seized varies with the species as well as its stage of development. All instars of *L.flavomaculata* and of *C.lunata* seized their prey mainly by the body, especially the abdomen, whereas the larvae, but not the adults, of *S.morelleti* seized them mainly by the legs. First instars of *E.concavus*, seized their prey mainly by the appendages, whereas subsequent instars favoured the body.

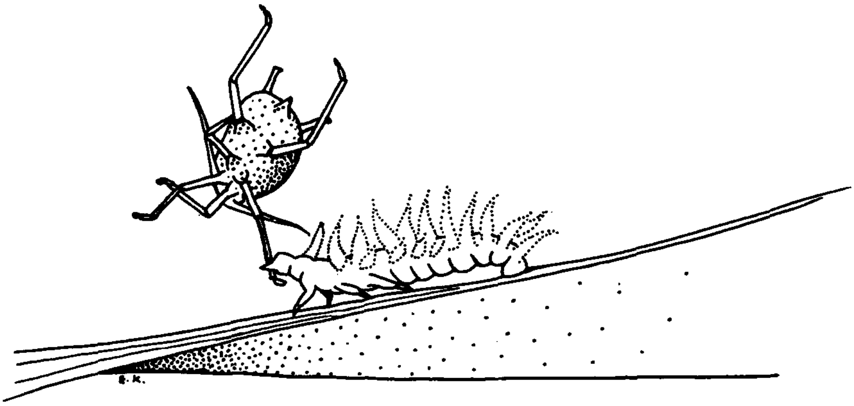

Fig. 4. Fourth instar larva of *S.morelleti* that has captured its aphid prey by the middle tibia (schematic, drawn from a photograph).

Table 7. Part of the aphid seized by the different instars of *S.morelleti* (10–15 replicates per instar)

Coccinellid instar	No. of aphids captured	Percentage aphids caught by				
		Antenna	Leg	Head	Thorax	Abdomen
First	75	1	99	0	0	0
Second	75	13	83	1	1	1
Third	75	13	73	1	0	12*
Fourth	75	15	83	0	0	3
Adult	54	0	6	6	15	74

* Caught mainly by siphunculi.

Table 8. Part of the aphid seized by the different instars of *E.concavus* (10–15 replicates per instar).

Coccinellid instar	No. of aphids captured	Percentage aphids caught by				
		Antenna	Leg	Head	Thorax	Abdomen
First	75	15	51	5	13	16
Second	75	1	24	12	20	43
Third	50	0	2	14	26	58
Fourth	50	0	2	4	32	62
Adult	50	0	0	16	30	54

(2) *The way in which the aphid was subdued*

The method used to subdue the prey was also found to vary between the different predator species. Some captured their prey with the aid of the fore legs, whereas others immobilised them by means of a toxic oral secretion.

Both larvae and adults of *L.flavomaculata* and of *C.lunata* made use of their fore legs in the capture of their prey, the aphid being lifted up and held in the legs for the duration of the meal. Although some of the older larval instars of both species seized small aphids only with their jaws, they quickly responded with their legs when the aphid struggled vigorously or when attacking relatively large aphids.

Larvae of *S.morelleti* did not use their fore legs but relied on another method of subduing their prey. On biting the aphid, a toxic secretion was immediately administered through the wound and rapidly immobilised the prey. All four larval instars of *S.morelleti* immobilised their prey in this way. The secretion was apparently part of the digestive fluid emanating from the gut. Subsequently during feeding, what appeared to be the same fluid was alternately regurgitated and sucked from the prey in the well-known method of extra-oral digestion reported for many predacious Coccinellids (Hagen, 1962). The immediate toxic effect, and the rapidity with which the prey became immobilised, was quite distinct from that produced by the mere sucking out of body fluids of the prey, as observed in *L.flavomaculata* and *C.lunata.* In the latter case there was no immediate forceful discharge from the gut, and the prey continued struggling for some time after being seized. However, regurgitation for purposes of imbibing liquid food did occur sometimes in these species, but usually at a later stage when the meal was well advanced and when the aphid had already assumed a collapsed appearance

