PREDATION BY THREE HEMIPTERANS ON THE NATIVE BUDWORM, *HELIOTHIS PUNCTIGER* WALLENGREN, (LEPIDOPTERA : NOCTUIDAE)

by

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A thesis submitted for the degree of
Doctor of Philosophy in the Faculty of Agricultural Science
at The University of Adelaide

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South Australia

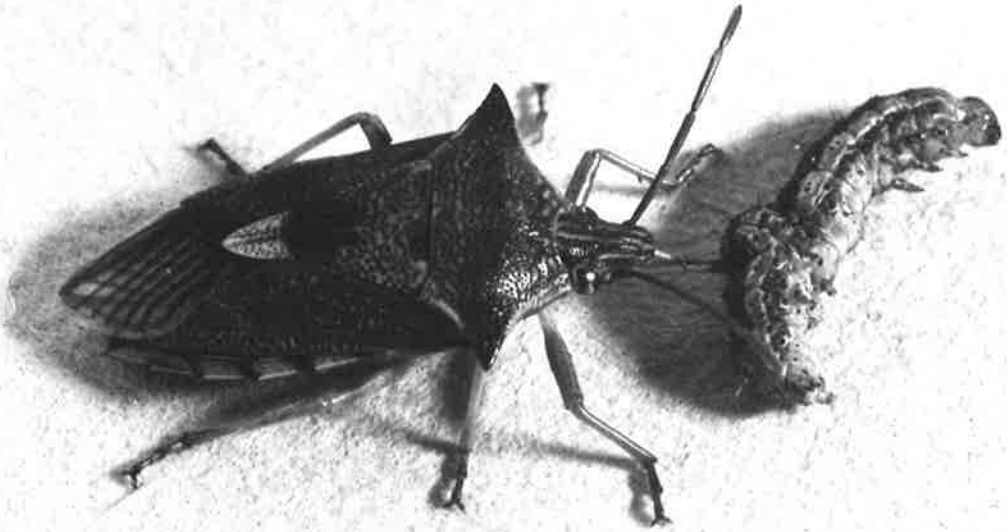
May 1981

To

My Parents

Frontispiece

Adult (♀) *Oechalia schellenbergii* feeding on late fifth caterpillar (killed in hot water).



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SUMMARY

Oechalia schellenbergii (Guerin-Menville), *Cermatulus nasalis* (Westwood) (Hemiptera : Pentatomidae) and *Tropiconabis nigrolineatus* (Dist) (Hemiptera : Nabidae) are common polyphagous predators found in lucerne fields and other places, where they variously prey upon the eggs and caterpillars of *Heliothis punctiger* (Wallengren) and on other pests of economic importance. *H. punctiger*, the native budworm, is a major lepidopterous pest, and a serious threat to the lucerne seed industry in Australia. Research was aimed at evaluating the significance of these predacious hemipterans in the bio-control of *H. punctiger*. Laboratory experiments were conducted using either a petri dish arena or simulated field conditions. Biological studies showed that all the species had a high reproductive potential, with *O. schellenbergii* having the greatest. Both this species and *T. nigrolineatus* had a wider range of functional temperatures than *C. nasalis*.

The first stages of the pentatomids were non-predacious, the second fed mainly on small caterpillars but also showed some response to eggs, later stages of the pentatomids appeared to prey exclusively on small to medium-sized caterpillars. Study of the searching behaviour of *O. schellenbergii* demonstrated that this species perceived its prey through movement of the latter, and that the speed of the prey determined the reaction of the predator. Slow-moving prey were much more prone to attacks than either the fast-moving or the stationary. The speed that elicited maximum predator response was quantified with a stepping motor and found to be 0.12 cms/second. Evidence for the

involvement of olfaction in prey perception was also established.

T. nigrolineatus preyed voraciously on *H. punctiger* eggs and small caterpillars but was unable to capture caterpillars bigger than the third stage. *O. schellenbergii* and *C. nasalis* failed to capture caterpillars bigger than the fourth stage, and even when encountering small caterpillars, captured only a proportion of them. Investigation of several predator-prey interactions revealed the presence of a wide variety of defense-ploys and retaliation tactics among the *H. punctiger* caterpillars. Large caterpillars were highly successful in making effective use of anti-predator-ploys, and hence were immune to predation. However, there was sufficient evidence to conclude that the attack behaviour of *O. schellenbergii* was related to the size of prey, as were the defense-ploys of the caterpillars when they were attacked.

Temperature did not affect the predators' maximum potential voracity over the range of 15 to 35°C with the exception of *T. nigrolineatus*, which consumed lower numbers of eggs at 30 and 35°C. But temperature had a great deal of influence on the actual daily feeding rates of the predators and their rates of development. Female predators always out-consumed their male counterparts, both as juveniles and as adults, and this relationship was independent of temperature and the complexity of the searching universe.

Complexity of the searching universe was of little consequence with regard to predation rates against large caterpillars. However, it resulted in reduced predation on first instar caterpillars, which were able to bore into lucerne fruits, flowers and buds, and thus were partially protected from predators.

Efficiency of capture of *O. schellenbergii* was estimated at 5 temperatures and the results indicated that it was dependent on temperature to a large extent. Efficiency was low at 15°C but increased with the temperature and assumed a near constant value at higher, sublethal temperatures.

Numbers of prey consumed by *O. schellenbergii* increased with prey density in a decelerating manner before levelling off at higher densities. Thus, *O. schellenbergii* showed a type-II functional response curve, in Holling's terms. Tests on the effect of temperature on functional response demonstrated that there was an interaction between the two at 15°C. A lower attack rate <u>a</u> and a longer handling time <u>Th</u> were the two key factors limiting the predator's response at low temperatures.

The overall impact of predators on *H. punctiger* populations and the reasons for the relatively low numbers of *O. schellenbergii* and *C. nasalis* observed in the field are discussed.

DECLARATION

The work presented in this thesis is my own unless otherwise acknowledged, and has not previously been published or submitted to any University for the award of any degree.

Muhammad Saeed Awan

May, 1981.

ACKNOWLEDGEMENTS

I am extremely grateful to my supervisors, Professor T.O. Browning and Dr. P.W. Miles for their advice, constructive criticism and encouragement during the course of this study and for critical reading of the manuscript.

I wish to express my sincere gratitude to Miss Prue Philips of the Biometry department and Dr. L. Laughlin for their advice and assistance with the statistical analyses and to Professor H.G. Andrewartha for his didactic and stimulating discussions with regard to the natural control of animal populations.

I am very grateful to Dr. D.A. Pucknell and Mr. R.C. Nash of the Electrical Engineering department, University of Adelaide, for lending me the stepping motor and Mr. J.H. Double, for designing the circuit to go with it for an experiment on the prey movement.

Thanks are due to the Waite Institute farm staff for maintaining the lucerne plots, to H.C. Nitsche and Co., for their kind permission to use their lucerne property at Pt. Gawler, and to library staff for their untiring cooperation in arranging many inter-library loans.

I am thankful to Mr. B. Palk for taking the photographs, to Mrs. Schonfeldt for photocopying, to Miss Tommie Seikman and Mrs. Margaret Brock for typing this thesis.

This study was financed by an award from the University of Sind, Pakistan. I am grateful to my alma mater for award and for the study leave to undertake this project. I also gratefully acknowledge the assistance of University Grants Commission of Pakistan for paying my fare.

It is a pleasure to thank my compatriot and former colleague, Dr. A.A. Munir and his wife for their kind treatment, which made our stay in Adelaide such a pleasant one.

Last, but certainly not the least, my special thanks to Zuhra, my wife, for her support and encouragement, particularly in the final writing up period.

1. GENERAL INTRODUCTION

1.1 ESTIMATE OF GLOBAL PEST DAMAGE TO CROPS

Ever since man began to raise crops he has been preoccupied with the problem of protecting them from insects and other pests. The struggle between man and insects for vital resource (food), began long before the dawn of human civilization, has continued unabated until now, and will undoubtedly last as long as the human race endures (Forbes, 1915 , in Metcalf *et al.*, 1962).

Reliable estimates of pest damage to crops are hard to gather, especially on a worldwide scale; nevertheless there is general, but somewhat conservative consensus that plant pests destroy one-third of the world's food and fibre each year (Janick *et al.*, 1974). Beirne (1967) estimated that average annual material loss due to pests (insects, plant diseases, nematodes and rodents) may be around 25-50 percent in Europe and North America where control measures are relatively more intensive, but it may reach up to 80 percent or more in third world countries. However, in a more recent estimate Pimentel (1978) reported loss of 48% of the world food to pests. This staggering annual loss, at a time when ½-1 billion humans are protein/calorie malnourished, reflects badly on control practices in use. Thus, there is greater need than ever before for better control strategies, aimed at preventing crop damages and obtaining higher yields.

1.2 PEST CONTROL PRACTICES AND ASSOCIATED PROBLEMS

Pest control technology is probably as old as human civilization. It began with cultural and physical methods, many of which have proved scientifically sound and are still in use. Although they reduced the injury level by several pests and provided adequate control against some, nevertheless cultural practices proved ineffective against pests with high damage potential and even primitive agriculturalists had to look for other means of control (Smith, 1978).

The search for additional methods of pest control led to the use of poisonous plant extracts and this later opened the door for other chemicals. Chemicals became fairly common in the 1800s. Furthermore, large scale farming, use of monoculture and the appearance of alien pests were instrumental in the greater use and development of insecticides. Thus, chemical control claimed wide approval, and this is understandable; other methods of control were largely in their nascent stages and chemicals were the only answer to pest problems (DeBach, 1974).

Thus, in subsequent years pesticides completely dominated the agricultural scene, evolved into compounds with spectacular toxicity and achieved the status of more powerful tools of pest control all over the world (Doutt and Smith, 1971). Moreover, development of broad spectrum and persistent organosynthetic insecticides was hailed as a major breakthrough in the pest control and chemistry was believed to be on the verge of providing complete answers to every pest problem. This enthusiasm, however, was not shared by a handful of workers in the field of biological control, who had observed some of the hazards associated with insecticides (e.g. Smith, 1941, 1944) and some purely academic entomologists (e.g. Wigglesworth, 1945) voiced their concern.

Smith's (1941, 1944) timely warning of insects' potential to develop resistance to insecticides and the probable consequences of control strategy based on insecticides alone, with no consideration for ecological principles involved, was largely ignored, and today there are over 200 examples of known resistance. The numbers of resistant species are increasing and some species of insects are becoming increasingly difficult to control with any of the insecticides (Wilson and Huffaker, 1976). Muir's (1978) recent estimate of known resistant species, including ticks and mites, is much larger. His estimate shows 305 species being resistant to one or several pesticides. Furthermore, insects' ability to degrade poisons and the induction of mixed function oxidase (a multi-purpose enzymatic degradation system) by the components of insecticide mixes (thought to be inert) have further confounded the insecticide dilemma (O'Brien, 1978).

Carson (1962) indicted insecticides with polluting environment, creating health hazards, exterminating beneficial and non-target species, and hence starting a chain of imbalances among the plant and animal biosystems. To her, the road to insecticides was a dead end and the answer to pest problems lay in the broadly based ecological approach. Pimentel (1978) expressed a similar view by calling insecticides "biological poisons" when they are used indiscriminately, often in large quantities than actually needed. Moreover, inefficient application technology further aggravates the problem and there is a great deal of evidence to blame insecticides for irreparable damage to many species of birds, fishes and beneficial insects.

Furthermore, increasing numbers of secondary pests achieve primary pest status after the introduction of synthetic insecticides and this is believed to be due to the disruption of the resident natural enemies (Ripper, 1956; Harpaz and Rosen, 1971; Huffaker *et al.*, 1971; Wood, 1971). Dramatic drop in the pest numbers after insecticide application is understandably euphoric for the farmer, but this euphoria is short-lived. The few pests that survive insecticides increase rapidly in the absence of their natural enemies, that normally keep their numbers down. This pest 'flare back' or resurgence is a common legacy of chemical control (Woods, 1974). Moreover, production and marketing costs of insecticides have gone up and this cost spiral is likely to continue as the prices of fossil fuels continue to rise (Pimentel, 1978).

1.3 BIO-CONTROL POTENTIAL OF NATURAL ENEMIES

The awareness of the hazards of indiscriminate use of insecticides and their side effects has highlighted the need for alternative methods of control, hence there is greater support for biologically based methods of pest control today than there was half a century ago. Although natural enemies of pests have been known for centuries, nonetheless awareness of their bio-regulatory role was pretty vague in early days. For example, Forbes (1880) wrote "the annihilation of all the established enemies of a species would, as a rule, have no effect to increase its final numbers." However, during the last few decades predators, parasites and pathogens have received a great deal of attention and some spectacular successes achieved in suppressing pest populations by natural enemies, have not only disproved Forbes' 'notion', but have demonstrated that natural enemies are a viable means of pest control.

Predators, parasites and pathogens are part of every animal's environment and they have a great deal of influence on its chances of survival and multiplication (Andrewartha and Birch, 1954). There are probably as many, or even more, entomophagous insects as there are prey or host species (i.e. 1 million species of natural enemies). Only a small proportion of them (15 percent) have been discovered. Furthermore, in their natural habitats, most phytophagous insects are attacked by more than one to several enemies and some have well over 100 recorded natural enemies (DeBach, 1974).

Howard and Fiske (1911) expressed the view that as many as 99 percent of the phytophagous insects were under natural biological control in their native habitats. This notion was strongly supported by Tothill *et al.* (1930).It is due to natural enemies that only 1-2 percent of potential phytophagous pests ever attain the stuatus of even minor pests (DeBach, 1974).

1.4 NATURAL ENEMIES AND POPULATION ECOLOGISTS

Population ecologists have significantly contributed to the understanding of the natural control of animal populations, both theoretically and practically. There are two main schools of thought in relation to natural control of animal populations. One, led by Nicholson (1954, 1958) and supported by a large number of ecologists, attaches considerable importance to the concept of 'natural balance' and regards density-governing (density dependent, as termed by Smith, 1935) factors responsible for bringing about the natural control. To them, natural enemies are one such factor.

However, the second school of thought represented by Andrewartha and Birch (1954), Andrewartha (1972) and supported by Thompson (1956), regards animal populations, for the most part, to be controlled by density-independent factors.

Nevertheless, importance of natural enemies is recognised by even those ecologists who argue that natural enemies sometimes, but not always, act in a density dependent manner. It is far easier to demonstrate their bio-control potential (by check methods) rather than to prove that this effect is achieved through a truly density-dependent action (Huffaker *et al.*, 1971).

1.5 ECONOMIC STATUS OF *H. PUNCTIGER*

H. punctiger is an endemic Australian species of a wellknown and widely studied genus of noctuid moths, with representatives found all over the world. In Australia this genus is represented by four species (Common, 1953; Kirkpatrick, 1961).

