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Defensive behaviour of the wheat aphid, *Schizaphis graminum* (Rondani) (Hemiptera : Aphididae), against Coccinellidae

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SYNOPSIS

An account is given of the behaviour of the wheat aphid, *Schizaphis graminum*, in response to attacks by two coccinellid predators *Scymnus morelleti* and *Exochomus concavus*. Various responses are described and their influence on predator efficiency is investigated.

INTRODUCTION

Although aphids have long been known to vary in their suitability as prey for Coccinellidae, reports in the literature on their ability to avoid predation are scanty. Aphids are known to avoid capture by being unpalatable and Dixon (1958) has recorded *Hyalopterus pruni* (Geoffroy) being rejected for this reason following seizure; other species such as *Megoura viciae* (Buckton) and *Aphis sambuci* L. have similar properties and when ingested retarded development or proved toxic to certain species of Coccinellidae (Blackman, 1967; Hodek, 1967). More palatable aphid species avoid capture by employing various behavioural responses which serve a defensive or evasive function. Dixon (1958), investigating the responses of the nettle aphid, *Microlophium evansi* (Theobald), against *Adalia decempunctata* (L.) showed that this prey avoided capture by kicking, by walking away and/or by dropping from the leaf; when seized it also immobilized the predator with a defensive secretion from the siphunculi. Similar use of chemical defence has been reported by Edwards (1966) for *Aphis fabae* (Scopoli), *Macrosiphum rudbeckiae* (Fitch.) and *Myzus persicae* (Sulzer). Other methods of escape such as by leaping have been recorded for *Eucallipterus tiliae* (L.) by Dixon (1958) and for *Drepanosiphum platanoides* (Schrank) by Kennedy and Crawley (1967).

Coccinellid predators of the wheat aphid, *Schizaphis graminum* (Rondani), a pest in the Orange Free State, South Africa, display considerable variation in predator efficiency due to differences in their method of attack and to the way they subdue their prey (Brown, 1972). However, behaviour of the prey itself could also influence predator efficiency and the present study is therefore concerned with the reaction of *S.graminum* to *Scymnus morelleti* (Mulsant) and *Exochomus concavus* Fürsch, two species of Coccinellidae commonly associated with this prey in the field.

Capture of prey by these two species sometimes involves seizure of prey by the legs, as well as the body, and injection of a toxic oral secretion into the prey. A full account of the predatory behaviour of these Coccinellids is given by Brown (1972).

MATERIALS AND METHODS

Batches of a desired instar of *S.graminum* were released on young wheat shoots standing in corked vials of water and allowed to settle on the preferred parts. The shoots were then placed in a rotating device beneath a Stereo microscope so that the aphids settled on both leaf surfaces could be kept under continuous observation; selected instars of unfed Coccinellids were then released amongst the aphids and their behaviour recorded. Observations were confined, as in nature to settled aphids, only individuals that were the target of attack or came within contact distance of a predator were considered. Except for the alate adult aphid, the reaction of all prey instars was examined. Following capture, the predator was removed so as to give the remaining aphids time to resettle before releasing the next predator. In order to obtain quantitative results, 15 replicates of each instar were tested against each prey instar and the type of behaviour elicited and number escaping were recorded. From the total number of attacks and proportion of escapes the percentage avoiding capture could then be calculated for each instar. Observations were conducted in the laboratory at temperatures ranging from 19–23° C which favoured aphid activity.

RESPONSES OBSERVED

All instars of *S.graminum* spend the greater part of their lives settled with their mouthparts inserted into the host plant. This sedentary attitude involves the arrangement of the appendages in a characteristic way with the antennae laid back over the body and the legs partly extended and spread out. From this position aphids reacted in one of several ways, depending on circumstances, when encountered by Coccinellidae which either prevented attack or enabled the aphid to take evasive action. Seven principal responses, described below, were distinguished.

Behaviour before seizure

Kicking reaction. When the leg of an aphid was contacted by a searching Coccinellid the aphid reacted by kicking. If the predator was very small in relation to the prey, such behaviour caused the predator to retire or, if executed sufficiently vigorously, to knock it off the leaf. In cases where aphids were seized by the tarsi, the predator was flailed about on the end of the limb until it let go. Defensive behaviour involving kicking has been recorded for *A.fabae* by Banks (1957) and for *M.evansi* by Dixon (1958), and adults of *D.platanoides* have been observed (Dixon, 1963; Kennedy and Crawley, 1967) to make similar movements when approached by neighbouring aphids.