Table 9. Efficacy of the toxic secretion injected into prey by the different larval instars of *S.morelleti*: time taken for fourth instar aphids to die after being seized

Coccinellid instar	No. of replicates	Mean time for all aphid movements to cease (minutes)
First	14	15·1
Second	15	5·4
Third	15	2·8
Fourth	15	2·4

Since larvae of *S.morelleti* invariably captured their prey by seizing an appendage, the secretion was usually introduced into the prey via a leg or antenna, although even the rostrum or siphunculus were on occasion used. The secretion was frequently ejected from the predator in such quantity and with such force that the prey sometimes assumed a turgid appearance immediately after being seized. The pressure was sometimes so great that the fluid oozed from other parts of the body remote from the traumatised appendage. The speed of action of the secretion, moreover, appeared to depend on the proximity of the injection site to the head and the anterior nerve ganglia. Individuals caught, for instance, near the base of an antenna were observed to be more rapidly immobilised than those caught by a hind leg.

Observations on the time needed to subdue fourth instar aphids by the different larval instars of *S.morelleti* showed that the action of the toxic secretion increased with each successive coccinellid instar, probably on account of increased dosage and toxicity (Table 9).

The secretion was not only toxic to *S.graminum*, but was observed to have similar lethal effects on *Myzus persicae* (Sulzer), *Macrosiphum rosae* (L.) and *C.elaeagni* seized by larvae of *S.morelleti*· No chemical analysis of this toxic secretion has been made, nor have the respective roles of digestive or other fluids been evaluated.

Unlike the larval instars, adults of *S.morelleti* used their legs to aid in capturing their prey. No instances of a toxic secretion being administered by the adult have ever been recorded.

Similar observations carried out on the larval instars of *E.concavus* showed that they also had the capacity to immobilise their prey by injection of a toxic secretion. However, immobilisation of prey by this means was mainly confined to the first two instars. Although older larvae have on occasion been observed to subdue their prey in this way, the majority invariably sucked out and drained the aphid of its body contents without immediately administering an immobilising agent. However, regurgitation of a dark fluid into the prey during feeding did sometimes occur in the older larvae, generally towards the end of the meal where it was apparently part of the normal feeding process, involving alternate suction and regurgitation of the liquid contents of the dead aphid. Third and fourth instar larvae of this species have on occasion been seen to grasp their prey with the fore legs, but this generally occurred when aphids were attempting to pull free. Many of these older larvae merely seized their prey with the mouth parts without the assistance of their fore legs or the aid of a toxic secretion. Adults of *E.concavus* made regular use of their fore legs to capture aphids. No instances of the prey being immobilised by a toxin were observed.

These observations show that valid differences in the method of attack occurred between certain species and their respective instars. Such differences in behaviour could obviously determine the outcome of an attack and would therefore influence the efficiency of a particular predator.

VI DISCUSSION

The four Coccinellids under investigation displayed variable efficiency in their capacity to capture different instars of *S.graminum* in the laboratory. Much of the variability observed between species could be ascribed to the different methods of attack employed by these Coccinellids and to the way the prey was overpowered once it had been seized. Of the four species, *L.flavomaculata* and *C.lunata* were the most efficient at capturing prey. The other two species, *S.morelleti* and *E.concavus*, were less efficient, especially in their early instars. Coupled with its numerical superiority in nature, the outstanding attack efficiency of *L.flavomaculata* leads one to conclude that it is the dominant predator associated with the wheat aphid. Although the efficiency of the larval instars of *C.lunata* compared well with those of *L.flavomaculata*, the former was rare in nature and could not therefore be considered as an important field predator.

