

THE EGG-PARASITE COMPLEX (SCELIONIDAE :
HYMENOPTERA) OF SHIELD BUGS (PENTATOMIDAE,
ACANTHOSOMIDAE : HETEROPTERA) IN
NEW ZEALAND

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Summary

Prior to the introduction of the egg-parasite *Asolcus (Microphanurus) basalis* (Woll.) to control the green vegetable bug *Nezara viridula* (L.) two *Asolcus* species were involved in the egg-parasite complex. One is restricted to acanthosomid and the other to pentatomid hosts. *A. basalis* is now known to accept the eggs of five pentatomid species in addition to those of *Nezara*. These same five species are also utilised by the resident scelionid species which however cannot utilise the eggs of *Nezara*.

Anatomical characters and biological characteristics which distinguish the scelionid species are described. Interspecific copulation is attempted, but crossing of the two species involved in the Pentatomidae does not occur.

Experiments designed to study both adult and larval dominance in the two closely allied pentatomid parasites indicate that, given equal opportunity, the resident species is more aggressive than *A. basalis*. Factors other than inherent dominance which may be responsible for field dominance are discussed.

It would appear that the laying of male producing unfertilised eggs is irregularly spaced in any sequence, but that there may be a tendency towards greater male production early in the laying life of the female.

INTRODUCTION

The egg-parasite complex of shield bugs in New Zealand has been a changing one in recent years. Three further host species have reached the country, and one parasite species has been introduced. The complex, however, is still a relatively restricted one in respect of numbers of species. The study of host relationships is biologically interesting and of importance economically.

Myers (1926) in his extensive biological notes on the more commonly encountered members of the Pentatomidae and Acanthosomidae, makes no mention of egg parasites.

During the summer of 1948-49, the egg parasite *Asolcus (Microphanurus) basalis* (Woll.) was introduced from Australian stocks to assist in the control of the green vegetable bug *Nezara viridula* (L.) (Cumber, 1951). In the course of this work it was noted that field collected eggs of *Cuspicona simplex* Walk. were parasitised by a species of *Microphanurus* which bred readily in captivity. Repeated attempts failed to induce this

species to utilise the eggs of *Nezara* however, which at that time were present in very great numbers. Field eggs of *Nezara* were frequently collected but there was no evidence of parasitisation before *Asolcus* was introduced.

Pendergrast (1952) in his studies on the Acanthosomidae recorded the presence of *Microphanurus* in the eggs of *Rhopalimorpha obscura* A. White from Paiaka (Foxton) in materials collected by the writer.

During 1962, a number of experiments using eggs of *Antestia orbona* Kirk., indicated that both *A. basalis* and the *Microphanurus* sp. earlier discovered on *Cuspicona* could use this host.

Since the introduction of *A. basalis* there has been a gradual decline in the severity of plant damage caused by *Nezara*. The parasite has been widely distributed and is now probably present in most districts where the host has, at one time or another, been reasonably plentiful. Although local populations of *Nezara* may continue to fluctuate seasonally, the present situation is satisfactory in the light of past experience.

The systematics of the Cydnidae, Pentatomidae, and Acanthosomidae are fully treated by Woodward (1953). The pentatomids involve the species *Cermatulus nasalis* (Westw.), *Oechalia schellenbergii* (Guérin-Meneville), *Dictyotus caenosus* (Westw.), *Glaucias amyoti* (A. White), *Antestia orbona* Kirk., and *Cuspicona simplex* Walk., which are shared with Australia; *Nezara viridula* (L.) which is cosmopolitan; and the endemic species *Hypsithocus hudsonae* Bergroth. The acanthosomids, *Oncacontias vittatus* (Fabr.), *Rhopalimorpha alpina* Woodw., *Rhopalimorpha lineolaris* Prend., and *Rhopalimorpha obscura* A. White are apparently endemic. There is no information concerning the arrival in New Zealand of the first four pentatomids mentioned above. However, *C. simplex* and *N. viridula* were first observed in New Zealand in 1944 and *A. orbona* in 1950.

HOST COMPATIBILITY

Successful distribution, adaptation, and the adoption of alternative hosts, are the factors most probably responsible for the reduction of the *Nezara* populations to a relatively low level after a period of some 14 years. One possibility of proving adaptation was lost through inadequate documentation of the 1949 experiments with *Nezara* and *Cuspicona*. The writer feels fairly certain that the alternative of *A. basalis* to *Cuspicona* eggs was unsuccessful, as were the attempts made with the resident *Microphanurus* from *Cuspicona* on *Nezara* eggs, but there is no definite record of this. Today the eggs of *Cuspicona* are readily accepted by *A. basalis*. However, the opportunity for adoption of further hosts by *A. basalis* was provided by the recently arrived *Antestia orbona*. The preliminary experiments with *A. orbona* suggested that the fall-off in *Nezara* numbers might be due to the adoption of alternative hosts. The present studies commenced with a view to examining this hypothesis.

The work has provided an opportunity for behaviour studies. Some of the reproductive habits described in detail by Wilson (1961) were noted

(Cumber, 1951) when recording the *A. basalis* breeding programme. The present complex, involving two closely allied competing species, is of very considerable interest.

Asolcus (*Microphanurus*) lives and breeds readily under laboratory conditions even in the absence of food for the adults (Fig. 1). Habits and performance under such conditions are always under some doubt in application to the field, but compatibility, and reproductive behaviour will vary little under the two conditions.