Bucking reaction. Aphids reacted in this way when the legs, especially the middle and hind ones, were stimulated or when predators attempted to crawl over their backs. Such a reaction consisted of synchronised kicking of both hind legs so that the body performed upward and forward movements, pivoting on the embedded mouthparts, and occurred in short bursts following contact. Similar behaviour has been reported for *A.fabae* (Ibbotson and Kennedy, 1951; Banks, 1957) and for *D.platanoides* (Kennedy and Crawley, 1967).

Swivelling reaction. An aphid stimulated on one side, especially on the middle leg, often swivelled away from the source of disturbance and in this way rapidly broke off contact with the predator. Aphids behaving thus generally turned through 90° to their long axis but some turned through 180° to face in the opposite direction.

When the above responses failed to deter an attack or when encountered by larger predators the following behaviour was observed.

Walking away. Aphids settled in the path of an approaching predator rapidly withdrew their mouthparts and escaped by walking away, either before or after being contacted. Aphids facing the predator apparently responded visually because their invariable first reaction was to lift the antennae and point them at the approaching predator when it was still a short distance away. Similar behaviour has been recorded for *M.evansi* by Dixon (1958).

Springing and dropping. When encountered by or before coming in contact with relatively large predators, aphids sometimes kicked strongly with both hind legs, released their mouthparts and somersaulted off the leaf. Others first freed their mouthparts and then simply dropped off the leaf. It was sometimes difficult to distinguish between the two responses, which are therefore combined, although in the former case they tended to travel horizontally away from the place of rest instead of vertically. Dropping has been reported for *M.evansi* and for *Euceraphis punctipennis* (Zett.) by Dixon (1958).

Behaviour after seizure

Pulling free. A violent struggle sometimes ensued following seizure and if the predator was small or if the prey was improperly secured in the jaws of the predator it pulled free and escaped. *M.evansi* responds in the same way (Dixon, 1958), often in combination with a discharge from the siphunculi.

Leg shedding. Adult prey severed their legs (autotomy) at the junction of the trochanter and femur when seized. In some, shedding was almost instantaneous, but in others a struggle ensued before the limb was shed. Individuals subjected to repeated attacks shed as many as three legs and resettled to resume feeding and reproduction. Shedding of the limbs was apparently dependent on a certain amount of tension being exercised on the captured limb and seemed most effective when the predator was positioned at right angles to the aphid. Shedding was prevented when the aphid was lifted off the leaf surface. Alate aphids were also able to shed their legs but in hundreds of observations on the immature stages none escaped in this way. Similar behaviour was recorded for the adults of several other species, such as *Myzus persicae*, *Brevicoryne brassicae* (L.) and *Capitophorus elaeagni* (del Guercio). Although Dixon (1958) briefly mentions *M.evansi* losing legs during encounters with Coccinellids, he did not record prey escaping by this means.

Although all instars of *S.graminum* responded by exuding a greenish liquid from the siphunculi which sometimes became smeared on the attacker, neither of the two species of Coccinellidae investigated ever appeared adversely affected by it. In *M.evansi* such behaviour serves an important defensive function (Dixon, 1958).

Defensive behaviour

The relative sizes of the different prey instars and corresponding predator instars are shown in figure 1. As can be seen there is considerable variation in size between the different stages of both predators, *E.concavus* being the larger, and between them and the wheat aphid. The type of behaviour shown is listed separately for each predator species below.