The efficiency of a particular coccinellid species varied with its stage of development as well as with that of its prey. Although small first instar Coccinellids were able to capture all instars of *S.graminum*, many aphids, especially the older instars, managed to escape. The first instar Coccinellid was always the least efficient at capturing prey. However, with each succeeding instar, individual efficiency improved until it attained its maximum in either the third or, more usually, the fourth instar. Adults of all coccinellid species were less efficient than their older larval instars. These findings substantiate the observations of Dixon (1959) on *Adalia decempunctata*; he found that efficiency increased with each succeeding larval instar and decreased again in the adult.

Since the older larval instars were the most efficient, third and fourth instars of

L.flavomaculata would be expected to have the most pronounced effect on the aphid population and hence exert maximum control. Blackman (1967), using different species of aphids as prey, found *C.septempunctata* to be a more efficient predator than *A.bipunctata* and that fourth instar larvae of both species were more efficient than first instars.

Discovery of an aphid colony by a newly dispersed first instar Coccinellid marks a turning point in its life and probably assures its subsequent survival. Inability to capture certain aphid instars will also affect survival of the individual, especially when prey is scarce. Fortunately, colonies of *S.graminum* usually contain all stages of development, and a wide choice of prey is thus always available. Impaired efficiency against certain of the larger prey, such as the apterae, would consequently not be such a critical factor, since younger and more vulnerable prey would always be available. Capture of the younger aphid instars would facilitate development, producing more mature predators which would in turn capture a greater proportion of the more difficult older aphid instars. Because they would be more easily captured, mortality due to selective feeding would probably be greatest amongst the younger aphid instars.

The efficiency of a predator also depended on the species of aphid that was attacked. Some aphids like *C.elaeagni* proved difficult to capture, and experiments with the larvae of *C.lunata* showed them to be less efficient against this aphid species than against *S.graminum.* According to Dixon (1958), the aphid *Microlophium evansi* was another extremely difficult species to capture. Adults of the sycamore aphid, *Drepanosiphum platanoides*, were also rarely captured by Coccinellids (Dixon, 1963); *Acyrthosiphon pisum* (Harris) and *Megoura viciae* Buckton also proved to be difficult prey species (Blackman, 1967). Variable efficiency in the capture of certain aphid species might also be responsible for a certain degree of host specificity, even amongst the more general aphid-feeding Coccinellids, and the relationship between predator and prey might be more specialised than was hitherto suspected, as suggested by Thompson (1951).

The Coccinellids studied here captured their prey either by some part of the body, i.e. the head, thorax and abdomen, or by some appendage, such as the antenna or leg. Depending on their preference, these predators might therefore be classified as either "body seizers" or "appendage seizers". On the basis of the method of capture, the larvae and adults of *L.flavomaculata* are predominantly body seizers, whereas, in *S.morelleti*, the larvae are predominantly appendage seizers and the adults body seizers. A similar transformation in the method of capture also occurred after the first instar in *E.concavus*: the first instar, and possibly a few second instar individuals, operate as appendage seizers, whereas subsequent larval instars, together with adults, operate as body seizers. Both larvae and adults of *C.lunata* captured their prey by the body, the larvae especially favouring the abdomen, and could hence be termed body seizers. Greater variation in the method of prey capture was found between the larval instars of the different species than between their adults.

Some aphid stages, especially the apterae, were capable of putting up a violent struggle after capture. In order to counteract this tendency and to prevent the aphid from escaping, several methods of subduing the aphid and making it more tractable were used by certain of the predators. During attack species such as *L.flavomaculata* and *C.lunata* sometimes made use of their fore legs to seize and overpower the aphid. Others, like the different larval instars of *S.morelleti*, as well as the first two instars of *E.concavus*, rapidly immobilised their prey by orally administering a powerful toxic secretion through the wound. This secretion proved fatal to all instars of *S.graminum* and was equally toxic to several other aphid species. The forceful injection of a potent toxic secretion, administered by biting as an aid to prey capture, as shown by the larvae of *S.morelleti*, displays all the characteristics of an insect venom (*sensu* Beard, 1963).