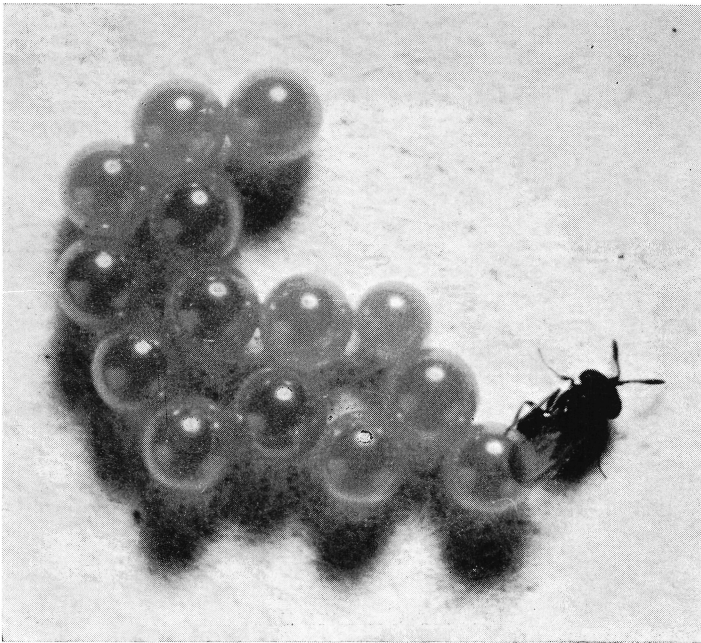


Photo: J. W. Endt

FIG. 1.—*Asolcus basalis* ovipositing in eggs of *Cuspicona simplex* which have been laid on filter paper.

Adult bugs in the families concerned overwinter as such, and commence laying following a short period of post-hibernation feeding and mating. The adults of some species, such as in *Rhopalimorpha*, have a relatively restricted range of host plants, and may be taken quite readily in spring. The same, however, cannot be said of the predacious species. The scope of the present work has been limited by the supply of adult bugs of the various species. However, sufficient material has been available to perform a number of host compatibility experiments. The majority of the egg materials used have been obtained by enclosing bugs singly, or in pairs, in 3 in. \times 1 in. corked glass tubes. Small amounts of the required food, and strips of filter paper for oviposition purposes, were provided. For larger species such as *Glaucias* and *Nezara*, a number of bugs of each species

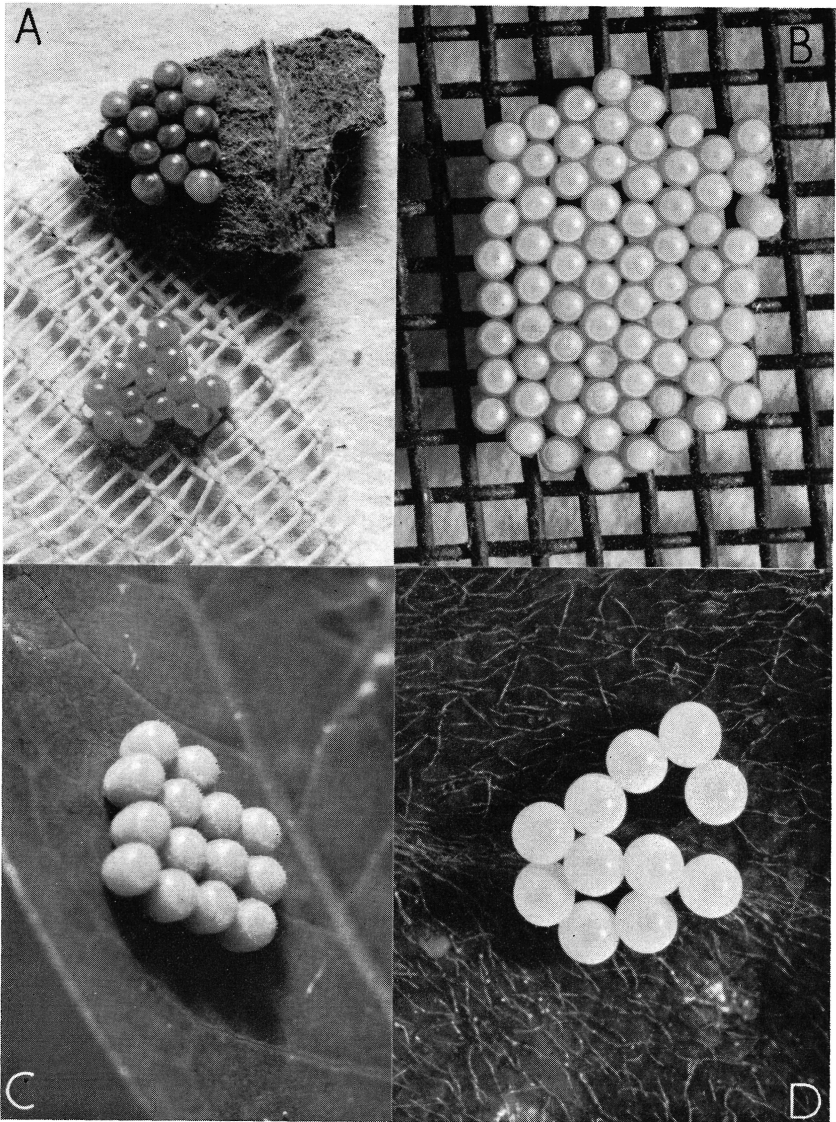


Photo: J. W. Endt

FIG. 2.—Pentatomid egg-masses: A—*Dictyotus caenosus*, the mass on the grape leaf has been parasitised in the field by *A. basalis*; B—*Nezara viridula* deposited on wire mesh; C—*Glaucias amyoti* on *Coprosma*; D—*Antestia orbona* on *Pittosporum*.