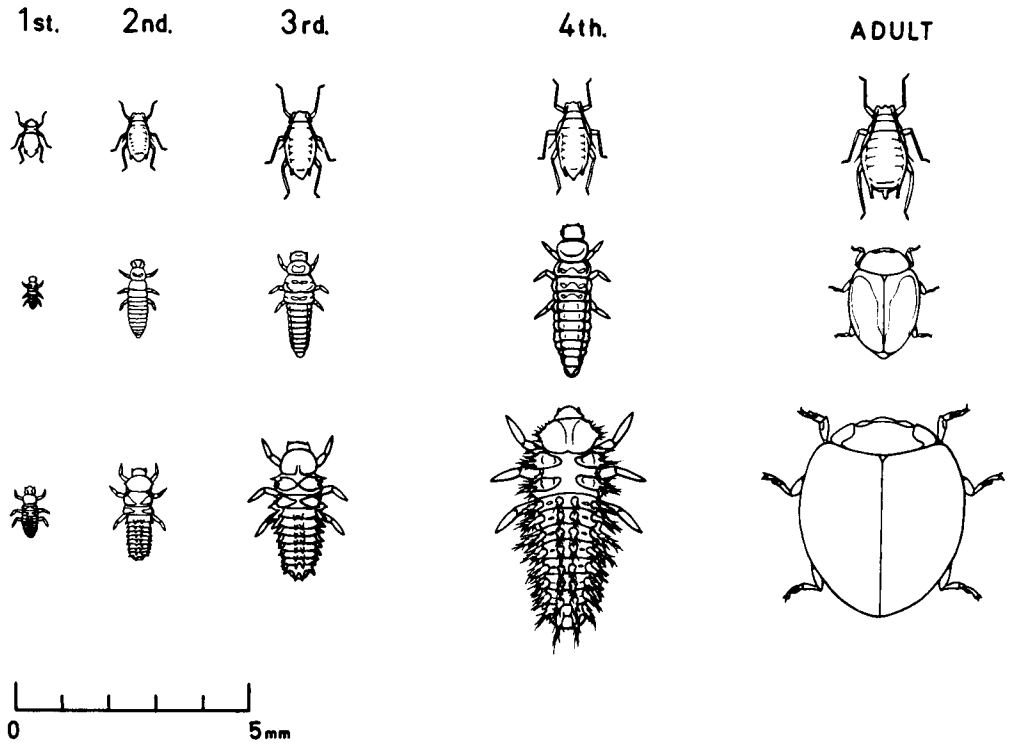

Fig. 1. Relative sizes of *S.graminum* and its two coccinellid predators, *S.morelleti* (above) and *E. concavus* (below).

Behaviour evoked by S.morelleti

Percentage prey escaping from the different instars of this predator are shown in figure-2a – e and the following behaviour recorded.

Escapes from first instar predators (fig. 2a). The commonest method of escape was by kicking and this ability improved with each instar, the percentage first, second, third and fourth instars escaping were 14, 18, 21 and 35 per cent. respectively with a maximum of 47 per cent. for adult prey. Apart from its small size, this predator had the habit of seizing prey by the tarsus which probably facilitated kicking. Although the majority of early prey instars responded immediately, certain of the older instars ignored the predator and in some cases remained settled with the predator feeding on their legs. Although initially unaffected, failure to respond ultimately proved fatal because of the toxic secretion introduced by this predator during feeding. Prey killed in this manner remained with their mouthparts embedded in the leaf. Adult prey shed their legs when seized, 29 per cent. escaping, 9 per cent. also pulled free and 2 per cent. repelled the predator by means of bucking movements. Ten per cent. first and 9 per cent. second instars reacted in the latter way when Coccinellids mounted their backs; a smaller number, 5 per cent. each, of both these instars also pulled free.

Escapes from second instar predators (fig. 2b). Kicking was less successful against this predator presumably because of its more persistent behaviour and preference for seizing prey by the tibia, only 6 per cent. third instars, 10 per cent. fourth instars and 17