H. punctiger, commonly called the 'native budworm' is widely distributed and common throughout Australia. It is the major lepidopterous pest in Australia, except in coastal and sub-coastal Australia, where *Heliothis armigera* becomes a more serious pest than *H. punctiger*.

Although the presence of two other *Heliothis* spp. has been reported in South Australia, the numbers involved in these reports were so low that it is safe to assume that *H. punctiger* is the major, if not the only species of *Heliothis* spp. occurring in South Australia, and all the reported damage refers to this species (Cullen, 1969).

In South Australia, *H. punctiger* attacks vegetables, fruit trees, cereals and many garden plants. *H. punctiger* caterpillars show marked preference for flowers and fruits of the host plants and adult moths deposit eggs on flowering host plants. This species becomes highly destructive when moths fly and converge on lucerne seed crop and peas in mid-summer when vegetation elsewhere becomes dry. The damage caused by caterpillars to lucerne seed crop (*Medicago sativa*) can be extremely high. Elsewhere in Australia its main targets are cotton, tomatoes, peas and maize (Helson, 1947; Richards, 1964; Wright and Nikitin, 1964).

1.6 NATURAL ENEMIES OF *H. PUNCTIGER* AND OTHER *HELIOTHIS* SPP. IN AUSTRALIA

Previously published information about the natural enemies comprises lists of "beneficial" insects found in cotton agro-ecosystem in New South Wales (Wright and Nikitin, 1964), and south-eastern Queensland (Bishop and Blood, 1976), and a study of egg parasites conducted by Twine (1973) in south-eastern Queensland. There is no report of any quantitative study of the interaction between *H. punctiger* and any of its natural enemies.

In South Australia, where *H. punctiger* is the only species of concern, the role of its natural enemies in suppressing its numbers has not received much attention, despite the fact that it has been speculated by earlier workers that natural enemies of *H. punctiger* reduce its numbers considerably (Cullen, 1969). *O. schellenbergii* is a potential predator of *H. punctiger* (Cullen, 1969). Cooper (1979) reported *O. schellenbergii* and *T. nigrolineatus* (previously known as *Nabis tasmanicus*) preying upon virus-killed caterpillars in the field and attributed to them an important role in disseminating the virus. These predators were found passing infective polyhedra with faeces for 6 days after feeding on dead caterpillars.

Among the other reported natural enemies of *H. punctiger* are tachinid parasites which parasitize larger larvae. Cullen (1969) reported 5 to 22.3 percent parasitism of *H. punctiger* caterpillars in the field. *H. punctiger* eggs are attacked by *Trichogramma australicum* and the degree of parasitism encountered may be quite high (Learmonth, pers. comm.). Furthermore, Cooper (1979) demonstrated that *H. punctiger* populations were susceptible to applied and natural control by pathogens. Successful results were achieved with *Bacilus thuringiensis* and nuclear polyhedrosis virus in the field and laboratory trials.

1.7 CONTROL OF *HELIOTHIS* SPP. IN AUSTRALIA AND ELSEWHERE

H. punctiger is controlled in Australia by organochlorine compounds, in particular DDT is extensively used against *Heliothis* spp. Nevertheless, scope of this insecticide is becoming limited as *H. armigera* has developed resistance against it (Broadley, 1977; Kerr, 1977).

Although there is no report of resistance to insecticides by *H. punctiger* so far, nevertheless the number of treatments required to avoid economic injury level has been on the increase for quite some time; this presages development of resistance in the near future.

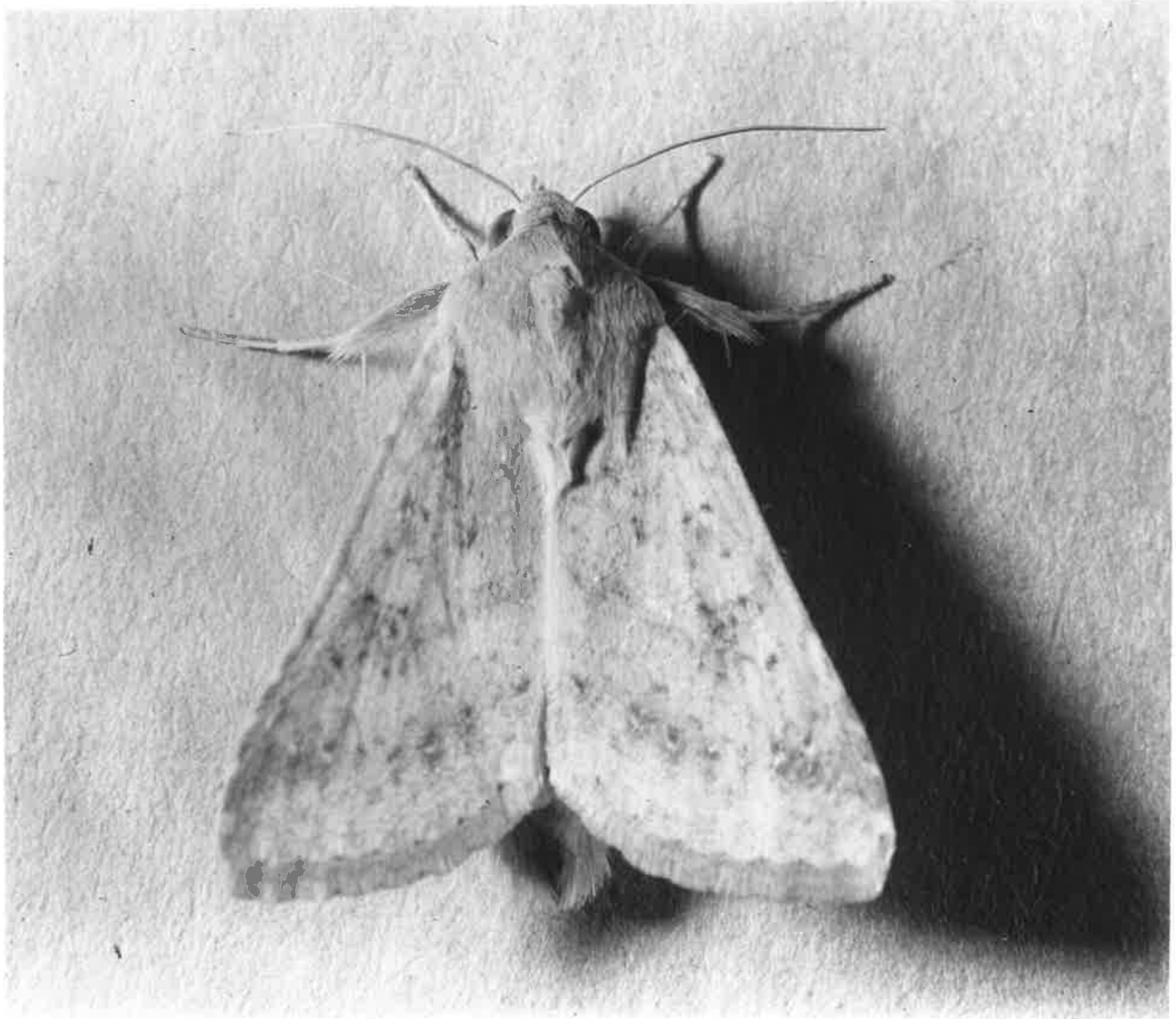
Thus, there is a growing need to minimise use of chemicals and devise pest management programmes for *Heliothis* spp. in Australia, as the results of such attempts in America have been encouraging.

Elsewhere in the world except America, *Heliothis* spp. are mainly controlled by chemical means and especially by organochlorines. This was true for America too, not long ago, but due to growing numbers of problems associated with insecticide applications (Doutt and Smith, 1971) emphasis has greatly shifted towards the conservation and use of natural enemies in the pest management programmes during the last decade or two (Pate *et al.*, 1972; Sterling and Haney, 1973).

Fletcher and Thomas (1943) and Ewings and Ivy (1943) demonstrated in laboratory and field studies that several predator species removed large numbers of bollworm eggs and caterpillars. There are around 600 species of predacious insects in the cotton ecosystem (Whitcomb and Bell, 1964). Furthermore, inundative releases of predator *Chrysopa carnea* (Neuroptera : Chrysopidae) have proved effective in controlling *Heliothis* spp. in field cages. Ridgway and Jones (1968, 1969) reported reduction in *Heliothis* spp. egg and larval population by *C. carnea* of up to 96 percent. Lingren *et al.* (1968) obtained promising results with *Geocoris punctipes*. Moreover, field cage tests conducted by van den Bosch *et al.* (1969) showed 96 percent mortality of *Heliothis* spp. attributable to several native predator species.

Furthermore, application of insecticides such as, Carbofuran, Disulfoton have been linked with higher mortalities of stilt bugs on tobacco (Elsey, 1973) and hence less predation by this species on tobacco budworm eggs. Moreover, Aldicarb used alone, or mixed with Disulfoton

Fig. 1.1 Adult *Heliothis punctiger* x 7.



reportedly exterminates predator populations of *Geocoris* spp. and *Nabis* spp. on cotton and predator numbers remain low for 45 days after each treatment (Ridgway and Jones, 1968).

1.8 BIOLOGY OF *H. PUNCTIGER*

H. punctiger is inactive in winter and spends this period in diapause. Its activity starts with large flights of adult moths in spring around September-October. It is not clear whether these adults emerge from local diapausing pupae or whether they migrate from other places. Cullen (1969), on the basis of his light trap data, specualted that the former was the case, and this notion is further supported by the fact that adults in the first spring flight reportedly had non-depleted fat reserves. This makes it untenable that moths may have migrated from any considerable distance. Nonetheless, studies on larval survival indicated that it is highly unlikely that large numbers of larvae in summer and autumn would enter diapause to account for such enormous flight of adults in spring.

A second flight of *H. punctiger* adults occurs in early December, followed by three more flights at approximately monthly intervals. In most of the lucerne growing areas in South Australia larvae resulting from December and subsequent flights are injurious to seed lucerne crop.

Female *H. punctiger* has reproductive potential of well over 1,000 eggs, which are deposited on lucerne flowers, terminal leaves and pods and eggs hatch in 2-3 days and caterpillars go through six larval instars, which in summer usually takes 10-14 days, while the duration of pupal stage that is spent underground is 12-14 days (Doull 1960).

1.9 OBJECTS OF THE PRESENT STUDY

Laboratory studies were carried out to gather information about the interaction between *H. punctiger* and its three common hemipterous predators. The specific objectives of the study were:

(a) To evaluate the effectiveness of *O. schellenbergii, C. nasalis* and *T. nigrolineatus* as predators of *H. punctiger*.

(b) To test the effects of temperature on their voracity under simple and complex searching conditions.

(c) To test the influence of temperature on their efficiency of capture.

(d) To evaluate their searching ability and determine the factors involved in prey finding.

(e) To study the effects of temperature on the functional response of predators.

(f) To study the selective predation by hemipterans and underlying reasons for selection.

(g) To examine the possible reasons for low numbers of *O. schellenbergii* and *C. nasalis* in the field.

Fig. 2.1 Rearing container with various stages of *O. schellenbergii* feeding on fifth instar caterpillars (killed in hot water).

2. METHODS FOR RAISING STOCK CULTURES

2.1 PREDATOR CULTURES

Cultures of predators, *Oechalia schellenbergii, Cermatulus nasalis* and *Tropiconabis nigrolineatus* were started from field collected adults each spring. Cultures were held in a room maintained at 28±2°C and 14L:10D. Adults were housed in large ventilated breeding containers with bases lined by paper towelling sheets and filter papers. This was necessary to minimise the effects of alerting and/or defensive odour produced especially by the 'stink bugs'. A band of 'Fluon' was applied near the base of the container (Figure 2.1) to keep the predators close to food source and mainly to prevent egg-laying on lids.

Predators were provided with a source of drinking water, 2-3 cm sections of bean (*Phaseolus vulgaris* L.) and large numbers of late fifth instar caterpillars killed under hot tap water. Lepidopterous larvae killed in this manner are known to be a suitable food source for predators from the works of Buttler (1966), Champlain and Sholdt (1967) and Samson and Blood (1979). Bean slices were replaced on alternate days; water was replenished whenever necessary. However, food (freshly killed caterpillars) was provided every day and remains of caterpillars due to previous feeding were removed. Predators were transferred to new containers once a week.

O. schellenbergii and *C. nasalis* laid eggs on filter papers and walls of containers. However, *T. nigrolineatus* laid eggs in bean slices. *Nabis* spp. reportedly lay eggs in plant material and materials suitable for oviposition include beans, sweetcorn and alfalfa stems (Taylor, 1949; Perkins and Watson, 1972; Hormchan *et al.*, 1976; Donahoe and Pitre, 1977).

Later, *C. nasalis* eggs had to be incubated at a lower temperature of 25°C because of their low viability at 28±2°C. However, newly emerged nymphs were returned to 28±2°C.

2.2 *HELIOTHIS PUNCTIGER* CULTURE

H. punctiger cultures were held under similar conditions as mentioned above (2.1) and cultures were started from field collected moths each spring. Six to seven pairs of moths were placed in a large container (18x20 cm) with slit lids on either side for paper towels. Ten percent honey solution, with 0.5 percent potassium sorbate as yeast inhibitor was provided as food for moths in plastic vials with cotton dental rolls projecting through the lids. Eggs laid on paper towelling were surface sterilized, incubated and the larvae reared as described by Browning (1979). The artificial diet for larvae was similar to that described by Griffith and Smith (1977), except that 1 $ml.kg^{-1}$ commercial formalin was added.

When *H. punctiger* caterpillars reached their third instar, they were separated and transferred individually to clean autoclaved glass vials, each holding sufficient food for complete larval development. Larger than third instar *H. punctiger* are cannibalistic (Ignoffo, 1965; Cullen, 1969; Cullen and Browning, 1978) in nature and hence if kept together would feed on one another. Some of the larvae, when they completed larval development and commenced wandering, were transferred to plastic vials with vermiculite, where they pupated and eventually emerged as moths, which were then used in the stock cultures. Larvae not immediately required for experiments were allowed to develop only until late fifth instar and were then transferred to cold room and held at 5°C, where they remained viable for long periods (3-4 weeks). Each day the required number of larvae were obtained from this stock and held at room temperature for 3-4 hours for revival and then used as food (2.1) for predator cultures.

Fig. 3a. Female *Cermatulus nasalis* x 10.

Fig. 3b. *Tropiconabis nigrolineatus* x 10.

3. BIOLOGICAL STUDIES

3.1 INTRODUCTION

Biologies of many predacious pentatomids have been studied by previous workers (e.g. LeRoux, 1960; Mukerji and LeRoux, 1965; Oetting and Yonke, 1971; Tostowaryk, 1971). Although *Oechalia schellenbergii, Cermatulus nasalis* and *Tropiconabis nigrolineatus* (formerly known as *Nabis tasmanicus*) have been reported as important mortality agenst of several lepidopterous larvae (e.g. Cullen, 1969; Cordingly, 1977; Cobbinah, 1978; Cooper, 1979) in Australia, nevertheless there is no published account of their biologies in the literature.