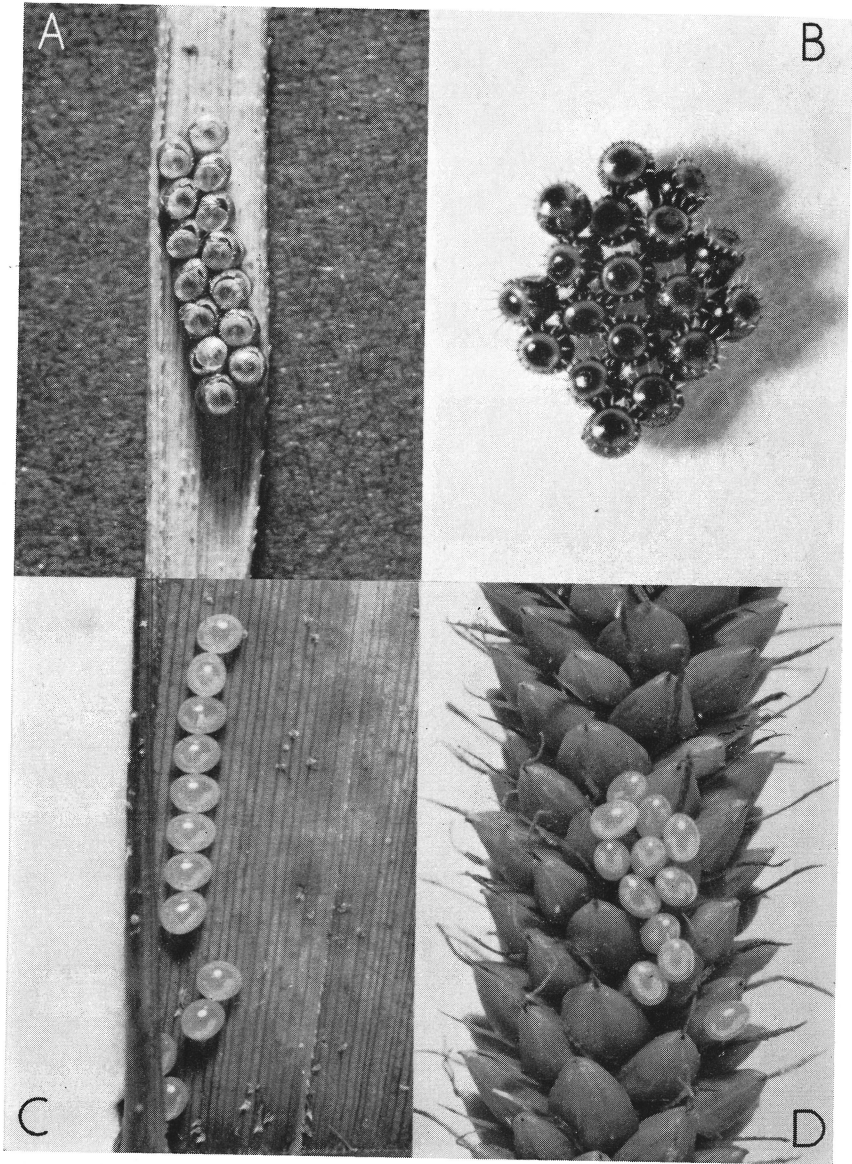


Photo: J. W. Endt

FIG. 3—Egg-masses: A—the pentatomid *Cermatulus nasalis* on *Gabnia xanthocarpa* following normal bug emergence; B—the pentatomid *Oechalia consocialis*; C—the acanthosomid *Rhopalimorpha lineolaris* on *Carex*; D—the acanthosomid *Rhopalimorpha obscura* on *Carex*.

were enclosed in 2 lb preserving jars. Eggs were removed regularly, dated, and placed in a refrigerator until required (Figs. 2, 3). Wherever possible recently laid eggs were used in experiments.

It seems probable, as indicated by Myers (1926), that with the majority of pentatomids there is one generation each year, and this would certainly seem to be true of the acanthosomids. Overwintering adults appear to live for several months and continue to lay periodically. This results in successions of nymphs and a rather confusing picture. It also seems probable, however, that in some species such as *Nezara* and *Cuspicona* there may be a second generation, which are the progeny of the earliest members of the first generation, seasonal factors doubtless having some bearing on the situation. This is borne out by the relatively large egg masses appearing early in March.

The existing evidence suggested that three species of *Asolcus* (*Microphanurus*) probably existed, namely, *A. basalis* (for convenience referred to as species B) the introduced species with relatively lighter coloured appendages; the native species originally detected on *Cuspicona* (referred to as species N or the resident species); and a smaller species (referred to as species A) with relatively dark antennae and light-coloured legs from the acanthosomid *Rhopalimorpha*. The following host-relationship experiments support the presence of these three distinct species.

Experiment 1 was set up on 10.12.63. Field collected eggs of *Cermatulus nasalis* taken at Paihia on 19.11.63 yielded adults with light-coloured appendages and presumed to be *A. basalis* (B). These were placed in the one tube containing eggs of the pentatomids *Antestia*, *Cuspicona*, *Dictyotus*, and *Glaucias*, and the acanthosomids *Rhopalimorpha lineolaris* and *R. obscura*. All the pentatomids were parasitised and parasites emerged successfully, but there was no parasitising of, or attempted oviposition in the acanthosomid eggs which all produced bugs. *Nezara* eggs were later made available to parasites emerging from the pentatomid eggs, as no eggs of this species were available at the setting up of the experiment. These were successfully parasitised, indicating that the above stock from *Cermatulus* were correctly assigned to *A. basalis*.

Experiment 2 was set up on 9.12.63. Field collected eggs of *Rhopalimorpha obscura* taken at Mt Albert on 28.11.63 yielded parasites of the small species A, with dark antennae and light-coloured eggs. These were placed in the one tube containing a series of eggs of the pentatomids and acanthosomids as used in Experiment 1. In this case only the acanthosomids were successfully parasitised.

Experiment 3 was set up on 20.12.63. Field collected eggs of *Antestia orbona* taken at Mt Albert on 9.12.63 yielded parasites of species N with the dark appendages. These were placed in a tube containing eggs of the pentatomids *Cuspicona*, *Dictyotus*, *Glaucias*, and the acanthosomids *Rhopalimorpha lineolaris*, and *R. obscura*. Only the three pentatomid species were successfully parasitised.

Experiment 4 was set up on 20.1.64. Field collected eggs of *Nezara viridula* taken at Paihia on 17.1.64 yielded parasites of the light-appendaged

A. basalis (B). These were placed in a tube containing eggs of the pentatomids *Antestia*, *Cuspicona*, *Dictyotus*, and *Glaucias*. All were successfully parasitised.