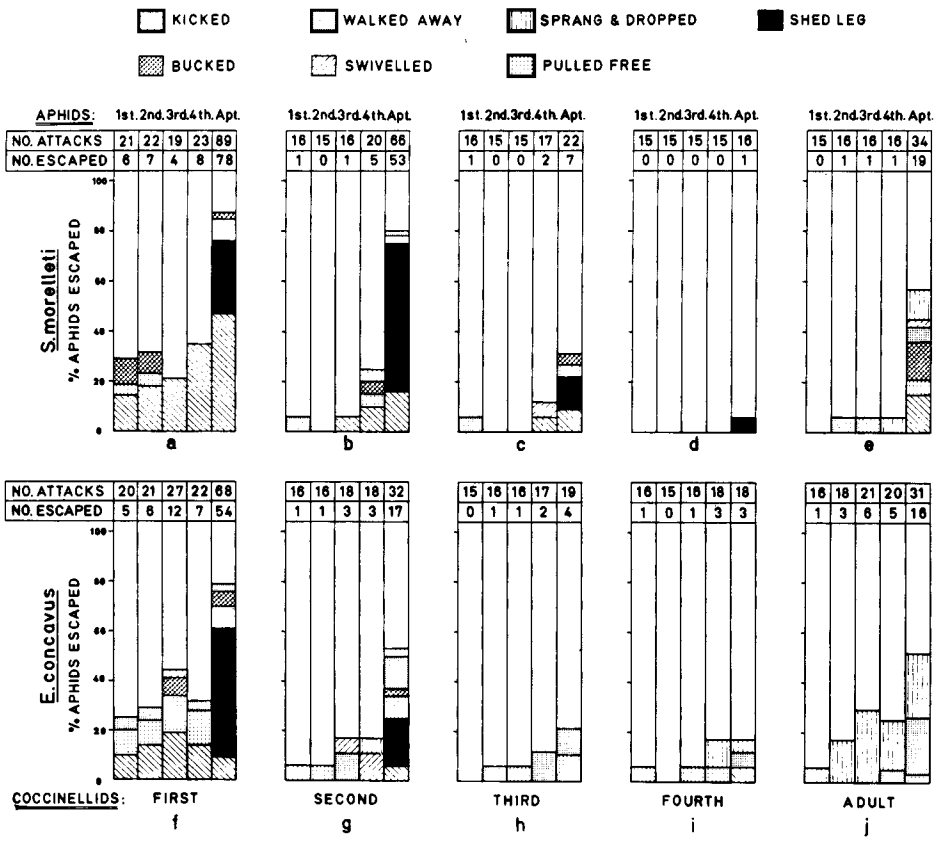

Fig. 2. Reaction of different instars of *S.graminum* to attacks by *S.morelleti* (a–e) and *E.concavus* (f–j), and percentage prey escaping; 15 coccinellids were tested against each aphid instars. Blocks denote different predator instars, columns denote different prey instars. The number of attacks observed and the number of aphids escaping are shown above each column.

per cent. adult prey escaped this way. Leg shedding consequently assumed greater importance and 59 per cent. of apterae escaped by this means. This was influenced by the increased toxicity of the oral secretion, only those apterae that shed their legs within seconds of seizure succeeded in escaping. In five individuals where times of 28, 60, 90, 90 and 120 seconds were recorded before the leg was shed, the delay proved fatal and all died from the toxin introduced at the time of attack. Escapes effected by walking away accounted for 6 per cent. of first instar and 2 per cent. adult prey escaping, whilst 5 per cent. in each case of fourth instars escaped by bucking, by springing and dropping and by pulling free. The latter reaction also enabled 3 per cent. of adult prey to escape.

Escapes from third instar predators (fig. 2c). Kicking was much less effective and only 6 per cent. fourth instars and 9 per cent. adult prey escaped. This was presumably due to the larger size of this predator instar and its habit of seizing prey by the tibia and femur. Leg shedding also proved less successful, only 14 per cent. adults escaping, probably on account of increased toxicity and/or dosage of the oral secretion which could be clearly seen as a dark discoloration advancing up the leg and streaming into the aphid's body.

Once it reached the base of the leg it evidently blocked the response, since shedding rarely took place after this had occurred. Of the apterae escaping, all shed their limbs 3–4 seconds after seizure. Five per cent. of this prey also escaped by bucking and by pulling free. One first instar aphid managed to walk away and one fourth instar swivelled out of reach.

Escapes from fourth instar predators (fig. 2d). Of the 76 attacks observed, only one aphid was successful in escaping. Toxicity of the oral secretion together with a tendency to lift prey in the air prevented all but one of the apterae from shedding their legs. Responses such as kicking, bucking and springing and dropping were unsuccessful. Indeed movement of any sort seemed disadvantageous, since it provoked immediate attack; prey remaining immobile was overlooked in preference to neighbouring individuals which moved.

Escapes from adult predators (fig. 2e). Somewhat different responses were evoked by this predator due to prey being seized by the body instead of the legs. Adult prey was reasonably successful, 15 per cent., respectively, escaping by kicking and by bucking, 12 per cent. by springing and dropping, 6 per cent., respectively, by pulling free and by walking away, and 3 per cent. by swivelling. One second, one third and one fourth instar escaped by walking away, by pulling free and by dropping from the leaf.