Knowledge of predator biology is not only essential for determining suitable rearing conditions, but is also important for extensive studies aimed at evaluating the effectiveness of predators. Thus laboratory experiments were conducted to estimate the reproductive potential of three species at various temperatures; their rates of survival and development were studied under different rearing conditions.

3.2 EGG INCUBATION PERIODS AND EGG VIABILITIES OF THREE SPECIES AT CONSTANT TEMPERATURES

3.2.1 Methods:- Egg batches of *O. schellenbergii, C. nasalis* and *T. nigrolineatus*, 6-12 hours old, obtained from stock cultures (cf. 2.1) were transferred to containers with distilled water (approximately 100 percent R.H.). These containers were then transferred to constant temperature rooms and cabinets held at 10, 12.5, 20, 25, 30 and 35°C respectively. Incubation periods for each species and the numbers of eggs that hatched were recorded.

Since the experiments on each species were carried out at different times, results could not be subjected to joint analysis. Thus, egg viabilities at different temperatures were tested by χ^2 test for each species and, if overall differences appeared significant, individual viabilities were further compared by the same test.

3.2.2 Results and Discussion:- No eggs hatched at 10 and 12.5°C (Table 3.1). This is in accord with the results of many authors on hemipterans (cf. Table 3.3). When examined under the microscope, after a period of 3 to 4 months, eggs appeared shrivelled and showed no signs of development. Thus, 10 and 12.5°C were below the egg development threshold and hence lethal to eggs. However, eggs of all species hatched at all other test temperatures except 35°C, where eggs of *C. nasalis* failed to hatch (Table 3.1). *O. schellenbergii*, on average, had shorter incubation periods at each temperature relative to the other two species and *C. nasalis* had the longest incubation periods of the three.

Egg viability of *O. schellenbergii* was significantly lower at 15°C relative to the other test temperatures, where it was similar (Table 3.1). Egg viability of *C. nasalis* was similar at 20 and 25°C but it was significantly lower at 15 and 30°C. However, viability of *T. nigrolineatus* was significantly lower at 35°C and similar at other test temperatures.

Table 3.1. Incubation periods and egg viabilities of three species at constant temperatures.

Species	n	Temp. ^{o}C	Mean incubation period in days ± S.D.	Numbers hatched	Percentage hatched	
O.schellenbergii	300	10	-	-	-	
	300	12.5	-	-	-	
	300	15	20.3 ± 0.4	204^{b}	68	
	300	20	8.1 ± 0.3	261^{a}	87	$\chi^2_4 = 14.2$,
	300	25	6.0	273^{a}	91	$P < 0.01$
	300	30	3.0	279^{a}	93	
	300	35	3.0	267^{a}	89	
C. nasalis	300	10	-	-	-	
	300	12.5	-	-	-	
	300	15	34.4 ± 0.6	210^{d}	70	
	300	20	19.1 ± 0.3	270^{c}	90	$\chi^2_3 = 132.5$,
	300	25	9.0	288^{c}	96	$P < 0.01$
	300	30	7.0	72^{e}	24	
	300	35	-			
T. nigrolineatus	300	10	-			
	300	12.5	-			
	300	15	28.2 ± 0.8	245^{f}	82	
	300	20	16.6 ± 0.4	267^{f}	89	$\chi^2_4 = 24.5$,
	300	25	8.2 ± 0.4	279^{f}	93	$P < 0.01$
	300	30	6.1 ± 0.3	234^{f}	78	
	300	35	5.2 ± 0.4	180^{g}	60	

Within species, numbers followed by different letters are significantly different from one another at the 5 percent level.

3.3 RATE OF DEVELOPMENT AND SURVIVAL OF JUVENILES OF THREE SPECIES

3.3.1 Methods:- Fifty first-stage nymphs of each species, 4-8 hours old after hatch, were transferred to 5 experimental temperatures in 65 mm plastic petri dishes. Predators were provided with drinking water (water-soaked dental roll) and plenty of food (cf. 2.1) (as the daily food consumption and rate of development bear a direct linear relation (Mukerji and LeRoux, 1965). Food and water were replenished every day and petri dishes were changed on alternate days. Stage duration of juveniles and their survival rate was recorded. The numbers of emerging adults were counted and sex ratios recorded for each species. Survival rate for each species at different temperatures was tested by X^2 analysis.

3.3.2 Results and Discussion:- Only juveniles of *T. nigrolineatus* completed development at 15°C. Juveniles of the other two species failed to develop further than the second stage; a large proportion of them died during the moult to the second stage and the few that moulted successfully to the second stadium did not develop further. Thus, 15°C appears to be below the nymphal development threshold of *O. schellenbergii* and *C. nasalis*. All the species developed at other test temperatures with different mortalities (Table 3.2). *O. schellenbergii* and *T. nigrolineatus* showed similar survivals at 20, 25, 30 and 35°C. But survival of *C. nasalis* was significantly less at 35°C (Table 3.2) indicating that this temperature was not suitable for their survival.

Moreover, juveniles of *C. nasalis* were relatively slow in development compared with the other two species, and *O. schellenbergii*

Table 3.2. Development periods and survival rates of juveniles of *O. schellenbergii*, *C. nasalis* and *T. nigrolineatus* at constant temperatures.

	Temp. °C	1st Stage n	1st Stage x̄ days ±S.E.	2nd Stage n	2nd Stage x̄ days ±S.E.	3rd Stage n	3rd Stage x̄ days ±S.E.	4th Stage n	4th Stage x̄ days ±S.E.	5th Stage n	5th Stage x̄ days ±S.E.	Cumulative nymphal period x̄ days ± S.E.	Sex Ratio ♀	Sex Ratio ♂	
O. schellengergii	15	50	-		-		-		-		-	-			
	20	50	2.3±.4	44	4.6±.6	36	4.8±1.1	36	7.6±1.9	25	11.1±2.1	30.4±6.1	13	12	
	25	48	1.3±.4	48	3.7±.5	40	4.5±1.3	35	4.8±1.1	25	8.2±1.2	22.5±4.5	13	12	$\chi^2_3=3.4$
	30	49	1.9±.2	44	3.4±.5	40	2.6±.9	39	2.8±.7	36	4.3±.8	15.0±3.1	17	19	$P>0.05$
	35	49	1.0	47	2.0	43	1.7±.4	40	2.3±.5	34	2.9±.7	10±1.6	18	16	
C. nasalis	15	50	-		-		-		-		-	-	-	-	
	20	50	5.3±.4	45	9.9±.9	43	7.8±1.2	42	8.7±1.5	39	14.1±7.0	45.8±7.0	21	18	$\chi^2_3=32.2$
	25	48	4.0±.2	44	5.2±.4	43	4.6±.7	41	5.4±1.3	40	9.4±1.4	28.5±4.0	20	20	$P<0.01$
	30	50	2.1±.3	48	3.0±.2	48	3.8±.3	43	3.9±1.0	37	4.8±1.0	17.6±2.8	18	19	
	35	50	2.0	37	2.5±.6	28	2.8±.7	19	3.7±1.0	3	6.3±.5	17.3±2.8	2	1	
T. nigrolineatus	15	50	12.2±.8	46	8.3±1.7	42	10.3±2.3	42	15.2±2.1	42	22.8±2.5	68.8±9.4	20	22	
	20	50	7.0±.6	45	5.8±1.0	44	5.9±.9	43	6.6±.6	43	10.5±.9	35.8±3.9	25	18	$\chi^2_3=2.4$
	25	50	3.1±.4	48	2.3±.6	46	2.4±.6	46	3.3±.8	46	5.4±.7	16.5±3.0	20	26	$P>0.05$
	30	50	2.0	47	2.0	45	2.0	44	2.0	44	3.0	11.0	24	20	
	35	50	2.0	40	2.0	43	2.0	36	2.0	33	2.8±.4	10.8±.4	15	18	

χ^2 test was based on the number of animals that reached adult stage.

appeared to be well adapted to higher temperatures, while *C. nasalis* showed better survival at low temperatures (Table 3.2). The average nymphal periods reported for the three species are well within the range of those reported by other authors (cf. Table 3.3).

Juveniles of all thress species stopped feeding before the moult and did not accept food for some time after the moult. This period was directly dependent on rearing temperatures. It was short at higher temperatures and longer at lower ones. This is in accord with the observations of previous authors (e.g. Jones and Coppel, 1963; Mukerji and LeRoux, 1965; Oetting and Yonke, 1971).

3.4 SPECIAL FEEDING HABITS OF FIRST STAGE JUVENILES OF *O. SCHELLINGBERGII* AND *C. NASALIS*

3.4.1 Introduction:- It was noticed in the stock cultures that first stage nymphs of *O. schellenbergii* and *C. nasalis* moved either towards the water source or towards the bean slices, after dispersal from eggs, and remained huddled there until the moult. They were seldom observed probing or feeding upon the caterpillars but were often seen probing the beans and dental rolls.

This experiment was conducted to test the non-feeding behaviour of first stage pentatomids.

3.4.2 Materials and Methods:- Eighty first-stage nymphs of *O. schellenbergii* and *C. nasalis*, 8-10 hours old, obtained from stock cultures before dispersal from eggs, were used in tests. They were divided into four batches of 20 each. The first batch of each species

Table 3.3. Comparative statement of reproductive biology of other hemipteran predators studies by previous authors.

Author and Year	Rearing Temps. in ^{o}C	Predator Species	Egg Incubation Period in days	Percentage hatch	Nymphal duration in days	Longevity ♀ in days	Longevity ♂ in days	Fecundity No. of eggs/♀	Sex Ratio	Overwintering Stage
Taylor (1949)	67-88	*Nabis alternatus*	9.0		16-30			127		Adult
Butler (1966)	15	*Orius tristicolor*	-							
	20		6.0		17.1					
	25		3.8		14.7					
	30		3.0		11.8					
	35		2.5		9.9					
	15	*Geocoris pallens*	-		-					
	20		16.0		55.5					
	25		6.8		24.1					
	30		5.1		14.7					
	35		-		-					
	15	*G. punctipes*	-							
	20		17.9		54.2					
	25		8.2		26.4					
	30		5.8		21.3					
	35		-		-					
Champlain and Sholdt (1967)	10	*G. punctipes*	-		-					
	15		46.5		-					
	20				53.9					
	25		16.0		31.0					
	27.2		10.7		25.4					
	30		8.1		22.1					
	35		7.1		17.8					
	40		5.0		19.0					
Jones and Coppel (1963)	22	*Apateticus cynicus*	14.0		30.1	94	107		1:1	
Mukerji and LeRoux (1965)	21-26.5	*Podisus maculiventris*	5.0	80	28-35	125.3	179.8	428.1	1:1	Adult
Oetting and Yonke (1971)	21-27	*P. placidus*	6.0	95	27.1				1:1	Adult
		S. fimbriatus	9.5		26				1:1	
Tostowaryk (1971)	26	*P. modestus*	15.3	88	59.0				1:1	Adult
Perkins and Watson (1972)	28	*R. alternatus*	6.5		16.3	37.3	35.2	223		
Dunbar and Bacon (1972)	23.9	*G. articolor*	14.0	89.8	48.3					
	26.7		7.6	86.5	25.5					
	30.0		5.8	88.2	21.2					
	32.2		5.5	88.0	15.1					
	35.0		4.5	77.1	14.1					
	23.9	*G. pallens*	12.3	80.3	42.2					
	26.7		7.1	86.6	24.1					
	30.0		5.6	84.8	16.4					
	32.2		4.9	72.0	14.1					
	35.0		4.1	83.0	12.1					
	37.8		-							
	23.9	*G. punctipes*	14.1	82.2	37.3					
	26.7		8.7	76.7	25.3					
	30.0		6.6	88.3	18.9					
	32.2		5.8	84.9	17.1					
	35.0		5.7	65.7	17.0					
	37.8		-							
Hormchan *et al.* (1976)	26-28	*T. capsiformis*				14.9	21.6	105		
Elsey and Lam (1978)	15.9	*Jalysus spinosus*			52.7					
	18.3				29.2					
	21.1				24.3					
	23.5				21.7					
	16.5				15.5					
	29.5				12.3					
	32.2				11.8					
	35.0				11.8					
Samson and Blood (1979)	18	*Nabis capsiformis*	17.2		30.2					
	23		9.4		19.0				1:1	
	28		6.5		12.8					

was released in individual 65 mm plastic petri dishes, with pieces of water-soaked dental rolls. The second batch was transferred to individual lucerne stems (10-12 cms) held in water-filled vials. The third batch was transferred to similar petri dishes with 20 *H. punctiger* eggs each. The final batch, that served as a control, was transferred to petri dishes with neither food nor water. Tests were replicated three times. Mortality in each group was monitored, the numbers of eggs eaten, if any, were recorded every 24 hours, and water was replenished in those treatments with a water source.

3.4.3 Results:- The first stage nymphs of *O. schellenbergii* and *C. nasalis* developed to the second stage in the presence of water or plant material, but failed to do so in the presence of *H. punctiger* eggs only.(Table 3.4). First stage nymphs of both species that had access to water or plant material probed these materials, and their abdomen appeared distended as compared to their counterparts with *H. punctiger* eggs alone, or without any source of water.

The nymphs with *H. punctiger* eggs alone or without any source of water dispersed after 2-4 hours and continued wandering until they died in a state of emaciation. However, nymphs with water or plant material did not show this wandering behaviour. They stayed on plant leaves and dental rolls until their next moult.

3.4.4 Discussion:- Development of non-predacious first stages in predacious species is probably an advantageous adaptive behaviour. First, it eliminates cannibalism during this stage and hence tends to increase predator populations. Cannibalism is of a common occurrence among predators with predacious first instars. The

Table 3.4. Developmental success of first stage *O. schellenbergii* and *C. nasalis* with different food sources at 28±2°C.

Predator species	No. tested	Material	No. successfully mounted to next stage	Stage duration in days
O. schellenbergii	60	Water	60	1.5
	60	Lucerne	60	1.5
	60	Prey (eggs)	0	-
	60	None	0	-
C. nasalis	60	Water	60	2.0
	60	Lucerne	60	2.0
	60	Prey (eggs)	0	-
	60	None	0	-

Table 3.5. Survival of second stage *O. schellenbergii* on lucerne plants.