In a further series of experiments attempts were made to induce the resident species (N) to utilise the eggs of *Nezara*, but none was successful, indicating that there had been no apparent adaptation in this direction since the 1949 experiments.

The results of experiments 1-4 are shown diagrammatically in Fig. 4. These experiments show conclusively that three scelionid species are involved in the pentatomid-acanthosomid complex. One scelionid species apparently is confined to the Acanthosomidae, although information in respect of *Rhopalimorpha alpina* and *Oncacontias vittatus*, the other two representatives of the family, is not available. There is experimental and/or field evidence from all pentatomid representatives (excluding sub-species) except *Hypsithocus hudsonae*. This is summarised in Table 1 which shows both field and laboratory compatibilities for parasite species B and N. This indicates that each of these two species may utilise the eggs of five species, namely, *Antestia*, *Cermatulus*, *Cuspicona*, *Dictyotus*, and *Glaucias*. Species N (resident species) does not utilise the eggs of *Nezara*. The eggs of *Oechalia*, for want of materials, have not been tested against species B (*A. basalis*). Thus the last-mentioned parasite has, in addition to *Nezara*, at least five compatible alternative hosts.

At Paihia in the Bay of Islands, field collections within a mile radius include *A. basalis* (B) from *Nezara*, *Glaucias*, and *Cermatulus* (these three at the one site), and the resident species (N) from *Cuspicona* and *Dictyotus*.

TABLE 1—Parasitisation of Pentatomid Species

Host	Parasite	
	Species B (<i>A. basalis</i>)	Species N (Resident)
<i>Antestia</i>	+	++
<i>Cermatulus</i>	++	++
<i>Cuspicona</i>	+	++
<i>Dictyotus</i>	+	++
<i>Glaucias</i>	++	+
<i>Nezara</i>	++	—
<i>Oechalia</i>	?	++

*field as well as experimental evidence.

SEPARATION CHARACTERS FOR THE *Asolcus* (*Microphanurus*) Spp.

The species of *Asolcus* (*Microphanurus*) (species A) which apparently is specific to the acanthosomids may be readily separated from those species (B, N) involved in the pentatomid complex, by its contrasting lightly

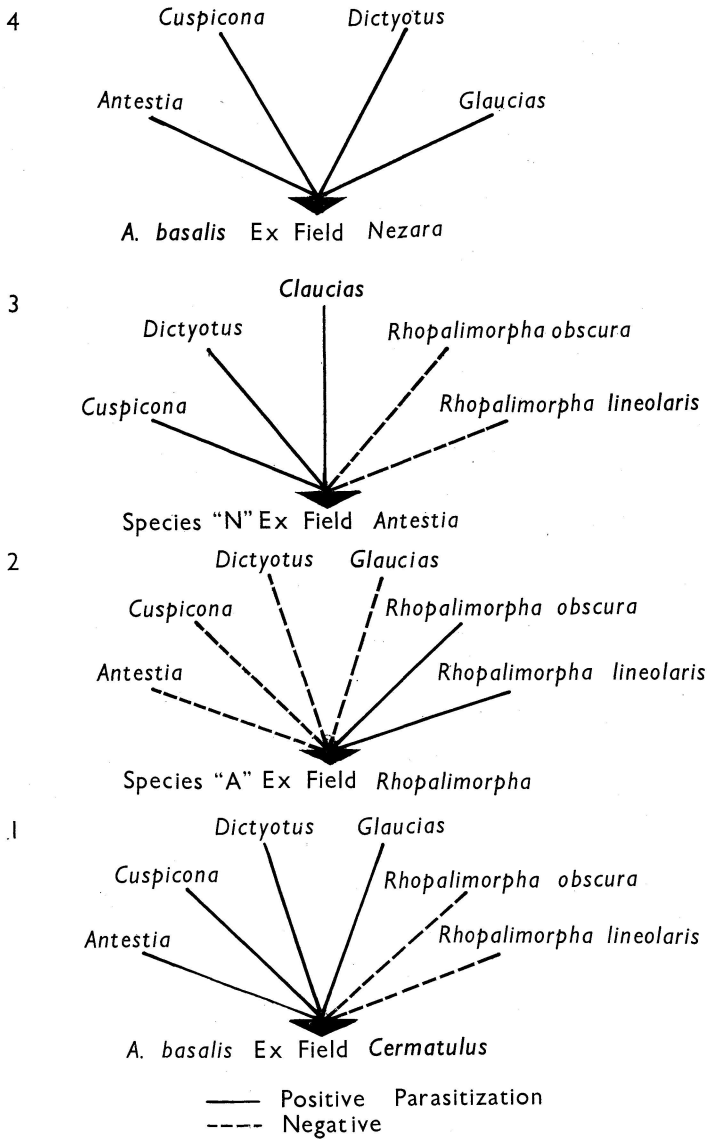


FIG. 4—Host compatibility results from four experiments using parasites from field collected eggs and eggs laid in captivity are shown. Successful parasitisation and parasite emergence are indicated by the solid rays.

coloured legs and darkly pigmented antennae, this latter depth of pigmentation being consistent throughout the length of the antennae. It is also a much smaller species, but the possibility of *Oncacontias*, with its larger eggs entering the complex cannot be overlooked.

It is the species which attack the pentatomids that mainly concern us here. *A. (M.) basalis* (B) and the resident species (N) are very similar in general appearance. However, there are anatomical characters and biological characteristics which serve to distinguish the two.

Anatomical Characters

The depth of pigmentation in the appendages has been mentioned above. The legs of *A. basalis* are much lighter coloured, as are the antennae—especially in their proximal segments. The wings, too, are lighter in colour, and the microtrichia smaller and more closely spaced. Punctuation of the dorsal areas of the thorax and head is finer in *A. basalis* giving a more silky appearance at lower magnifications. A comparison of the original stock (dry-mounted) materials with present-day specimens indicates that the former may have been even lighter in appendage pigmentation.

Biological Characteristics

Characteristics which separate the two species include oviposition stance, incubation period, host compatibility and depth of staining of host eggs.