Rapid immobilisation of the prey by the larvae of *S.morelleti* has high survival value for this predator. In the first instance it is advantageous on account of the small size of the predator relative to that of its prey, which gives the aphid an advantage over the predator. Secondly, it is advantageous because seizure of the prey by the legs increases the likelihood of the predator being flailed about and becoming dislodged.

Regurgitation of a toxic secretion into the prey, which immobilises and aids in its capture, is hardly surprising when one considers that the method of extra-oral digestion necessitates the introduction of digestive secretions into the body of the prey. Since the larvae of *S.morelleti* only imbibe food in the liquified state, these digestive secretions serve to liquify and degrade the body contents of the prey and make them more assimilable to the predator. It is noteworthy that most carnivorous beetles secrete enzymes such as protease and lipase during digestion in order to hydrolyse proteins and fats in their food (Wigglesworth, 1953). According to Beard (1963), the enzyme protease was one of the active ingredients of the salivary venom of the reduviid bug, *Platymeris rhadamanthus* Gerstaecker, which disrupts the intercellular matrix and causes dissolution of the tissue of the prey. Similar enzyme activity could account for the toxicity of the gut fluid of the larvae of *S.morelleti*, but confirmatory analysis of the fluid is needed.

Although immobilisation of the prey by injection of toxic secretions is known for several other Coleoptera, such as the larvae of certain Dytiscidae and Carabidae (Balduf, 1935), it has hitherto not been recorded in the Coccinellidae. Beard (1963), in his extensive review of insect toxins and venoms, made no mention of its occurrence in Coccinellidae and in a recent personal communication confirmed that he had not previously come across this method of prey immobilisation by members of this family. About the only reference to this method of capture by Coccinellidae, as far as the writer is aware, is that of Smit (1917), who very briefly mentioned the narcotic effects of the feeding of *Scymnus* (=*Pullus*) *casstroemi* Mulsant on its aphid prey.

VII SUMMARY

Lioadalia flavomaculata (DeGeer), *Scymnus morelleti* Mulsant, *Exochomus concavus* Fürsch and *Cheilomenes lunata* (F.), predators of the wheat aphid, *Schizaphis graminum* (Rondani), in the Orange Free State province of South Africa showed considerable variation in their ability to capture prey. *L.flavomaculata* was one of the most efficient species, as well as the most abundant in the field, and it is suggested that this species was the dominant predator. Although *C.lunata* was equally efficient, it never achieved importance because of its relative scarcity in the field. *S.morelleti* and *E.concavus* were relatively inefficient, especially in their early instars.

The efficiency of a particular coccinellid species varied with its stage of development. First instars were always the least efficient, but efficiency improved with each succeeding instar and attained its maximum in either the third or more usually the fourth instar. Adults were less efficient than their older larval instars.

Predator efficiency also depended on the species of aphid that was involved. *Capitophorus elaeagni* (del Guercio) proved more difficult to capture than *S.graminum*. Efficiency varied not only with the species of aphid but also with its stage of development,

older aphids being more difficult to capture than the early instars. Because of this, mortality would be greatest amongst the early aphid instars.

Much of the variability in efficiency can be ascribed to the different methods of attack employed by each coccinellid species and to the way their prey was overpowered. The prey was captured either by part of the body (head, thorax or abdomen) or by some appendage such as the antenna, leg or even the siphunculi. The method employed varied with the species and was also influenced by the stage of development of the predator. Larvae of *L.flavomaculata* and *C.lunata*, and adults of all four species, used their fore legs to seize and overpower their prey. All four larval instars of *S.morelleti* and the first two instars of *E.concavus*, however, rapidly immobilised *S.graminum* by administering a toxic secretion through the bite; these secretions proved equally toxic against several other aphid species.

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