Temperature °C	n	Survival (h) ± S.D.	n	Survival (h) in control	t P
20	10	127 ± 42	10	44.4 ± 5.7	t=6.1, P<0.01
25	10	55.2 ± 8.3	10	20.4 ± 5.7	t=11.0,P<0.01
30	10	36.2 ± 9.8	10	16.8 ± 6.1	t=5.1,P<0.01

older nymphs prey upon either unhatched eggs or newly emerged siblings. This has been reported for *Adalia decempunctata* (Dixon, 1959), *Nabis alternatus* (Perkins and Watson, 1972), *Orius tristicolor* (Askari and Stern, 1972), *Geocoris punctipes* (Champlain and Sholdt, 1967), *Leis conformis* (Maelzer, 1978) and *Chrysopa carnea* (Butler, 1971). Second, it precludes the hazards of searching, finding and capturing prey. Furthermore, if first stages of *O. schellenbergii* and *C. nasalis* were similarly predacious, they would be able to handle only very small prey and these would have to be available at required densities, either throughout the season or completely synchronized with the life cycle of the predators, a situation that does not appear to exist in the field. However, once these predators moult to the second stage, they are larger, more mobile and perceive and capture prey more efficiently, and this extends the variety of prey items they can handle. Thus, the chances of survival of these predators would appear to be improved by being non-predacious in their first stages.

Previous authors have also reported that predacious pentatomids do not require any animal food during the first stage and that they develop to the second stage after imbibing water alone (e.g. Mukerji and LeRoux, 1965; Tostowaryk, 1971). Furthermore, Mukerji and LeRoux (1965) were able to take *Podisus maculiventris* to the third stage on apple leaves and drops of water, despite its later dependence on predation.

Some authors (e.g. Prebble, 1933; Mukerji and LeRoux, 1965; Oetting and Yonke, 1971) speculated that the first stages of predacious pentatomids might prey upon unhatched eggs or their emerging siblings. Nonetheless, there was no evidence of such predation in either of the species. Some of the egg-masses showed 100% hatch and all the nymphs moulted to the next stage.

Present observations do not agree with Coppel and Jones' (1963) observations, who reported that the presence of water increased survival of first stage predacious pentatomids but water alone was not enough for development.

3.5 ASSESSMENT OF THE ROLE OF LUCERNE IN SUSTAINING SECOND STAGE *O. SCHELLENBERGII*

3.5.1 Introduction:- First stage *O. schellenbergii* either do not feed or take only water or sap and successfully moult to the next stage (cf. 3.4). It was of interest to determine whether lucerne alone would be sufficient for further development. Previous reports indicate that some general predators can subsist solely on plant foods. *Geocoris punctipes* develops to maturity on some plant foods, but lengthened stadia and infertility of the adults indicate that animal food is essential for development (Stoner, 1970). Nevertheless, the ability to survive on plant food alone may add to a predator's survival, particularly when prey are scarce in the field (Stoner *et al.*, 1975).

This experiment was conducted to investigate whether *O. schellenbergii* can subsist on plants alone or plant material is only of temporary survival value. The possibility that interaction between temperature and fasting might have a bearing on the readiness of predators to take plant juices was also tested by carrying out observations at three different temperatures.

3.5.2 Materials and Methods:- Sixty second-stage *O. schellenbergii,* 4-8 hour old after moult to second stage, were obtained from stock cultures and divided into six lots of 10 each. Thirty lucerne stems (8-10 cm) obtained from the field were thoroughly washed to remove any other insects or mites, and then held in water-filled vials. These stems were then transferred to ventilated plastic containers. Second-stage *O. schellenbergii* were then released individually on stems and containers were transferred to constant temperature rooms held at 20, 25 and 30°C and 12L:12D. In controls equal numbers of bugs were released in similar, but empty, containers (without water) at each test temperature. Predators were observed every 12 hours and their mortalities were recorded.

3.5.3 Results and Discussion:- Predators on lucerne plants lived significantly longer than their counterparts in controls (Table 3.5). Nevertheless, none of them completed development on plants alone and all died within the same stadium. This indicates that animal food was necessary for further development. The increased survival on plants may either be due to the bugs having obtained some nourishment from the plants or it may be due to the greater humidity among the leaves. Thus, lucerne is either not a suitable food source or it is not sufficient alone for further development.

Plant materials have been shown to be of survival value to many predators by previous authors (cf. Stoner, 1970, 1972; Tamaki and Weeks, 1972). Furthermore, it is noteworthy that due to their 'plant-feeding habits' many hemipteran predators are susceptible to systemic poisons (Ridgway *et al.*, 1967).

3.6 EVALUATION OF THE EFFECT OF TEMPERATURE ON THE FECUNDITY AND LONGEVITY OF *O. SCHELLENBERGII* AND *C. NASALIS*

3.6.1 Methods:- Males and females of each species (1-2 days old) were paired in 65 mm plastic petri dishes. The number of replicates was 16 per test temperature for *O. schellenbergii* and 20 for *C. nasalis*. Petri dishes with paired predators were transferred to 15, 20, 25, 30 and 35°C. They were provided with plenty of food (killed large caterpillars, cf. 2.1), bean slices and water-soaked dental rolls. Food and water was replenished each day. Petri dishes were changed on alternate days until oviposition started, after which they were changed daily and the number of eggs laid were counted under the microscope.

Data were gathered on pre-, inter- and post-oviposition periods, numbers of egg batches laid, eggs per batch, and survival of both sexes of the two species at each test temperature.

Analysis of Data:- Data on fecundity and longevity were subjected to analysis of variance. Data on fecundity of *O. schellenbergii* at 15°C were not included in the analysis. Data were transformed to logarithms.

3.6.2 Results:- The two species behaved differently. There was no mating in *C. nasalis* and none of the females laid any eggs ~~at~~ 15°C. However, there was some mating activity in *O. schellenbergii* at this temperature. Five pairs were seen in copulation after 15-17 days and their matings lasted for 4-5 days. Furthermore, some of these females laid one egg batch after 70-90 days with few eggs ($\bar{x} = 4.5$/♀). At other test temperatures several matings were observed in both species.

Both species showed normal reproductive activity at 20°C. The pre-oviposition, inter-position and post-oviposition periods were relatively longer in *C. nasalis* at each test temperature than *O. schellenbergii* (Table 3.6).

Reproductive potential of both species was higher between 25 and 30°C, but *O. schellenbergii* appears to be well adapted to higher temperatures (Table 3.6). Moreover, *C. nasalis* laid fewer egg masses/female than *O. schellenbergii* (Table 3.7).

Both species laid eggs in rows; there were fewer rows (3-4) in *O. schellenbergii* than *C. nasilis* (4-5). Occasionally both species laid eggs individually glued to the bases of petri dishes. In the field, both species lay eggs on leaves, usually in the upper part of the lucerne stem. On four occasions *O. schellenbergii* eggs were laid on lucerne stems near the shoot. These eggs were deposited in two tightly packed columnar rows. Number of eggs per mass was always higher in *C. nasalis* both in laboratory and field. The maximum number per egg mass in *O. schellenbergii* was 62 while for *C. nasalis* it was 84. However, the most common number of eggs per batch for the former species was 14 and for the latter it was 56.

The maximum number of eggs laid by a single female *O. schellenbergii* was 1,301 and this resulted from 36 egg batches at 30°C. However, *C. nasalis* laid 821 as a maximum number/female in 19 egg masses at the same temperature.

At 35°C *O. schellenbergii* laid significantly more eggs than *C. nasalis* (Appendix 1). Furthermore, at 25°C it laid more eggs than at 20°C. Differences at other temperatures were non-significant.

Table 3.6. Effect of temperature on pre-oviposition, inter-oviposition, post-oviposition and fecundity of *O. schellenbergii* and *C. nasalis*.

Species	Temp. °C	Pre-oviposition			Inter-oviposition			Post-oviposition			No. of eggs laid		
		n	$\bar{x}$ days ± S.E.	Range	n	$\bar{x}$ days ± S.E.	Range	n	$\bar{x}$ days ± S.E.	Range	$\bar{x}$	± S.E.	Range
O.schellenbergii	35	12	3.1±0.1	2-4	-	-	-	-	-	-	268	±72	7-727
	30	15	4.4±0.2	3-7	2	1.0	-	6	1.5±0.5	1-4	351	±91	2-1301
	25	15	7.8±1.3	4-24	49	1.2±.09	1-4	6	3.1±1.4	1-10	414	±77	23-1111
	20	15	11.5±1.0	8-22	43	2.2±0.2	1-8	13	7.0±1.7	1-19	134	±31	11-467
	15												
C. nasalis	35	11	6.1±0.3	5-8	7	2.1±0.5	1-5	8	12.0±1.9	2-17	35	±7	8-77
	30	13	7.1±0.7	6-15	71	2.1±0.1	1-6	8	6.1±1.7	2-17	333	±81	8-82
	25	13	23.1±5.3	8-86	57	5.8±0.6	1-33	9	7.0±3.3	1-33	258	±46	46-534
	20	6	34.3±4.8	23-56	8	11.1±4.1	1-39	3	53.0±34.3	6-120	121	±14	70-151

Table 3.7. Effect of temperature on the number of egg batches/female laid by *O. schellenbergii* and *C. nasalis* at different temperatures.

Species	Temperature °C	Mean No. of Egg Batches ± S.E.
O. schellenbergii	35	10.8 ± 1.7
	30	16.5 ± 3.8
	25	17.4 ± 2.8
	20	5.2 ± 1.0
	15	1
C. nasalis	35	1.7 ± 0.3
	30	7.3 ± 1.7
	25	5.0 ± 0.9
	20	2.3 ± 0.4
	15	-

C. nasalis laid significantly less eggs at 35°C than other test temperatures. Differences at other temperatures were not significant (Appendix 1).

3.6.3 Longevity of males and females of *O. schellenbergii* and *C. nasalis* at constant temperatures:-

Males of both species, on average, lived longer than females at each test temperature (Table 3.8) and this observation is in agreement with results reported by other workers (see Table 3.3). Mukerji and LeRoux (1965) attributed lower female longevity to body 'wear and tear' and due to male predation on females. However, no male predation on females was observed in this study. Longevity of both species increased as the temperature decreased (3.8). (See Appendices 3 and 4).

Both species showed longer life spans at 15°C but *C. nasalis* had the longest. Some individuals of *C. nasalis* lived more than 7 months at 15°C (when there was accidental breakdown of temperature in the constant temperature room and observations were discontinued). At that time there were still 6 females and 4 males alive. It is likely that *C. nasalis*, at 15°C, undergoes a reproductive diapause. Furthermore, their long survival at this temperature suggests that they probably overwinter in the adult stage. Many predacious pentatomids have been shown to overwinter in the adult stage (cf. Table 3.3). Moreover, twice during field observations, *C. nasalis* males and females were found preying upon syrphid larvae in July and August (mid-winter months in South Australia). This further supports the notion that *C. nasalis* not only overwinters in adult stage, but also remains active throughout the winter and does not spend winter in hibernation quarters.

Table 3.8. Life span of *O. schellenbergii* and *C. nasalis* males and females at different temperatures.

Species	n	Temp. °C	Mean life span of ♀ in days ± S.E.	Range	Mean life span of ♂ in days ± S.E.	Range
O. schellenbergii	16	35	11.0 ±2.1	3-33	20.5±2.8	6-38
	16	30	18.1 ±3.0	5-44	26.3±3.1	7-46
	16	25	29.6±3.9	3-59	39.0 ±3.5	13-56
	16	20	31.3±3.6	18-68	41.7±5.1	12-73
	16	15	77.9 ±10.0	19-138	82.1 ±10.2	29-171
C. nasalis	20	35	16.2±1.5	7-28	22.4±2.7	1-46
	20	30	24.0 ±3.6	4-61	42.0 ±4.4	1-89
	20	25	44.9±5.9	4-97	47.0±7.6	7-124
	20	20	51.4±8.5	5-150	65.6±9.4	1-160
	20	15	140.5±15.8	7-120	110.2±15.2	21-210

O. schellenbergii, on the other hand, were never found in the field after the end of May until early October. Nonetheless, their long survival at 15°C indicates that probably this species too overwinters as adults. Adults of this species ceased feeding at 15°C and adopted unusual postures by prostrating their front legs and antennae forward and being motionless for several days. These individuals, on average, lived longer than others. However, the limited amount of mating and egg-laying activity raises the possibility of *O. schellenbergii* overwintering in the egg stage. Evidence, although circumstantial, points to the contrary. For instance, it is the adult stage that appears in the field in spring. Moreover, their dark and dusty colours appear similar to the colours of adults held at 15°C, as against the bright dark reddish colours of adults held at higher temperatures. The plausible reason for some reproductive activity may be the high rearing temperatures for stock cultures, where some egg maturation might have occurred before the animals were transferred to 15°C.

3.7 OBSERVATIONS ON COURTSHIP AND MATING BEHAVIOUR OF *O. SCHELLENBERGII* AND *C. NASALIS*

Ten males and females of each species were held individually in 65 mm plastic petri dishes and given plenty of food for 14 days. At the end of this period they were paired in petri dishes, one pair at a time. Observations were made on the courtship behaviour of males and the time they spent in courtship and mating was recorded.

Moreover, the time reproductive adults wasted in courting unresponsive females was ascertained by pairing 1 day old females with 14 day old males.

3.7.1 Results and Discussion:- *C. nasalis* males did not show any elaborate courtship behaviour. Males made the first move. They approached females with vibrating antennae and touched them against females. He then quickly mounted on her and slid back with projected aedegus, brining his posterior end underneath hers. At this stage a responsive female lifted her abdomen and made room for the male's approaching body and stayed motionless until the male established the contact. After which, males turned over and the two sexes faced in opposite directions. However, females determined the direction of movement.

When paired with unresponsive females, males attempted many courtships, but females simply walked away. Furthermore, when aggressively held in one position, they did not lift their abdomen to let the male establish contact. *C. nasalis* males quickly abandoned unresponsive females and their mating time was relatively short (Table 3.9) as compared to *O. schellenbergii*.

Table 3.9. Courtship time and mating durations of *O. schellenbergii* and *C. nasalis* at 27°C.

Species	Age in days ♀	Age in days ♂	Mean time in mins spent in courtship ± S.D.	Mean mating time in hrs ± S.D.
C. nasalis	14	14	-	3.2 ± 0.7
	1	14	-	-
O. schellenbergii	14	14	0.8 ± 0.9	3.8 ± 0.7
	1	14	3.6 ± 1.3	-

O. schellenbergii males, however, displayed an elaborate courtship behaviour. They initiated the courtship by stroking their antennae against the female and grasped her with fore legs from the anterior, around the lateral spines and pushed her up and down several times while vibrating antennae against her back. Thereafter they turned around with protruding aedegus and brought their posterior end in line with her side and slid back to establish the contact. A responsive female at this moment lifted her abdomen and kept it lifted until the male established contact. Males continued to stroke the female's body until the contact. After that stroking stopped and males turned over to face in the opposite direction.

When unresponsive *O. schellenbergii* females were paired with older males, males spent considerable time in futile courtings. They repeated all the events of courtship behaviour and spent more time in each of them, but failed to establish contact, since unresponsive females did not lift their abdomen. Time of single courting against unresponsive female was significantly longer than a courting against responsive female (Table 3.9).