The oviposition stance involving the position of the wings is quite characteristic of the species. In *A. basalis* (B) the wings lie almost touching the top of the eggs during oviposition, with a slight tendency for one wing to be raised above the other. In the resident species (N), the wings are held vertically—almost at right angles to the body and well away from the egg surface.

An experiment set up on 29.1.64 was designed to compare incubation periods in the two species. A mass of 14 refrigerated *Cuspicona* eggs was used, half the eggs being given to B parasites ex *Glaucias* (Paihia, 17.1.64) and half to N parasites ex *Dictyotus* (Paihia, 17.1.64), numbers of females being used in each instance. Oviposition commenced within five minutes of egg introduction. In species B, males appeared on 11.2.64 and 4 males and 3 females had emerged by 13.2.64. In species N, the males did not appear until 13.2.64, females appearing on the same day. The full complement of 2 males and 5 females had emerged by 14.2.64. The experiment was conducted at room temperature. Further experiment is desirable using B and N parasites from the one host species. However, it would appear that the incubation period of the resident species (N) may be 1–2 days longer than that of *A. basalis* (B).

The further characteristic of host incompatibility has been mentioned above. If any uncertainty of the species is entertained, presentation of *Nezara* eggs will settle the question. These will be acceptable only to *A. basalis* except for the rare instance described later, when wing stance will provide conclusive evidence.

During incubation the wall of the bug egg becomes noticeably darkened. This feature, together with the habit of chewing a hole in the operculum rather than forcing it off neatly as in the normal bug emergence, enables the fate of old egg-masses to be determined at a glance. In *Cuspicona* differences in the amounts of pigment deposited by *A. basalis* and the resident species N are apparent. Species N, which as an adult is the more heavily pigmented, deposits less of the darkening substance on the inner wall of the egg. With practice it is possible to determine which species has emerged from the egg, especially where mixed parasitisation of the one egg-mass has occurred. Occasionally the pigment is deposited between segments of the parasite larva once this has reached a relatively immobile stage, and this remains as darkened lines indicating the indentations.

AN ANOMALOUS FEMALE FROM FIELD COLLECTED EGGS OF *Oecharia*

Reference is made above to the inability of the resident species of *Asolcus* (*Microphanurus*) (N) to parasitise the eggs of *Nezara* successfully. However, a single case of attempted parasitisation has been observed.

On 7.2.64 an egg mass of *Oecharia consocialis* containing 30 eggs was taken from *Rubus* fruits near Whangarei. Subsequently parasites of the darker resident species emerged from all eggs. In order to verify the parasite species involved, two egg-masses, one of *Nezara*, the other of *Cuspicona*, were introduced. The eggs of the latter received immediate attention and the typical vertical wing stance of species N was apparent. Later in the day a single female was noted attempting to utilise the eggs of *Nezara*. The wing stance again was typical of species N. The early attempts at oviposition were lengthy as if mechanical difficulties in piercing the egg or in actual laying were being experienced, but later oviposition times were more normal. The female was isolated and allowed to continue undisturbed oviposition. Forty-three eggs of *Nezara* were supplied. Nineteen of these failed to produce bugs, the eggs initially taking on the appearance typical of parasitisation.

Although typical recognition wiping of eggs occurred following oviposition, indicating that eggs were probably inserted and bug development was prevented, no parasites emerged. This would appear to indicate a chemical barrier even where the occasional individual does regard the eggs as suitable for oviposition.

ATTEMPTS TO CROSS THE SPECIES

Attempts were made to cross the males of *A. (M.) basalis* with females of the resident species N. A dominance trial set up on 4.2.64 with eggs of *Cuspicona* provided an opportunity to test the cross. On 18.2.64 emergences from the egg-mass comprised 2 males of *A. basalis*, 2 females of *A. basalis*, and 2 females of species N. The dominant male remained on the egg-mass as the females emerged. Copulation, which usually takes place immediately

after the female leaves the egg, was obviously successful in the case of *A. basalis*. Attempts were also made to copulate with the females of species N. Apart from mating on the egg-mass there may be additional peripheral mating. Adequate opportunity for this was provided in the present experiment. The females of each species were then given egg-masses of *Cuspicona*. In both cases parasitisation was successful. However, whereas the females of *A. basalis* produced both male and female offspring (2 males, 23 females), species N females produced only males (13), indicating that mating had not been successful.

An attempt was made on 5.3.64 to cross the males of resident species N with virgin females of *A. basalis* from eggs of *Nezara* taken at Paihia on 27.2.64. The experiment involved the use of 5 females and 3 males. Refrigerated eggs of *Nezara* were provided. Attempted copulation was noted and oviposition proceeded normally. However, only males (47) emerged from the egg-masses indicating again that mating had not been successful.

INTER-SPECIFIC DOMINANCE TRIALS

When two closely allied parasite species compete for a number of host species, the factors which result in the one or the other becoming dominant are often obscure. Such factors may include ability to locate the host, times required for the completion of each generation, the aggressiveness and strength of the adult individual and of the larval stages, adequacy of the ovipositor for penetration, acceptability of the hosts, relative fecundity, and the suitability of prevailing climatic conditions. Although more evidence is required from field studies to establish that in any one area the host species is usually concerned with the one parasite species, present evidence suggests that this may be so.

A considerable number of experiments have been carried out to examine the question of dominance in both the adult and larval stages. For the most part eggs of *Cuspicona* have been utilised. These are reasonably easy to obtain by laboratory caging of field-collected adults. They are usually deposited in somewhat compact masses of about 12-14 eggs on the filter paper strips provided. Diagrams of such masses are readily made and the individual egg positions indicated. Both species of parasite work apparently undisturbed under the artificial light requirements of the stereoscopic microscope which allows a close study of behaviour during experiments.

Marking of Eggs following Oviposition

Cumber (1951) drew attention to the marking procedure adopted by *Asolcus* following oviposition in the host eggs and suggested that it served to distinguish those eggs which had been stung. Wilson (1961) reviewed the relevant literature and further described the marking in *Asolcus*.