Behaviour evoked by E.concavus

The percentage aphids escaping from the different instars of this species are shown in figure 2f–g. Responses evoked by the first two instars are similar to those described for the larvae of *S.morelleti*, but subsequent responses are different. This is due to a change in predatory tactics: first instar larvae and, to some extent, second instars seizing prey by their legs whereas later instar predators favour the body. In these circumstances the behaviour of prey may be summarised as follows.

Escapes from first instar predators (fig. 2f). Kicking was moderately effective enabling 10, 14, 19, 14 and 9 per cent. respectively of first, second, third, fourth and adult prey to escape. Pulling free accounted for 10, 10, 15 and 14 per cent. escapes by the first four instars and for 9 per cent. by adult prey. Adults invariably shed their legs before these could be pulled free, resulting in 53 per cent. escapes, the remainder escaped either by bucking or walking away. Five per cent., respectively, of first and second instars to with 4 per cent. of fourth instars, walked away from the predator. Bucking enabled 7 per cent. third instar prey to escape.

Escape from second instar predators (fig. 2g). Kicking was less effective and 6 per cent. adult prey escaped by this method. Increasing preference for the aphid's body reduced leg shedding by apterae to 19 per cent. and walking away accounted for 13 per cent. The latter reaction enabled 11 per cent. third instars to escape, while 6 per cent. each of first, fourth and adult prey escaped by springing and dropping. Swivelling enabled 6 per cent. of third and 11 per cent. of fourth instars to escape. One second instar and 9 per cent. adult prey pulled free and one adult escaped by means of bucking.

Escapes from third instar predators (fig. 2h). Prey was seized by the body and 6 per cent. second instars, 12 per cent. third instars and 11 per cent. adults escaped by walking away; pulling free enabled 6 per cent. third instars and 11 per cent. adults to escape.

Escapes from fourth instar predators (fig. 2i). Prey attempting to walk away was overtaken and captured, only one adult aphid escaped in this way. A small percentage,

6 per cent. in each case, of first, third and fourth instars escaped by pulling free. Prey attempting to drop from the leaf was often intercepted, although 11 per cent. fourth instars and 6 per cent. apterae escaped by this means. One aptera repelled an attack by kicking.

Escapes from adult predators (fig. 2j). An interesting feature here was the high percentage of aphids which sprang and dropped, 6 to 29 per cent. of the different prey instars thus escaping. Five per cent. of fourth instars and 23 per cent. of adult prey escaped by walking away. Frequent use of the fore legs in capturing prey reduced the incidence of pulling free and only 3 per cent. adults escaped by this means.

DISCUSSION

These observations show that there is a reasonable expectation of survival in *S.graminum*, at least against certain predator instars, and that the species is not entirely defenceless. Different prey instars were also not equally susceptible to predation, resistance by certain of the older instars, especially apterae, was more effective and all instars were better at escaping from first instar predators. Discovery of prey by a newly hatched Coccinellid sees the completion of a critical stage in the life cycle of the predator which must locate its food within a specified time or succumb from starvation. If faced however with the additional problem of prey that is superior to the predator's best method of attack then the Coccinellid's chances of survival could be appreciably reduced. This might help explain the failure of predators to sometimes develop on aphids which appear suitable as food for their adult stages.

Seven different responses with presumed defensive function have been described in the behavioural repertoire of *S.graminum*. Other kinds of predators (and parasites) might however evoke different responses which still require evaluation. Under restraint, for instance, aphids discharge a secretion from their siphunculi and although this did not deter even the smallest predator investigated, an aphid from the field was collected with a dead Aphidiid parasite affixed to its siphunculus suggesting greater efficiency against parasites. Reaction to predators depended on the method of attack, species of predator involved and its stage of development, there being an advance in efficiency with each successive instar; longer reach, greater oral capacity and increased toxicity of the immobilising agent, increased handling time and more rapid reaction time, all served to improve predator efficiency. The aphid instar was also important, adult prey for example being able to shed their legs. The importance of the instar and its size relative to that of the predator has been emphasised in *M.evansi* by Dixon (1958).