Neither *O. schellenbergii* nor *C. nasalis* placed their heads underneath the female's terminal segments and lifted them up, an observation widely reported for pentatomids (Mukerji and LeRoux, 1965; Mitchell and Mau, 1969; Nilakhe, 1976; Harris and Todd, 1980). Furthermore, mating periods recorded in this study are shorter than those reported by others (e.g. Coppel and Jones, 1963; Mukerji and LeRoux, 1965). Moreover, present observations indicate that both species became responsive after 2-3 days and not immediately after the hardening of their cuticles, as reported by Couturier (1938) for *P. maculiventris*.

In addition, both sexes required a meal before starting reproductive activity.

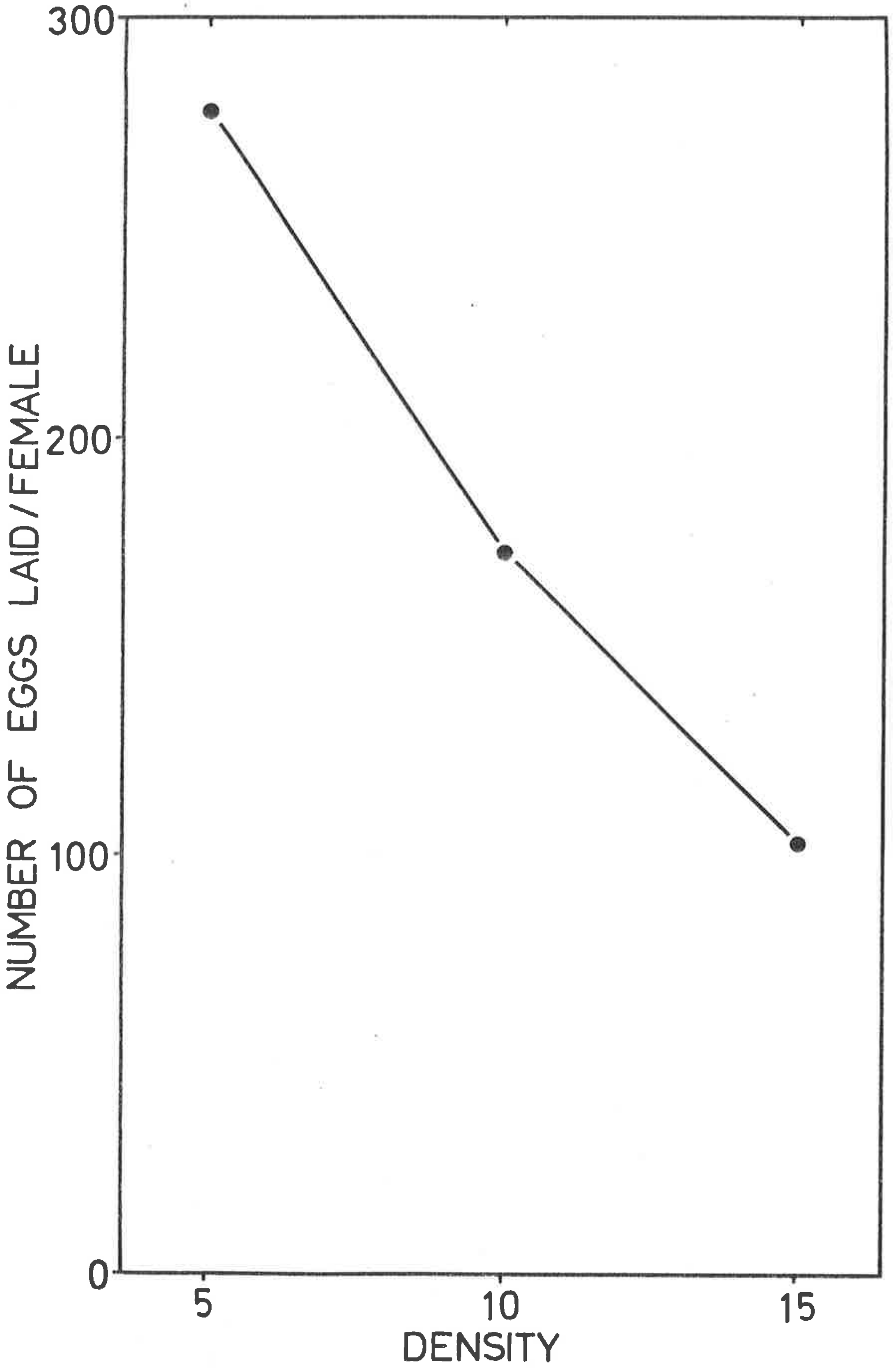
Present observations are contrary to the reports of Mitchell and Mau (1969) and Nilakhe (1976), who indicated that in most pentatomids, if one partner died during copulation the other failed to disengage and died too. None of the *C. nasalis* males or females died during mating. However, fifteen females of *O. schellenbergii* died during mating, but males were able to free themselves within 24 hours.

3.8 EFFECTS OF CROWDING ON THE FECUNDITY OF *O. SCHELLENBERGII*

3.8.1 Methods:- Similar to those described in Section 2 (cf. 2.1), except that smaller containers (13 cm x 13 cm) were used. Adults 1 day old were released in these containers at the rate of 5 pairs, 10 pairs and 15 pairs/container and given plenty of food.

3.8.2 Results and Discussion:- Crowding had dramatic effects on fecundity (Figure 3.1); the number of eggs per female decreased as the number of predators per container increased. This was mainly due to mutual interference among the predators and it became more evident in the later part of the experiment, in particular at higher predator densities. Females died earlier (cf. 3.6) than males and disproportionate ratios of two sexes intensified the interference. Males' disrupted females' feeding activities by engaging them in forced courtings and futile matings. Often when the female dislodged one male, another one subjected her to similar courtings. Furthermore, males often disturbed egg-laying females, which then walked away from oviposition sites without laying full

Fig. 3.1 Average number of eggs laid per female by *O. schellenbergii*, when held at densities of 5, 10 and 15 pairs/container.


300
200
100
0
NUMBER OF EGGS LAID / FEMALE
5
10
15
DENSITY

complement of eggs. The other two factors that probably contributed to the results obtained were lower food requirements of males, as they spent less time feeding and their longer sexual viability. Older males were as aggressive and polygamous as the younger ones.

Results described are in accord with those of Mukerji and LeRoux's (1965) on *P. maculiventris*, Kuchlein's (1966) on predatory mite, *Typhlodromus longipilus* and Evan's (1976) on *Anthocoris confusus*.

3.9 ESTIMATE OF LONGEVITY AND FECUNDITY OF *T. NIGROLINEATUS* AT 25°C

3.9.1 Materials and Methods:-

Similar to those described in Section 3.6.1.

3.9.2 Results:-

Females lived longer than males, but the difference between the two was not statistically significant (Table 3.10) as is found in most studies (Table 3.3). This is opposite to that of *O. schellenbergii* and *C. nasalis* in which males live longer.

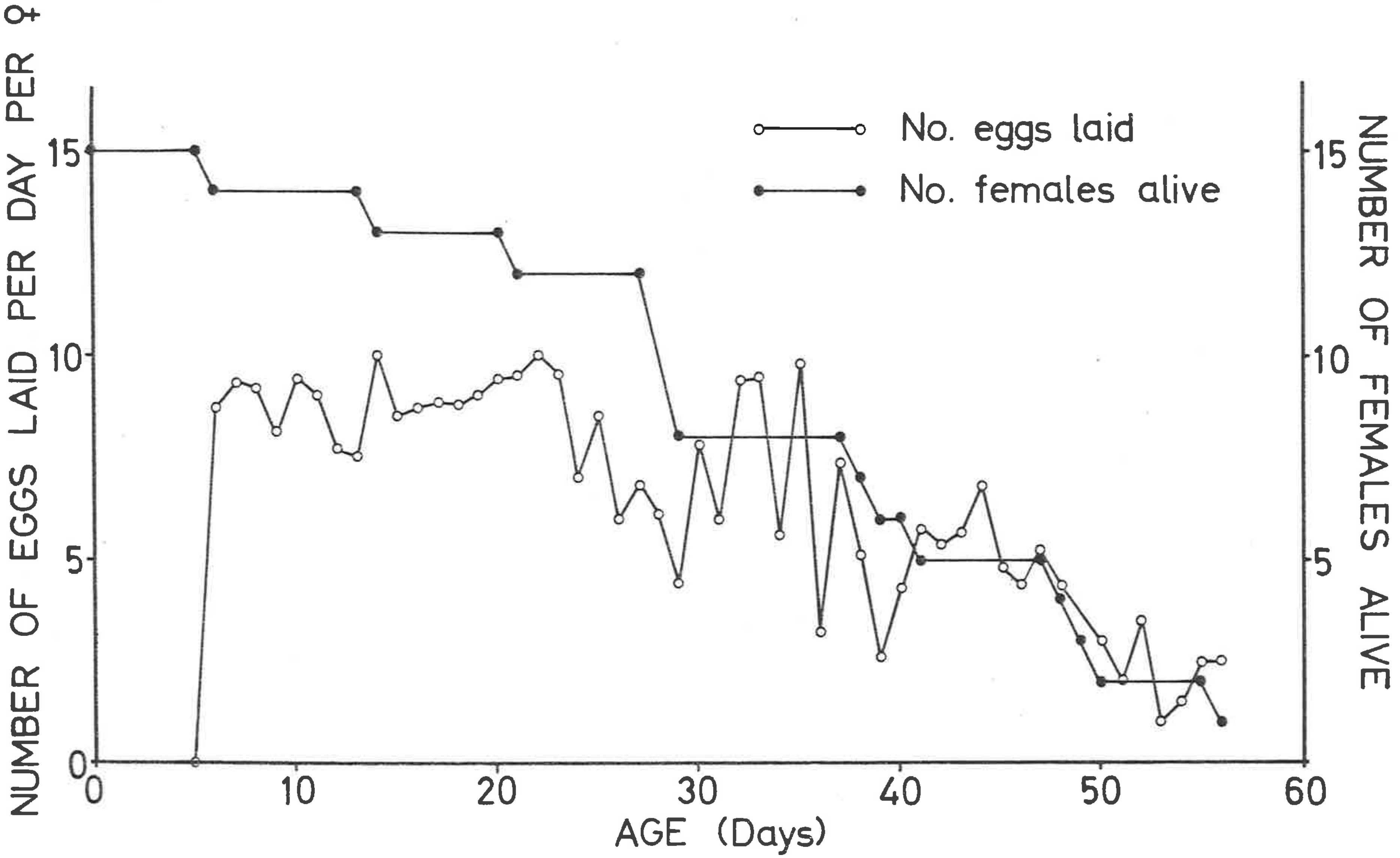
Table 3.10. Fecundity and longevity of *T. nigrolineatus* at 25°C

n	Mean number of eggs laid	n	$\bar{x}$ life span of ♀ in days ± S.D.	n	$\bar{x}$ life span of ♂ in days ± S.D.
14	260 ± 104	15	37 ± 13	15	29 ± 13

$t = 1.6, \quad P > 0.05$

T. nigrolineatus females commenced egg-laying on the 6th to 7th day, eggs were often laid in rows and 6-10 eggs were deposited at a time. Eggs were laid continuously by individual females during the first two weeks of the oviposition period (Figure 3.2). However, egg-laying became intermittent with senescence and they stopped laying a few days before death. For comparative differences between the present results and those reported by previous workers see Table 3.3.

Fig. 3.2 Survival and age-specific fecundity of *T. nigrolineatus* at 25°C. (Data for the last surviving female not included in the figure).


NUMBER OF EGGS LAID PER DAY PER ♀
0
5
10
15
No. eggs laid
No. females alive
NUMBER OF FEMALES ALIVE
15
10
5
0
10
20
30
40
50
60
AGE (Days)

4. VORACITY

4.1 VORACITY OF THREE HEMIPTERANS AGAINST EGGS OF *H. PUNCTIGER*

4.1.1 Introduction:- Previous workers (e.g. cf. 1.7) in laboratory and field cage tests have demonstrated that predators have a great deal of impact on the populations of lepidopterous pests. Among the hemipterans thought to be important in this regard are the spined stilt bug, *Jalysus spinosus* (Hemiptera : Berytidae), a leading cause of mortality of eggs of tobacco budworm and hornworm (Lawson, 1959; Elsey and Stinner, 1971); *Geocoris* spp. which significantly reduce egg and small larvae of tobacco hornworm (Gilmore, 1938), bollworm, *Heliothis zea* (Lopez *et al.*, 1976) and the soybean looper, *Pseudoplusia includens* (Richman *et al.*, 1980) and members of the genus *Podisus* which are major bio-control agents of tree defoliators (LeRoux, 1960; Mukerji and LeRoux, 1965).

van den Bosch and Hagen (1966) reported that the pirate bug, *Orius tristicolor* was a voracious predator of small noctuid larvae. Whitcomb and Bell (1964) showed that *Zelus exsanguia, Z. cervicalis* and *Z. socius* (Hemiptera : Reduviidae) had the potential to reduce popualtions of bollworm, *H. zea,* cabbage looper, *Trichoplusia ni* and the cotton leaf perforator, *Buccalatrix thurberiella* to low levels. Lingren *et al.* (1968) provided supportive evidence and maintained that *Z. renardii* consumed large numbers of bollworm eggs and larvae, in particular under simple searching conditions.

Bell and Whitcomb (1964) studied the incidence of predation of eggs of *Heliothis* spp. in cotton fields and concluded that predators with piercing and sucking mouth parts caused far greater egg mortality than any other groups of predators.

Voracity of predators (van Emden, 1966; Kehat, 1968) is one factor that determines their effectiveness. Predator mobility, the maximum number of prey they can consume, and the prey population levels are some of the parameters likely to affect predator voracity (Russell, 1970). Tamaki *et al.* (1974) advocate that before attempting to augment a predator's effectiveness by either modifying its environment or by introducing new predators, voracity of the resident predators must be appraised. Furthermore, information on the feeding capacity of predators on target pest species is required in order to take full advantage of their bio-control potential or to integrate them into biological, chemical and cultural control practices (Lingren *et al.*, 1968).

Experiments on voracity of *O. schellenbergii, C. nasali* and *T. nigrolineatus* were carried out as part of an indepth look at their effectiveness as predators of *H. punctiger* eggs and caterpillars. This information is lacking in the literature and it is likely to enhance knowledge about their potential as bio-control agents and allow them a properly evaluated role in the pest management of *H. punctiger*. The principal objectives of experiments on voracity were to determine (1) the numbers of eggs or caterpillars eaten per predator per stadium under simple and complex searching conditions, (2) the effects of temperature on voracity of the predators, (3) the preferences of smaller predators for eggs and small caterpillars, (4) the minimum numbers of prey needed for development of the predators and (5) their survival rate under unfavourable conditions. Experiments were conducted in two parts and are described as such.