During the course of the present experimental work there were frequent indications of the efficiency of the marking process which involves the criss-cross wiping of the tip of the ovipositor over the egg above the

point of oviposition. Where a single female was concerned with one egg-mass, it was common for all 13 or 14 eggs to be parasitised in about half an hour. Although the position of the eggs parasitised in any sequence was quite at random over the egg-mass, the detection of unparasitised eggs up to the last one was for the most part rapid and sure.

In Experiment 21, set up on 11.2.64 and using a mass of 16 eggs of *Cuspicona*, a female of *A. basalis* was allowed to sting and wipe seven eggs before her removal. On the following day the female was reintroduced when she stung a further six eggs before removal. Only one of these latter had been stung the previous day. This was done inadvertently, after examining an adjacent unwiped egg. Unfortunately the female died before reintroduction on the third day. However, the experiment showed clearly that the wiping marks were recognised after 24 hours.

But there can be no doubt that this wiping mark is of no interspecific significance. In experiments where the two parasite species were working together, one would utilise the eggs stung and wiped by the other only seconds before, and despite the usual careful inspection with the antennae. Similarly in experiments involving larval dominance where egg-masses were given first to one species and then to the other, there was no indication of interspecific recognition.

Thus the question of inter-specific dominance is in no way confused by the wiping recognition procedure. It is a specific device concerned with economy in oviposition.

Phases of Dominance

When single females of the two species are introduced to a single egg-mass, they may exhibit all stages of behaviour from disinterest to extreme keenness to oviposit depending upon factors of past oviposition, hunger, etc. Dominance would appear to come into operation only when the first wave of oviposition pressure has passed. This may represent the clearing of the basal egg from each ovariole. With the passing of this wave, some time is probably required for maturation and readiness of further eggs. At this stage dominance becomes a product of past ownership and familiarity with the egg-mass. There is no indication that inter- and intraspecific dominance operate in a different manner.

In some experiments, as indicated above, the female of one species would show no interest in the egg-mass, and the other individual would successfully sting all eggs. In cases where two females who had not laid any eggs, and were apparently under equal oviposition pressure were utilised, both would settle down to laying perhaps four eggs each without signs of animosity, and these could involve eggs already utilised by the other. However, as the numbers of unstung eggs decreased, animosity appeared and increased.

Having established dominance, the factor of temporal advantage begins to operate. The female chased from the mass usually does not return immediately but waits until the domineering one has recommenced oviposition. She then returns timidly to the mass and commences oviposition usually well away from the other. The domineering one finishes oviposition

first and is able to chase the other off again before its oviposition and recognition wiping is completed. This procedure is repeated until (in small egg-masses) all eggs are parasitised, the domineering individual thus retaining a temporal advantage. The habit of laying at random over the mass rather than starting at one end and working through is a useful mechanism in maintaining dominance through periodic inspection.

In nature it is probable that egg-masses are rarely found simultaneously by two or more females so that oviposition pressure is released and the domineering character has time to build up before further females find the egg-mass. While awaiting maturation of ova the domineering female will stay with the egg-mass. The resulting parasite emergence (in large egg-masses) may thus occupy a number of days. In the field, parasites from the one egg-mass are probably, for the most part, the offspring of the one female.

There is no doubt about the ability of the female to dominate the egg-mass even though she is not ready for further oviposition. During periods when she is not actually involved with repelling intruders she will adopt a characteristic on-guard-but-resting attitude in which the head and thorax are raised and the antennae hang straight down. Any intruders appear to waken the female readily. A recommencement of oviposition may sometimes be induced by tapping the glass tube, but this will usually only involve one stinging before the resting attitude is again adopted.

Adult Domination Trials

The following three experiments throw light on the question of dominance through oviposition pressure and ownership boosted morale.

Experiment 7 was set up on 3.2.64 using a pair of females which had not laid, namely *A. basalis* (B) from eggs of *Glaucias* collected at Paihia, and resident species N from eggs of *Antestia* taken at Auckland. These were simultaneously introduced to 14 freshly laid eggs of *Cuspicona*. There was no antagonism until nine eggs (B = 5, N = 4) had been parasitised at which stage the typical pattern of antagonism and struggle for dominance appeared. The egg-mass was removed when all eggs had received attention. The resulting offspring comprised 5 adults of B (1 male, 4 females) and 9 of N (1 male, 8 females). At the end of the experiment it was not clear which individual was dominant despite marked antagonism.

The same two adults were utilised in Experiment 10 set up on the same day (3.2.64). This involved a further fresh egg-mass of *Cuspicona* containing 11 eggs. Here female N established dominance from the beginning of the experiment which produced 1 female of B, and 1 male and 9 females of N.

The same females were used in Experiment 13 set up on the same day (3.2.64) and using a further egg-mass of *Cuspicona* involving 13 newly laid eggs. In this case, since N had established dominance in the previous experiment, B was first introduced on her own and allowed to parasitise 10 eggs. N was then introduced and there was immediate conflict, B on this occasion however, maintaining dominance until all eggs had been

parasitised. Apart from a short interlude, B maintained dominance until removal on the following morning. The resulting emergences were all of species B (3 males, 10 females).

In these three experiments which were carried out on the same day and using the same pair of parasites, the sway of dominance is of some interest. In the first, the odds as reflected in the offspring were fairly even ($B = 5$, $N = 9$). In the second N established undoubted dominance ($B = 1$, $N = 10$). The third experiment reversed the situation prevailing in the second. This was achieved by giving a temporal advantage to the female previously dominated ($B = 13$). Temporal is used here in the sense of a continuous undisputed ownership period—a morale-boosting period as opposed to the temporal advantage mentioned above which is established in the early stages of dominance while both are attempting oviposition, only the one individual having time to oviposit successfully.