Kicking was most effective against small predators, especially the early instars of *S.morelleti* which attempted to seize prey by the extremities of the legs. Later instars were not only larger but favoured capture by the femur and tibia which probably hampered kicking. Predator size also influenced certain of the other responses, more prey for example struggled free from first instar *E.concavus* than from later instars and more prey responded to the adult predator by walking away and especially by springing and dropping. It was evident from the way prey responded while the predator was still some distance away that visual perception of the beetle was enhanced. That aphids show a well developed visual response to nearby objects has been demonstrated by Ibbotson (1966). According to Dixon (1958) characters such as shininess, coloration and form increased the responsiveness of the nettle aphid to adults of *A.decempunctata*.

An unusual method of escape was shedding of legs by adult prey but was not peculiar to this species, having been observed by the writer in several other species of aphids as well. Although alate aphids could also shed their legs, immature aphids were unable to do so. Shedding of legs was of course only effective against those predators that seized prey by the legs, such as the larval stages of *S.morelleti* and the early instars of *E.concavus*. Such adaptation should provide good protection from predators which capture prey in this way; its failure against certain of these predators was due to the efficacy of the toxic immobilising secretion and superior predatory tactics such as lifting prey in the air.

As would be expected in a group with only limited vagility and where organs for rapid escape are poorly developed, the majority of responses shown such as kicking, bucking, swivelling and leg shedding were of a static nature, performed while the aphid was settled on the leaf. Active escape was limited to walking away and to springing and dropping and were generally carried out after the deployment of static defences. The dropping response is a special case where gravity is utilised as a means of escape, operating in effect as a form of active escape normally only possible with the aid of specialised locomotory or flight organs. The development of an additional springing component in *S.graminum* permits its use even when settled on a horizontal surface. Escape behaviour by dropping from the host plant is of course known for many families of insects.

The majority of responses recorded for *S.graminum* operate before capture, once seizure occurred the chances of escape were considerably reduced for, apart from leg shedding, the only means of escape possible was by pulling free.

It is concluded that predator efficiency rests not only on the method of attack and the way in which the prey is subdued, but also on the defensive behaviour of the aphid itself. Significantly enough this takes place here in the case of an apparently susceptible prey species and emphasises the specialised nature of the relationship between the predator and its prey, a fact not always fully appreciated when planning biological control.

Prey perception by the Coccinellids under investigation occurred only after actual contact so that the first warning the predator has of prey is after colliding with it. Since aphids settle with legs extended around them and point their antennae at approaching predators, the chances are that the predator will encounter one of these appendages before contacting the body of the aphid. Observations on *Lioadalia flavomaculata* (DeGeer), another Coccinellid predator of the wheat aphid, show that after contacting the leg of a settled aphid, the predator groped around until it located and seized the body. However, against other species of aphids which possessed longer legs, like *C.elaeagni* such behaviour proved less successful as the predator had difficulty in reaching the body before the aphid reacted and escaped. The responses shown by certain aphids and the way they arrange their legs on the leaf while settled, leads one to suspect that many aphids use their appendages as an early warning system, enabling them to take evasive action and make their escape. Present results reveal that in certain circumstances they will even sacrifice their limbs as a second line of defence. Conceivably therefore aphids with long appendages will stand better chance of escape than those with short appendages, as suggested by Kaddou (1960).

SUMMARY

The wheat aphid, *Schizaphis graminum* (Rondani), despite its apparent vulnerability to predators, evades capture in a number of characteristic ways from *Scymnus morelleti* (Mulsant) and *Exochomus concavus* Fürsch, two coccinellid predators of this aphid in the

Orange Free State province of South Africa. Seven different type of defensive responses were distinguished. *Kicking*, *bucking*, or *swivelling* were employed while the aphid remained settled on the leaf, active escape behaviour was limited to walking away and *springing and dropping*. After capture the prey could sometimes escape by *pulling free* or *shedding a leg*. *S.graminum* perceives predators mainly by tactile stimuli, although visual perception was also important especially for adults.

Older aphid instars were more successful in evading attack than the younger instars and apterae proved the most successful. Factors such as the aphid instar, the method of attack employed, the species of predator and its stage of development were important in determining the reaction of the prey. Defensive behaviour on the part of the prey would influence predator efficiency and could constitute an additional hazard for small predators which happen to encounter aphids with superior defence systems.

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