Experiments on Egg Predation

4.1.2 Materials and Methods:- Newly emerged first stage *T. nigrolineatus*, second stage *O. schellenbergii* and *C. nasalis* were obtained from stock cultures and deprived of food for 24-36 hours at 27°C and used as test animals. Three samples of 5 individuals of each species were tested at a time, and tests were replicated three times. Test animals were raised on eggs alone until they reached the adult stage or died. Eggs used in tests were 10-12 hours old, mainly laid overnight on paper towels. Eggs were washed in 1.5 percent aqueous sodium hypochlorite solution then rinsed with distilled water and transferred to 65 mm plastic petri dishes. Eggs were examined under the microscope and damaged eggs were removed and replaced. The numbers of eggs provided to three predator species are shown in Table 4.1.

Table 4.1. Number of eggs provided per day to three hemipteran predators.

Species	Predator Stages				
	I	II	III	IV	V
T. nigrolineatus	20	25	35	50	75
O. schellenbergii	-*	70	140	250	400
C. nasalis	-*	70	140	250	400

* Non-predacious.

After each 24-hour interval predators were transferred to new petri dishes with appropriate numbers of eggs, and the eggs eaten in previous petri dishes were recorded. When predators reached the adult stage, their sex was noted. Because the observation interval was only once a day and most of the predators take 6-8 hours to commence feeding after moulting, it was not feasible to estimate the numbers consumed in each instar and thus data for the whole nymphal period were pooled for males and females for each species.

Analysis of Data:- Data were analysed by analysis of variance. Individual samples showed similar variability and one-third of animals died in *C. nasalis*. This reduced the sample size in some replicates and probably was the reason for an unproportionate increase in the variance with increase in the mean. To stabilize the variance, the data were transformed to logarithms.

4.1.3 Results:- Results of the experiment are presented in Table 4.2.

Table 4.2. Mean number of eggs eaten by three hemipterans at 28 ± 2°C

Species	n	Sex	Numbers reached adult stage	Mean number of eggs eaten ± S.D.	P
T. nigrolineatus	15	♀	8	310 ± 8)	**
		♂	7	264 ± 16)	
O. schellenbergii	15	♀	7	846 ± 35)	**
		♂	7	781 ± 23)	
C. nasalis	15	♀	6	1258 ± 77)	**
		♂	4	1078 ± 37)	

** $P < 0.01$. Differences between species were significant at 1 percent level.

Unfed predators of the three species showed different behaviour when released in petri dishes with eggs. *T. nigrolineatus* were the first to notice and prey upon *H. punctiger* eggs and their response to eggs was immediate. *O. schellenbergii* and *C. nasalis* on the other hand, spent considerable time in searching the arena and walked over eggs several times before sensing them. However, once they accidentally probed and consumed an egg, the remaining eggs were rapidly discovered and eaten. Moreover, with continuous predation on eggs, the predators became more efficient at preying upon eggs.

T. nigrolineatus showed normal stadia comparable to individuals raised on caterpillars, and the emerging adults were of normal size. However, *O. schellenbergii* and *C. nasalis* had normal durations of only the second and third stages. Fourth and fifth instars of these species were of longer durations, and the emerging adults appeared smaller in size. This was especially the case with the females of the two species.

C. nasalis, the largest of the three species of predators consumed significantly more eggs ($P < 0.01$) than the others; and *O. schellenbergii* consumed more eggs than *T. nigrolineatus* (Table 4.2 and Appendix 4). Furthermore, there were significant differences in relation to sex. Female juveniles of each species consumed more eggs than their male counterparts (Table 4.2) and these differences were significant (Appendix 5).

4.1.4 Discussion:- The poor response of *O. schellenbergii* and *C. nasalis* to *H. punctiger* eggs, their prolonged stage durations, especially in the later part of their development, with feeding exclusively on eggs, and the smaller sizes of emerging adults indicate that either eggs are unprofitable items of food or the later stages of predacious pentatomids are not behaviourally adapted to prey upon eggs. Earlier workers have shown that predacious pentatomids when raised on eggs alone fail to reach adult stage. For instance, Waddill and Shepard (1975) noted that *Podisus maculiventris* and *Stiretrus anchorago* (Hemiptera : Pentatomidae) when raised on eggs of Mexican bean beetle, *Epilachna varivestis* did not complete their development beyond the second stage. However, the number of eggs offered by these authors were too low to permit development. Richman *et al.* (1980) demonstrated that *S. anchorago* adults failed to recognise the presence of eggs of soybean looper, *Pseudoplusia includens* on plants. But the number of eggs (16/plant/day) exposed to predators was again extremely low. On the other hand, Lopez *et al.* (1976) demonstrated that *P. maculiventris* adults not only preyed upon eggs under simple searching conditions, but also under complex searching conditions.

The apparent failure of *O. schellenbergii* and *C. nasalis* to recognise the presence of *H. punctiger* eggs in simple searching conditions for such a long time has important implications for their role as egg predators of lepidopterous pests in nature. Of all the stages, the second and third are more likely to act as egg predators, but their response or efficiency in finding eggs is limited. However, their ability to make use of eggs as prey and survival on them alone indicates that at times, egg predation can be of survival value, particularly in the absence of other suitable prey. Nevertheless, the resultant subnormal size of the adults may not contribute much to the later generations. Insect fecundity is a function of their body weight and size (Miller, 1957; Jacobson and Blakeley, 1958; Hough and Pimentel, 1978), and very small females are unlikely to contribute significantly to an increase in predator populations.

Normal stage durations of *T. nigrolineatus* and their immediate response to *H. punctiger* eggs indicate that this species is probably a more important egg mortality factor in nature.

Conclusion:- The results of this experiment suggest, albeit inconclusively, that *O. schellenbergii* and *C. nasalis* are not important as egg mortality agents of *H. punctiger*. But *T. nigrolineatus* is a potentially significant egg predator.

4.2 FOOD PREFERENCES OF IMMATURE STAGES OF *O. SCHELLENBERGII* AND *C. NASALIS*

4.2.1 Introduction:-

Observations on egg predation (cf.4.1.3) indicated that predacious pentatomids showed a rather poor and delayed response to eggs. Both species are polyphagous and, in nature, polyphagous predators make use of a wide variety of prey species, nevertheless some show strong preferences for a particular stage of the prey. Thus, *Orius tristicolor* (Hemiptera : Anthocoridae), a general predator, preys upon aphids, lepidopterous eggs and small larvae but shows a strong preference for thrips (van den Bosch and Hagen, 1966; Aguilar and Ehler, 1977). Some general predators, such as *Zelus renardii* and *Z. exsanguis* (Hemiptera : Reduviidae) are indiscriminate feeders and only the availability and the size of prey limits their choice (Edwards, 1966; Ables, 1978). Furthermore, some general predators prey exclusively on/or show preference for a particular stage of prey. Lawrence and Watson (1979) demonstrated that *Geocoris punctipes* preferred *Heliothis virescens* eggs over larvae and the first stages of this predator preyed exclusively on eggs. But this may well be due to their inability to capture caterpillars.

The aim of these experiments was to establish (1) which stages of *H. punctiger* are preferred by immature stages of *O. schellenbergii* and *C. nasalis* in the event of a choice, and (2) what is the duration of food conditioning, if there is any.

4.2.2 Materials and Methods:-

Experiment 1.

Choice between equal numbers of eggs and first instar caterpillars by second stage predators.

Ten newly emerged individuals of second stage *O. schellenbergii* and *C. nasalis*, deprived of food for 24-36 hours at 27°C were used as test animals. Twentyfive freshly laid eggs and 25 one day old caterpillars were transferred to 65 mm plastic petri dishes with lids covered with Parafilm to prevent larvae from escaping. These petri dishes were exposed to predators for 8 hours and at the end of this time, the number of eggs and caterpillars eaten in each of the ten treatments were recorded.

Experiment 2.

Choice between three stages of prey: eggs, first and second instar caterpillars in ratios of 5:5:1 (actual numbers (25:25:5).

Test procedure as in Experiment 1.

Experiment 3.

Choice between eggs and first instar caterpillars by bigger predators.

Test procedure and numbers exposed similar as in Experiment 1.

Experiment 4.

Choice between two larval instars (first:second) by third stage predators (25:1).

Test procedure same as in Experiment 1.

Experiment 5.

Food conditioning.

A random sample of 10 second stage *O. schellenbergii* were obtained immediately after moulting and were raised on eggs up to the fourth stadium. They were then deprived of food for 24-36 hours and given a choice between three stages of prey in ratios of 5:5:1 (actual numbers being eggs 25 : first instar caterpillars 25 : second 5).

4.2.3 Results:-

Experiment 1.

Second stage *O. schellenbergii* and *C. nasalis* showed a strong preference for first instar caterpillars of *H. punctiger*. A preference for caterpillars was much stronger ($P < 0.01$) in *C. nasalis* (Table 4.3) than in *O. schellenbergii* ($P < 0.05$). Despite the apparent preferences for caterpillars both species showed a behavioural response to eggs, and on many occasions the predators stretched out the proboces towards the larvae which, due to their agility, moved out of position; and if the probosces touched eggs they were preyed upon.

Experiment 2.

Both predators oriented to and attacked the large caterpillars (second instars) first. But after several futile attacks, they turned towards first instar caterpillars and preyed upon them consistently thereafter. Both species showed significant preference ($P < 0.01$) for caterpillars over eggs (Table 4.4). Moreover, predation on eggs declined further with a widening choice of larval prey (Table 4.4). In this experiment too, *C. nasalis* showed a greater preference for the caterpillars than did *O. schellenbergii*.

Experiment 3.

Predation on eggs decreased with predator age (cf. Experiment 1). Third stage *O. schellenbergii* preyed almost exclusively on the caterpillars and no eggs were eaten by *C. nasalis* (Table 4.5).

Experiment 4.

Third stage predators showed preferences for caterpillars of different sizes. *C. nasalis* showed greater preference ($P < 0.01$) than *O. schellenbergii* ($P < 0.05$) for the large caterpillars (Table 4.6). However, these differences may be attributed to the size differences of the two predator stages. Third stage *C. nasalis* are the larger of the two, and were capable of handling and consuming large numbers of larvae.

Experiment 5.

Effects of food conditioning were short-lived or probably non-existent. Fourth stage *O. schellenbergii* were not attracted to eggs even when previously reared on them (Table 4.7). The predators' response to caterpillars was similar in pattern to that of individuals raised on larval prey. Insect predators do not show longlasting effects of food conditioning (Murdoch and Marks, 1973).

Table 4.3. Prey consumed by second stage *O. schellenbergii* and *C. nasalis* when given choice between eggs and first instar *H. punctiger* larvae.

Predator stage	n	Prey provided		Prey eaten		Chi-square value	P
		Eggs	Larvae	Eggs	Larvae		
2nd stage							
O. schellenbergii	10	25	25	27	49	$\chi_1^2 = 6.3$	*
C. nasalis	10	25	25	6	74	$\chi_1^2 = 57.8$	***

* $P < 0.05$ *** $P < 0.01$

Table 4.4. Prey consumed by second stage *O. schollenbergii* and *C. nasalis* in the event of choice between eggs, first and second larvae.

Predator stage	n	Prey given			Prey eaten			Chi-square value	P
		Eggs	1st	2nd	Eggs	1st	2nd		
2nd Stage									
O. schellenbergii	10	25	25	5	15	35	2	$\chi_2^2 = 29.9$	***
C. nasalis	10	25	25	5	2	42	3	$\chi_2^2 = 68.5$	***

Table 4.5. Prey consumed by third stage *O. schellenbergii* and *C. nasalis* in case of choice between eggs and first stage *H. punctiger* larvae.

Predator stage	n	Prey given		Prey eaten		Chi-square value	P
		Eggs	Larvae	Eggs	Larvae		
3rd Stage							
O. schellenbergii	10	25	25	7	95	$\chi_1^2 = 75.9$	***
C. nasalis	10	25	25	0	141		

Table 4.6. Prey consumed by third predator when given choice between first and second instar larvae.

Predator stage	n	Prey given		Prey eaten		Chi-square value	P
		Eggs	Larvae	Eggs	Larvae		
3rd stage							
O. schellenbergii	10	25	5	12	30	$\chi_1^2 = 7.7$	*
C. nasalis	10	25	5	6	34	$\chi_1^2 = 19.6$	***

Table 4.7. Effects of food conditioning on *O. schellenbergii* (raised on eggs to the fourth stage).

Predator stage	n	Prey provided		Prey eaten	
		Eggs	2nd larvae	Eggs	2nd larvae
4th Stage					
O. schellenbergii	10	25	5	0	43

4.2.4 Discussion:- Results of choice experiments further strengthen the evidence gathered in relation to poor predation of *O. schellenbergii* and *C. nasalis* on eggs of *H. punctiger*. The preferences of the immature predators of the two species for caterpillars suggest that they are mainly larval predators.

There are conflicting reports about egg predation behaviour of predacious pentatomids (cf. 4.1.6). My observations on *O. schellenbergii* and *C. nasalis* indicate that they take a long time to perceive the eggs (4.1.4) but are capable of feeding on eggs alone and reach to maturity on them.

In particular their apparent poor perception of eggs raises many questions and points to a number of possibilities: (1) It is likely that predators respond to prey movement and if so, eggs, being immobile, would not be noticed and hence not preyed upon; (2) It is also possible that caterpillars possess some chemical signal (kairomone) that is lacking in eggs; (3) The eggs are possibly unprofitable items of food and hence these predators have become behaviourally adapted to ignore the eggs. This last possibility may be true of the later stages of the predators, not for the second stage, whose ability to capture large caterpillars is limited. Thus, the first two possibilities will be explored in experiments on 'searching behaviour'.

Conclusion:- Present observations clearly demonstrate that *C. schellenbergii* and *C. nasalis* show a strong preference for caterpillars over eggs of *H. punctiger*. This preference increases with age and the size of predator, and is so strong that both species can be categorized as larval predators.

4.3 EFFECT OF TEMPERATURE ON THE VORACITY OF *T. NIGROLINEATUS*

4.3.1 Introduction:- Observations on the egg predation indicated that *T. nigrolineatus* was a potential predator of *H. punctiger* eggs (cf. 4.1.3). It was of particular interest to know if its voracity was independent of temperatures. Frazer and Gilbert (1976) expressed the view that predation studies under laboratory conditions do not represent true field conditions. All such studies should be supplemented by field experiments and if possible laboratory studies should be conducted under variable temperatures. They argued that temperature had a single effect on prey, as it influenced its rate of development, but a double effect on predators, as it not only affected their rate of development but also their predation rates.