In a further pair of Experiments (3, 5) set up on 30.1.64 and 31.1.64, adults which had not laid previously were utilised. On the first day 13 eggs of *Antestia* were introduced. Both females laid a number of eggs before the typical animosity developed and by the end of the day the N female was dominant. The offspring were 1 female of B, and 1 male and 11 females of N. Next day (Experiment 5) the females were given 10 freshly laid eggs of *Cuspicona*. In this case antagonism commenced immediately but dominance was assumed and maintained by B. This egg-mass produced 1 male and 9 females of B. In the first experiment N found the egg-mass one minute before B, whereas in the second B found the egg-mass some 2-3 minutes before N. This may well have had some bearing upon successful dominance.

The question of the inherently more aggressive species may be determined only by a series of experiments in which apparently equal opportunities are given to pairs of females of similar status. The results of a number of such experiments are given in Table 2. Although overall results of such experiments based on emergences may indicate relative adult aggressiveness, the situation is complicated by the fact that the adult of one species does not recognise the oviposition wipe marks of the other, and both may oviposit in the one egg. The question of larval aggressiveness thus enters into any results based on emergence of adults. In the confusion caused by antagonism and combat, apart from the non interspecific recognition, intraspecific recognition may become less acute and result in super-parasitisation. Experiments designed to test interspecific larval aggressiveness and dominance are described below.

The apparently dominant females as indicated by behaviour during the experiments are indicated in Table 2. These results point to the resident species N as being the more aggressive.

Larval Dominance Trials

Four experiments were set up to examine larval antagonism. Except on very rare occasions only the one individual emerges from the single host egg. Since eggs are sometimes parasitised several times larval elimination and/or parasite egg destruction must occur.

TABLE 2—Dominance Trials

(B = *A. basalis*, N = Resident species)

Experiment No.	Date	Eggs in Mass	Offspring				Apparently Dominant Female (by observation)
			B		N		
			Females	Males	Females	Males	
2	30.1.64	10	—	—	7	3	N
3*	30.1.64	13	1	—	11	1	N
5	31.1.64	10	9	1	—	—	B
7*	3.2.64	14	4	1	8	1	?
8	3.2.64	3	—	—	2	1	N
9	3.2.64	3	—	—	3	—	N
10*	3.2.64	11	1	—	9	1	N
14*	4.2.64	14	4	2	3	—	N
15	4.2.64	14	12	2	—	—	N
28	15.2.64	13	12	1	—	—	?
29*	15.2.64	10	1	6	2	1	?
30*	15.2.64	13	7	2	4	—	?
Totals		128	51	15	49	8	

*Trials involving emergences of both species.

Apparent dominance was not noted in Experiments 28, 29, 30.

In Experiment 11 commenced on 31.1.64, an egg-mass of *Cuspicona* comprising 15 eggs was mass-parasitised with *A. basalis*. Subsequently (3.2.64) N parasites from eggs of *Antestia* were introduced. Parasitisation commenced immediately, there being no recognition of previous oviposition. However, it soon became obvious that the parasites were not happy with the egg-mass and antagonism developed earlier than is normal. Difficulties in penetration may have been experienced because of changes in egg membranes caused by developing larvae already within. A new egg-mass provided for behaviour comparison purposes was soon adopted in normal fashion. The parasites were allowed to remain with the egg-masses for several hours. The first egg-mass produced 1 male and 12 females of *A. basalis* and 2 females of species N, these latter emerging several days after the others. This experiment indicates clearly that species N may superimpose itself upon *A. basalis* even after a period of several days. The chances that the two eggs were missed in the original mass-parasitisation are very remote.

Experiment 25 set up on 15.2.64 involved an egg-mass of *Cuspicona* comprising seven eggs. This was first presented to *A. basalis* until all eggs had been stung. It was then immediately given to species N until all eggs had received attention. This egg-mass produced 2 males and 5 females of species N.

In Experiment 26 set up on 15.2.64, six eggs of *Cuspicona* were first

given to species N. When each had received attention they were presented to *A. basalis*. This egg-mass produced 2 males and 3 females of species N, and 1 male of *A. basalis*.

Experiment 27, also set up on 15.2.64 and involving 8 eggs of *Cuspicona* followed the sequence of Experiment 25 with *A. basalis* being first introduced to the egg-mass. One female of *A. basalis* and 3 males and 4 females of species N emerged.

In summarising information from the dominance experiments four features bear consideration.

Firstly, in 7 of the 9 adult dominance experiments in which a close watch was maintained on behaviour, the resident species N emerged as dominant.

Secondly, even though species N may be the more aggressive inherently, when females which have not laid eggs are presented simultaneously with an egg-mass, the initial overriding influence of, and initial preoccupation with oviposition, does allow the less dominant species to produce offspring.

Thirdly, if we select only those adult dominance trials (marked with an asterisk in Table 2) which include emergences of both species, and sum these, the figure of N = 41, B = 29 which emerges suggests dominance by N. The information from trials designed specifically to test inter-specific larval competition also indicates strongly that the larvae of species N are the more successful.

Fourthly, dominance as a factor of established possession apparently overrides any differences in inherent aggressiveness. This is a feature well known in social Hymenoptera.

In attempting to apply these experimental results to the field the obvious difference lies in the timing of interspecific adult contact. Female parasites emerging from egg-masses do so over a period of several days and soon disperse after fertilisation by the male dominating the egg-mass. It seems probable that in nature two individuals of the different species will rarely discover the same egg-mass at intervals sufficiently short to allow mixed parasitisation during the initial pre-antagonism wave of oviposition pressure. The significance of interspecific larval dominance will depend upon the length of the period that the dominating female stays with the egg-mass once parasitisation is complete. Although there is little information on this point, it seems probable that this period is usually sufficiently long to prevent successful super-parasitisation.

No attempt has been made to discover which predominates when male and female larvae compete in the one egg—a situation which may be studied experimentally but which is unlikely to occur frequently in nature.

FACTORS INFLUENCING THE SEX OF PARASITE OFFSPRING

In *Asolcus* (*Microphanurus*) male brood is produced from unfertilised eggs. Infertile females produce male brood quite readily. The fertilised female, however, has the capacity of producing both male and female brood. The factors responsible for sperm retention are not clearly understood.