4.3.2 Materials and Methods:- Same as described in Section 4.1.2.

4.3.3 Data Analysis:- The data were treated as 11 values for females and 10 for males. Since the average number of eggs eaten by males was vastly different and less than females at each temperature, the two sexes were analysed separately. The missing values due to deaths of the animals during tests were replaced by new ones by (GENSTAT).

4.3.4 Results:- Results of the experiment are presented in Table 4.8.

Sex effects:- Results shown in Table 4.8 indicate considerable differences in the numbers of eggs eaten by male and female juveniles. Female juveniles always ate more than their male counterparts under each test situation.

Table 4.8. Number of eggs consumed by *T. nigrolineatus* male and female nymphs at 5 constant temperatures.

Temperature	n	Sex	Mean No. of eggs eaten ± S.D.	Mean nymphal period in days ± S.D.
15°C	10	♀	311.6 ± 9.6	71.4 ± 8.4
	10	♂	254.6 ± 13.2	69.9 ± 6.1
20°C	11	♀	315.0 ± 7.4	34.8 ± 1.1
	9	♂	253.7 ± 10.4	32.2 ± 1.4
25°C	11	♀	313.0 ± 7.9	17.6 ± 0.5
	10	♂	254.3 ± 18.7	16.6 ± 0.5
30°C	9	♀	274.1 ± 13.0	12.3 ± 0.7
	8	♂	289.2 ± 13.0	11.7 ± 0.8
35°C	9	♀	260.6 ± 10.8	11.5 ± 0.5
	9	♂	183.2 ± 10.9	10.8 ± 0.6

Temperature effects:- Male and female juveniles of *T. nigrolineatus* consumed, on average, similar numbers of *H. punctiger* eggs at 15, 20 and 25°C; their voracity was independent of temperature (cf. Table 4.8 and Appendices 5 and 6). Temperature did not affect their total feeding capacity, but it did affect the average daily rate of egg consumption and the number of feeding days (Table 4.8). This has also been shown for *Geocoris punctipes* (Crocker *et al.*, 1975) and for *Coccinella 7-punctata* (Hodek, 1957; Hukusima and Sakurai, 1963 - in Hodek, 1967).

Furthermore, temperature had a singificant influence on the voracity of both sexes at 30 and 35°C. Their total feeding capacity was significantly less ($P < 0.01$) at these temperatures (Table 4.8). Thus, interaction between temperature, sex and voracity became apparent at 30 and 35°C. It can be summed up by describing that females ate similar numbers of eggs at 15, 20 and 25°C. They ate less at 30 and 35°C (cf. Appendix 5). Furthermore, they took more eggs at 30°C than at 35°C. Males showed no significant differences at 15, 20 and 25°C, but they consumed significantly less eggs at 30 and 35°C (cf. Appendix 6).

4.3.4 Discussion:- Similar average egg consumption by *T. nigrolineatus* male and female nymphs at 15, 20 and 25°C is of ecological interest. Average summer temperatures in South Australia are around 25°C and it is unlikely that temperature would adversely affect their voracity. Furthermore, their ability to remain active and eat as many eggs at 15°C and 20°C suggests that *T. nigrolineatus* is more likely to interact with *H. punctiger* populations and reduce their numbers early in the season.

Although *T. nigrolineatus* is a voracious egg predator of *H. punctiger*, caution must be exercised in interpreting the results. *T. nigrolineatus*, like other nabids, is a polyphagous predator and preys upon a wide variety of prey, such as aphids, lygus bugs, and small lepidopterous larvae. van den Bosch and Hagen (1966) listed aphids, leaf hoppers, lygus bugs, spider mites and small lepidopterous larvae as potential prey for *Nabis* spp. Unless all the potential prey species are given to predators in laboratory studies, it is inappropriate to make assumptions about the effectiveness of any predator. Tamaki and Weeks (1972) offered *Nabis americoferous* a choice along the above mentioned lines between aphids and noctuid larvae and noted that *N. americoferous* were superior to other predators in reducing small noctuid larvae. Nagauda and Pitre (1978) obtained similar results with *Reduviolous roseipennis* (Hemiptera : Nabidae). Furthermore, Lopez *et al.* (1976) demonstrated in cage tests in the field that *R. roseipennis* effectively reduced egg populations of soybean looper, *Pseudoplusia includens* and that *Tropiconabis* spp. preyed voraciously on both eggs and small caterpillars.

Lower predation rates of both male and female juveniles in the present study at 30 and 35°C may be explained in terms of faster rates of development at these temperatures (Table 4.8).

4.4 ESTIMATE OF THE NUMBERS OF *H. PUNCTIGER* EGGS EATEN BY *T. NIGROLINEATUS* DURING THEIR LIFE SPAN

4.4.1 Introduction:- *T. nigrolineatus* responded to *H. punctiger* eggs immediately, whereas *O. schellenbergii* and *C. nasalis* showed poor response to eggs (cf. 4.1.3). This experiment was conducted to ascertain the total number of *H. punctiger* eggs that *T. nigrolineatus* would eat in its life time.

4.4.2 Methods:- Same as described in Section 4.1.2, except that the number of eggs exposed to predators per day was 70.

4.4.3 Results and Discussion:- Female *T. nigrolineatus* were more voracious and ate significantly more eggs ($P < 0.01$) than males. Furthermore, their life span was significantly longer than males (Table 4.9) and their daily rate of predation was relatively higher than males.

Table 4.9. Number of eggs eaten by *T. nigrolineatus* males and females in their life spans at 25°C.

Sex	n	Mean number of eggs eaten ± S.D.	Life span in days ± S.E.	Average eggs eaten/day
♀	15	933 ± 97	40.6 ± 3.5	22.9
o	15	498 ± 45	29.3 ± 3.4	16.4
		$t = 4.0$, $P < 0.01$	$t = 2.2$, $P < 0.05$	

Both sexes consumed higher number of eggs during the first week, but after that they behaved differently. The males' daily food consumption declined gradually with the age; there were many 1-2 days interval during which they did not take any food and they stopped feeding 2-3 days before death. Females' predation rate remained similar, although in some individuals it increased during the oviposition period; daily egg consumption declined sharply when females stopped laying eggs, shortly before death. Females also stopped feeding two to three days before death.

Different predation rates due to sex have been discussed (cf. 4.3.4). Differences in the overall predation are much evident in *T. nigrolineatus*. This sharp difference is probably due to shorter life span of males than females.

4.5 EXPERIMENTS ON LARVAL PREDATION

4.5.1 Evaluation of the effectiveness of *O. schellenbergii*, *C. nasalis* and *T. nigrolineatus* against first instar caterpillars

4.5.2 Methods:- Three predacious species were given various numbers of *H. punctiger* larvae as shown in Table 4.10.

Table 4.10. Numbers of *H. punctiger* caterpillars exposed to predators per day.

Stage of prey	Predator Stages				
	I	II	III	IV	V
T. nigrolineatus					
First instar	15	20	30	40	60
Second instar	2	4	5	6	8
Third instar	1	1	1	1	2
O. schellenbergii and *C. nasalis*					
First instar	*	50	100	200	300
Second instar		5	10	15	40
Third instar		3	5	6	12
Fourth instar		1	1	2	4
Fifth instar		1	1	1	1

* First stage *O. schellenbergii* and *C. nasalis* do not take any animal food.

Similar numbers of caterpillars were used in experiments under 'simple' or 'complex' searching conditions. In simple searching conditions caterpillars placed on strips of artificial diet were exposed to predators, while in complex searching conditions caterpillars were released on lucerne stems 12-16 cms and then exposed to predators. Numbers eaten were counted at 24-hour intervals and predators transferred tp new petri dishes or plants held in containers with same number of larvae. Adequate controls were maintained to account for the missing caterpillars or larval mortality due to natural causes. A random sample of 5 predators of a particular stage was tested at a time and tests were replicated three times.

Analysis of Data:- Data on predation against first instar caterpillars by 3 species were subjected to analysis of variance. Since first stages of *O. schellenbergii* and *C. nasalis* are non-predacious, data on numbers eaten by first stage *T. nigrolineatus* were not included in the analysis. Furthermore, due to unequal numbers of survivals in the fifth stage, data on this stage were analysed separately to test the differences between species, interactions between sex X species, sex X conditions, species X conditions, sex X species and conditions.

However, data on predation by second, third and fourth stage predators were analysed jointly to test the differences between these stages, interactions between stage X conditions, species X conditions, species X stages and species X stage X conditions. Data were transferred to logarithms due to large variability.

Table 4.11. Numbers of first instar caterpillars eaten by three species. at 28 ± 2°C. Mean values shown are the corrected means for missing larvae.

Species	n	Searching conditions	Mean numbers of caterpillars eaten*						Survival**
			I	II	III	IV	V♀	V♂	
T. nigrolineatus	15	Simple	6.1	14.2	28.4	39.8	87.9 ***(9)	62.8 (6)	15
O. schellenbergii	15		-	27.1	72.3	167.1	597.9 (5)	289.7 (5)	10
C. nasalis	15		-	41.5	109.5	221.2	771.6 (3)	395.9 (5)	8
T. nigrolineatus	15	Complex	4.5	10.0	17.2	35.4	58.4 (9)	50.5 (6)	15
O. schellenbergii	15		-	19.6	60.8	161.2	421.0 (5)	280.3 (5)	10
C. nasalis	15		-	20.5	93.0	192.2	529.5 (4)	354.3 (3)	7

* Mean values shown are the corrected means for the missing caterpillars.

** Actual numbers.

*** Number of replicates.

Data on predation against second and third instar caterpillars, showed very low variability especially in the earlier predator stages, therefore data on predation in each instar and under two sets of conditions were compared by Mann-Whitney U-test.

4.5.3 Results:- Results of predation against first instar caterpillar by three species are shown in Table 4.11.

All three species when raised on first instar caterpillars alone reached adult stage under two experimental conditions. *T. nigrolineatus* appeared to be normal in size in each stage and their stage durations (Table 4.12) were normal and comparable to ones observed previously (cf. Chapter 3). So also were the younger stages of *O. schellenbergii* and *C. nasalis*, but the fourth and fifth stage durations of pentatomids were unusually long (Table 4.11) and the size of emerging predators was small. This may be an indication of unprofitability of first instar caterpillars to larger pentatomids or simply reflects the difficulty of their capturing sufficient small prey to provide an adequate quantity of food. Many of the pentatomids died while moulting to the fifth stage or during the final moult and *C. nasalis*, the largest of the three species, showed greater mortality followed by *O. schellenbergii* (Table 4.10); there was no mortality in *T. nigrolineatus*.

Table 4.12. Stage durations of *T. nigrolineatus*, *O. schellenbergii* and *C. nasalis* when raised on first instar *H. punctiger* at 28 ± 2°C.

	Instar durations in days ± S.D.					
	I	II	III	IV	V♀	V♂
T. nigrolineatus	2.5±.4	2.0±.3	2.5±.4	3.0±.5	4.2±.7	4.0±.4
O. schellenbergii		2.8±.6	3.7±.5	4.1±1.0	10.5±2.3	9.5±2.6
C. nasalis		4.4±.5	4.0±.7	5.1±1.4	12.4±3.2	10.0±3.6

Furthermore, caterpillars eaten in individual stages were significantly different, within the species and between the species (Table 4.11, Appendix 7), Searching conditions also showed significant effect on the numbers of caterpillars eaten. Interactions between species and instars, species and conditions, instars and conditions and species x instar and conditions were all significant (cf. Appendix 7). Nevertheless, only the last interaction was of particular interest. Second and third stages of each species consumed significantly less ($P < 0.05$) caterpillars on plants. However, fourth stages of *O. schellenbergii* and *T. nigrolineatus* showed increase in searching ability and took similar numbers under two sets of conditions but fourth stage *C. nasalis* did not show improved searching ability.

Fifth stage predators showed significant differences due to sex (Table 4.11 and Appendix 8) between species and within species. Differences due to sex were independent of searching conditions. Significant interaction between species and conditions was due mainly to *C. nasalis* consuming more prey than either of the two species and *O. schellenbergii* eating more than *T. nigrolineatus*. Within species *O. schellenbergii* consumed similar numbers of caterpillars ($P > 0.05$) under two conditions. Other two species consumed significantly more ($P < 0.05$) caterpillars under 'simple' searching conditions.

4.5.4 Predation on second instar caterpillar:- Table 4.13 shows the results of this experiment. First and second stages of *T. nigrolineatus* failed to capture second instar caterpillars despite many attacks due to the latter's defense ploys. However, from third stage onwards, *T. nigrolineatus* readily attacked and captured second instar caterpillars, although it took the hemipteran considerable time and skilled use of a novel attack strategy to overpower the resistance of the caterpillar. The unique attack behaviour of third and fourth stage predators consisted of a sudden pounce on the caterpillar, seizure of the anterior and posterior ends of caterpillars in the front raptorial legs and insertion of the stylets in the middle of the body. This tactic reduced the impact of caterpillar's defense ploys to minimum. Nevertheless, if predators failed to grasp both the ends of caterpillar simultaneously during the initial pounce the hemipteran could not withstand the lashings of the wriggling and squirming caterpillar and released it. When presented with their prey in a petri dish, fifth stage and adult *T. nigrolineatus* were often seen to use an additional attack behaviour; they touched the prey with front tarsi repeatedly, until the caterpillar became inured to contact, then pounced on the caterpillar and put their front tarsi on the two ends of the caterpillar and kept them pressed against the floor of the petri dish until the insertion of the stylets and immobilization of the caterpillars had been completed. This observation is consistent with Arnold's (1971) report on the attack behaviour of *Nabis* spp.

In general, the number of caterpillars consumed increased with predator age, and fifth stage females of each species consumed more caterpillars than fifth stage males (Table 4.13).

All the stages of *O. schellenbergii* and *C. nasalis* readily preyed upon second instar caterpillar and attained maturity without any mortality. Thus indicating the suitability or high nutritive value of this caterpillar for development, compared with eggs (cf. 4.1) and first instar caterpillars (cf. 4.5.3). Predation pattern of these

Table 4.13. Numbers of second instar caterpillars eaten per stage by 3 species.

Species	n	Searching conditions	Mean numbers eaten per stage I	 II	 III	 IV	 V♀	 V♂	Survival
T. nigrolineatus	15	Simple	0	0	1.0b	2.0d	5.5c	3.7h	15
O. schellenbergii	15			1.3 a	3.0a	7.4b	35.6f	24.5i	15
C. nasalis	15			1.9a	3.2a	12.2c	48.4g	30.5i	15
T. nigrolineatus	15	Complex	0	0	1.0a	2.0d	4.7e	3.0b	15
O. schellenbergii	15		-	1.2a	2.8a	7.3b	35.1f	24.2i	15
C. nasalis	15			1.7a	3.0a	12.0c	45.7g	30.3i	15

Means followed by similar letters in each columnare not statistically significant at 5 percent level when compared by Mann-Whitney U test.
Mean value in each row underlined show significant differences due to sex when compared by the same test.