Two possibilities have been examined in the present work. In one the case of the sex of successive parasitisations has been examined in a number of experiments, and in the other successive individual parasitisations spaced by varying intervals have been studied.

In Table 3 Experiments 5, 12, and 13 involve females which had laid eggs previously. Adults of the alternative species were present in these tests but domination was complete. Experiments 19, 20, 21, and 23 involve single females which had not laid previously. With the exception of Experiment 12, the tests involve *A. basalis* oviposition.

TABLE 3—Sex of Successive Parasitisations
(+ = Male, — = Female)

Experiment No.	Order of Egg Laying													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
5	—	—	—	—	—	—	—	—	+	—				
12	—	—	+	—	—	—	—	—	—	—	—	—	—	—
13	+	—	—	—	—	—	—	+	+	—	—	—	—	—
19	+	+	+	+	—	+	—	+	+	—	+	—	—	+
20	—	+	—	—	+	—	+	—	+	+	—	+	—	—
21	+	—	—	+	+	+	—	+						
23	—	+	—	—	—	—	+	—	+	+				

It is obvious from Table 3 that the timing of male and female producing eggs in any succession follows no regular pattern. The much higher percentage of males (52%) in Experiments 19, 20, 21, and 23 where new females were used as opposed to females which had laid previously (14%) in Experiments 5, 12, 13, suggests that in general the male producing eggs may be laid more commonly in the earlier stages of oviposition. This, in addition to the shorter incubation period of the male, would help ensure that males were on hand whenever the females emerged from the egg-mass.

Experiments 35 to 39 set up on 20.2.64 involve a series of trials designed to gain information on the effect of delayed oviposition. Field collected parasites of species N from eggs of *Oechalia* taken at Whangarei were used. On the day previously, mass parasitisation of a single egg-mass allowing a minimum of oviposition had occurred. The intervals at which single ovipositions were permitted ranged from the minimum of less than one minute in the control where the female was allowed continuous oviposition, to an interval of not less than one hour. Results are summarised in Table 4. These experiments involved the mapping of all egg-masses and the recording

of all eggs utilised and the times involved. The females were quite amenable to handling being warded off the mass when each oviposition and marking was completed, the egg-mass being removed rather than attempting the removal of the female. The speed with which each parasite found the egg-mass when reintroduced was quite remarkable and indicated a recognition of the materials. Table 4 indicates that although there may be some reduction in the percentage of males where intervals between ovipositions are increased considerably, e.g., more than one hour, the evidence is insufficient to prove the point. It is apparent however that intervals ranging from 1 to 20 minutes do not affect the percentage of males significantly.

On the purely mechanical side the possibilities of sperm availability being restricted in the early stages of oviposition, or in short supply in the latter stages, suggest themselves. There is some evidence for the former in the above comparison of those females that had, or had not laid eggs, but there is no evidence that fertilisation is a function of time variations between successive ovipositions.

TABLE 4—Effect on Sex of Offspring of the Time Interval between Successive Ovipositions

Experiment No.	Period Occupied	Average Interval (min.) and Range	Number of Eggs Utilised	Percentage Males
35	9.20 a.m. - 1.42 p.m.	19 $\frac{1}{4}$ (16 - 30)	13	31
36	9.32 a.m. - 1.57 p.m.	18 (16 $\frac{1}{2}$ - 28)	14	14
37	9.53 a.m. - 4.41 p.m.	34 (30 - 45)	11	9
38	10.13 a.m. - 4.39 p.m.	61 $\frac{1}{2}$ (60 $\frac{1}{2}$ - 64)	7	0
39	10.31 a.m. - 11.13 a.m.	less than 1	14	14

DISCUSSION

Results in the various sections have been discussed at the appropriate places. It is pertinent, perhaps, to make some general comments on the apparent status of *Nezara* as a pest and to suggest the situation which may well exist in respect of the pentatomids and acanthosomids and their scelionid parasites in this country.

There has been no suggestion that the acanthosomids are of any economic significance. They appear to be largely restricted to our native monocotyledonous plants, with the possible exception of *Oncacontias*. On occasion *Rhopalimorpha* may be reasonably common on *Carex* spp. but there is only the one generation which is completed fairly early in the summer.

The pentatomids, however, may be of considerable importance as evidenced by *Nezara* before the introduction of *A. basalis*. In attempting to

assess the factors responsible for the general relatively low incidence of *Nezara* which has been attained some 14 years after the introduction of *A. basalis*, the possibility that the already present species N is now directly assisting, is virtually ruled out. It cannot be induced to use the eggs of *Nezara* successfully, and attempts at crossing the species have been unsuccessful.

A. basalis has extended its host range, as has the resident species N, to include the further pentatomid species that have reached the country. It is difficult to visualise any benefit accruing to the apparently less aggressive parasite species. It is obvious that *A. basalis* does swell its numbers in some areas by utilising species, in addition to *Nezara*, such as *Cermatulus* and *Glaucias*, as seen at Paihia.

Nezara is a very prolific species, each female producing several egg-masses some of which may contain in excess of 80 eggs. These are utilised solely by *A. basalis*. This parasite, on reaching an area of moderate *Nezara* population, has every chance of reaching greater numbers than resident species N which is restricted to the smaller egg-masses of other species. Once dominance in numbers has been established, it is likely that more and more of the alternative hosts in the immediate vicinity will be utilised by *A. basalis*. If some of these hosts have an extended season—*Cuspicona* may belong here—this will swell the overwintering parasite reservoir and help retain dominance in the following season. The possibility of one of the alternative hosts being a relatively early one in spring and aiding parasite build up just before *Nezara* egg-laying commences cannot be overlooked.

There is good reason to suspect that the lower incidence of *Nezara* now experienced in the majority of once troublesome areas is due to delicate state of biological balance which may easily be upset where insecticides are directed against minor populations of the pest.

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