Table 4.14. Numbers of third instar caterpillars eaten per stage by three species.

Species	n	Searching conditions	Mean numbers eaten per stage I	 II	 III	 IV	 V♀	 V♂	Survival
T. nigrolineatus	15	Simple	0	0	0	0	1.3b	1.0c	15
O. schellenbergii	15			1.0a	1.2a	2.4a	7.3a	3.4a	15
C. nasalis	15			1.4a	2.1a	3.4a	9.6a	6.0a	15
T. nigrolineatus	15	Complex	0	0	0	0	1.2b	1.0c	15
O. schellenbergii	15			1.0a	1.2a	2.3a	6.8a	3.3a	15
C. nasalis	15			1.3a	2.0a	3.2a	8.3a	5.8a	15

two species was similar to *T. nigrolineatus*. They consumed systematically more caterpillars in each subsequent stage (Table 4.13). Fifth stage females ate more caterpillars than males and their food consumption was almost three times that of all the preceding stages.

Furthermore, all the species consumed similar number of caterpillars under the two experimental conditions, thus indicating that complexity of the searching arena was of little consequence as far as predation on second instar caterpillar was concerned. Juveniles of *O. schellenbergii* and *C. nasalis* consumed significantly more caterpillars than *T. nigrolineatus* (Table 4.13). However, differences between the latter two appeared only in the fourth and fifth stages.

4.5.5 Predation on third instar caterpillar:- The first four stages of *T. nigrolineatus* were unable to capture third instar caterpillars. Nevertheless, fifth stage males and females captured such prey by using their unique attack behaviour (cf. 4.5.4). Normally a single third instar caterpillar was sufficient to satiate a fifth stage *T. nigrolineatus*; some females attacked and killed a second caterpillar, but it was always abandoned only partially consumed. However, differences between the two sexes were non-significant (Table 4.14).

Second stage *O. schellenbergii* and *C. nasalis* mostly killed one caterpillar and became satiated. However, some *C. nasalis* attacked and killed a second caterpillar but abandoned it partially consumed. They spent considerable time and attacked several times before succeeding in capturing a third instar caterpillar. Third stage *O. schellenbergii* captured similar numbers of caterpillars. In other words, one-third instar caterpillar is more than sufficient to satiate both second and third stages of *O. schellenbergii*. But in the previous experiment, it is clear that as the predators grow older their food requirements increase and hence they consume different numbers of caterpillars. As shown in previous experiment individual stages of each species captured and consumed similar numbers of caterpillars under two experimental conditions and fifth stage female was more voracious than fifth stage male (Table 4.14).

4.5.6 Predation on fourth and fifth instar caterpillars under simple searching:- Fifth stage *T. nigrolineatus* were unable to capture fourth instar caterpillars. Even their diverse attack behaviour (cf. 4.5.4) failed to overcome strong retaliation by large caterpillars (cf. Chapter 9). Furthermore, second stage *O. schellenbergii* and *C. nasalis* also failed to capture fourth instar prey (Table 4.15) nonetheless, a large number of them persistently attacked caterpillar on its prolegs and probably were able to acquire their critical food requirements and hence moulted to next stage after a slightly delayed stage duration. Only a small number of third stage *O. schellenbergii* actually killed fourth instar caterpillar and most of them, like the second stage, moulted to the next stage without killing the prey. Relatively more of the third stage *C. nasalis* killed fourth instar caterpillars, but some that failed to do so still moulted to next stage. From fourth stage onwards predators of both species were able to capture fourth instar caterpillars, but not before a long and fierce struggle between the two, lasting for many hours.

Except few females, none of the juveniles of *O. schellenbergii* and *C. nasalis* captured firth instar caterpillars. Even the female nymphs of two species had limited success against them when confronted with the fifth instar caterpillars which were more aggressive and used their

Table 4.15. Numbers of fourth and fifth instar caterpillars eaten by three species.

Species	n	Prey instar	Searching conditions			Predator Stages			
				I	II	III	IV	V♀	Vo
T. nigrolineatus	10	Fourth	Simple						
O. schellenbergii	10			-	0(6)	0.2(7)	1.0	2.0	1.5
C. nasalis	10			-	0(5)	0.7(2)	2.0	3.5	2.5
T. nigrolineatus	10	Fifth	Simple						
O. schellenbergii	10			-	0(5)	0(5)	0(8)	0.1	0(4)
C. nasalis	10			-	0(6)	0(4)	0(4)	0.2	0(3)

Numbers in parentheses show numbers of predators that moulted to next stage without killing the prey.

defense ploys much more effectively (cf. Chapter 9). Some predator stages again moulted to next stage (Table 4.15) without killing the caterpillar. An exception was the fifth stage females of both species which moulted to next stage only when they had actually killed the caterpillar, but this was achieved only by attacking the caterpillar during its ecdysis, a time when it is defenseless and easy to capture.

4.6 DISCUSSION

Results of experiment on predation against first instar caterpillars may be compared with experiment on egg predation (cf. 4.1.3). Slow development of *O. schellenbergii* and *C. nasalis* coupled with their small size, evidently demonstrates that eggs and first instar caterpillars are not suitable items of food for advanced stages of predacious pentatomids or that such prey provide only marginal returns for the search and/or feeding effort involved. It may be supposed, therefore, that *O. schellenbergii* and *C. nasalis* are unlikely to prey upon first instar caterpillars in nature. This view is consistent with field observations. None of the predators, collected from the field, at different intervals and times of the year, over four years appeared as small as predators raised either on eggs or first instar caterpillars. This does not imply that suitable *H. punctiger* larvae are always present in lucerne patches. At certain periods of the growing season, *H. punctiger* populations reach very low levels (Cullen, 1969). Nonetheless, these low population levels do not affect the size of *O. schellenbergii* and *C. nasalis* to a great extent, since they also prey upon other lepidopterous larvae. Moreover, on many occasions advanced stage predators were seen preying upon large coccinellid larvae.

But their capability to make use of very small and unprofitable caterpillars in the absence of suitable or preferred ones is of advantage and possibly of survival value. General predators are known to survive on unsuitable and non-preferred food in the absence of preferred ones. Waddill and Shepard (1975) noted that *Stiretrus anchorago* survived on *Galleria mellonella*. Furthermore, comparison between predation under simple and complex conditions, against first instar caterpillar, showed significant differences for second and third stages of each species. In other words, complex searching conditions lowered their overall predation. In nature, variables such as plant height, cover, and prey densities would have a great deal of influence on the predation potential of predators. Thus, behaviour patterns of predators and prey and the searching conditions should be taken into account while relating laboratory studies to field conditions. In this study, the lower predation against first instar caterpillars was mainly due to its 'refuge' seeking behaviour. Moreover, although predators may feed to their maximum capacity under simple conditions, but may not necessarily do so under more complex conditions, where a proportion of their time is spent in finding the prey. Other workers have also reported low predation rates under complex searching conditions (cf. Lingren *et al.*, 1968; Lopez *et al.*, 1976). However, individual stages of three species showed similar predation under simple and complex searching conditions against large caterpillars (Tables 4.13 and 4.14), thus indicating that lucerne plants do not provide protection to large caterpillars as is the case with first instar caterpillars.

Stage durations of *T. nigrolineatus* while preying on first instar caterpillars were comparable to those reported in Chapter 3. This indicates that this species is probably more important as predator of eggs or small caterpillars. Leigh and Gonzalez (1976) reported that nabids were potential predators of very small lygus bugs on cotton. Furthermore, inability of various *T. nigrolineatus* stages to capture large caterpillars suggests that this species would selectively prey upon eggs, first and second instar caterpillars.

Limited success of second and third stages of *O. schellenbergii* and *C. nasalis* against large caterpillars indicates that these stages would probably be restricted to feeding on small caterpillars as well. However, their high survival rates and normal stage periods, comparable to those observed previously (cf. Chapter 3), when preying upon second and third instar caterpillars, indicate that these two species would probably act as mortality agents of small to medium-sized caterpillars. This observation is consistent with the results reported by previous workers (e.g. Tamaki and Weeks, 1972; Waddill and Shepard, 1975; Richman *et al.*, 1980). The inability or limited success of *O. schellenbergii* and *C. nasalis* against fourth and fifth instar caterpillars (Table 4.15) lends further support to the contention that pentatomids mainly prey upon small to medium-sized caterpillars. Although caution must be exercised in projecting laboratory studies to field situations, nonetheless behaviour patterns such as attack behaviours of predators or defense ploys of caterpillars are unlikely to be different in the two situations. In other words, if a predator fails to capture a large caterpillar in the laboratory it is not likely to capture it in the field either.

However, persistent attacks by small predators on the prolegs of large caterpillars is a useful strategy and is apparently of survival, value. Small predators are probably able to acquire their critical food requirements by persistent attacks on prolegs. This would enhance their survival in nature in the absence of prey suitable for immobilization, for Tostowaryk (1971) noted that if earlier stages of *Podisus modestus* did not ingest animal food early in each stadium (except first stage), they became emaciated and hence were unable to capture prey and died of starvation. It is not unusual for predators to moult to the next stage on very little food. There is an immense difference between what a predator can consume when food is abundant, and its minimum requirement for food (LeCato and Collins, 1976). Inability of *O. schellenbergii* and *C. nasalis* female fifth stage predators to moult to the adult stage, without killing the fifth instar caterpillar can also be explained in terms of their food requirements. Their critical food requirements are probably larger than other stages and the most food they can acquire without killing the prey is presumably not sufficient to get them through to next stage.

Total mortality of *T. nigrolineatus* against fourth instar caterpillar and failure of its small stages to acquire basic food requirements from large caterpillars (Table 4.15) can probably be explained and related to the morphology of their probosces. The long and slender probosces are effective against eggs and first instar caterpillars, where no struggle is involved. But where fierce struggle is involved predators have to hold the caterpillars in their legs firmly before they can insert their stylets and if they fail to grasp the caterpillar, which they often do, against large caterpillars, they cannot hold the caterpillar with proboscis alone. Crocker and Whitcomb (1980) noted that slender beaks of *Geocoris* spp. were not physically suited to struggle with large prey.

4.7 SURVIVAL OF *O. SCHELLENBERGII* AND *C. NASALIS* FEMALES WITHOUT FOOD AND MINIMUM FOOD REQUIREMENTS OF THEIR JUVENILES

This experiment was conducted to ascertain (1) the longevity of females of two species under unfavourable conditions (without food), and (2) to determine the basic food requirements of the two species. Since the predators respond to second instar caterpillars, they were the prey chosen for the tests.

4.7.1 Methods:- Ten newly emerged females of *O. schellenbergii* and *C. nasalis* were housed in 65 mm plastic petri dishes and deprived of food. They were provided with drinking water and their mortality was recorded.

4.7.2 Results:- It is obvious from the results (Table 4.16) that both predators had similar life spans without food. In both species, predators showed increased searching activity during the first 5-8 days, but this activity declined gradually and predators tended to spend more time in 'resting' (resting here means being inactive), close to the water source.

Table 4.16. Survival of *O. schellenbergii* and *C. nasalis* females without food at 25°C.

Species	n	Mean life span in days ± S.D.	Range	
O. schellenbergii	10	16.3 ± 9.5	5-36	t=1.32, P>0.05
C. nasalis	10	22.9 ± 12.4	4-46	

4.8 MINIMUM FOOD REQUIREMENTS OF JUVENILES OF TWO PENTATOMIDS AND THE INFLUENCE OF QUANTITY OF FOOD ON THEIR STAGE DURATIONS

4.8.1 Methods:- Newly moulted individuals of *O. schellenbergii* and *C. nasalis* (second to fifth stage) were given various numbers of weighed second instar caterpillars (3.5 ± 0.2 mgs) in 65 mm plastic petri dishes and their survival and stage durations were recorded.

Data Analysis:- Stage duration of predators, at the food level, where they attained 50 percent or more survival were compared with stage durations at higher food levels by the t test.

4.8.2 Results:- Results are presented in Table 4.17.

Both second stage predators attained 100 percent survival on one second instar caterpillar and their stage durations were not significantly shorter if they were given more. In the case of third stage predators all survived on one caterpillar; but when provided with two caterpillars stage durations were significantly shorter in *O. schellenbergii* (Table 4.17), but not in *C. nasalis*.

Fourth stages of both species failed to survive on one caterpillar, they lived for a long time but none of them was able to moult to the next stage. Nevertheless, when provided with two caterpillars both species attained slightly more than 50 percent survival. Addition of one more caterpillar to their diet had dramatic effect on their stage durations and survival rates, however (Table 4.17). Survival increased to 100 percent and stage durations declined significantly.

Fifth stages of both species had different food requirements due

Table 4.17 Critical food requirements of *O.schellenbergii* and *C.nasalis* and their stage durations at different food levels at 30°C.

Species	n	Predator stage	No. of prey provided	No. of survivors	Stage durations	t value	P
O. schellenbergii	10	II	1	10	3.2 ± 0.4	$t = 0.37$,	$P>0.05$
	10	II	2	10	3.1 ± 0.7		
	10	III	1	10	3.7 ± 0.4	$t = 3.39$,	$P<0.01$
	10	III	2	10	2.9 ± 0.5		
	10	IV	1	-	-		
	10	IV	2	7	5.8 ± 1.3	$t = 5.0$,	$P<0.001$
	10	IV	3	10	3.3 ± 0.6		
	10	V♀	1-4	-	-		
	10	V♀	6	6	10.6 ± 2.4	$t = 4.1$,	$P=0.001$
	10	V♀	8	10	6.7 ± 1.3		
	10	V	1-2	-	-		
	10	V	3	7	7.0 ± 1.4	$t = 4.3$,	$P<0.001$
	10	V	4	10	4.6 ± 0.8		
C. nasalis	10	II	1	10	3.4 ± 0.5	$t = 0.94$,	$P>0.05$
	10	II	2	10	3.2 ± 0.4		
	10	III	1	10	4.5 ± 0.4	$t = 0.73$,	$P>0.05$
	10	III	2	10	4.3 ± 0.6		
	10	IV	-	-	-		
	10	IV	2	6	10.1 ± 1.9	$t = 10.3$,	$P<0.001$
	10	IV	3	10	3.5 ± 1.5		
	10	V♀	1-8	-	-		
	10	V♀	10	5	15.4 ± 2.0	$t = 8.0$,	$P<0.001$
	10	V♀	12	8	8.1 ± 1.2		
	10	V	1-4	-	-		
	10	V	5	6	7.1 ± 1.8	$t = 5.5$,	$P<0.001$
		V	7	10			

Data for the amount of food, where survival was less than 50% are not shown in the table.

to sex (Table 4.17). Females of each species required more food than males. Fifth stage females of *O. schellenbergii* failed to survive on four or less caterpillars and their survival on 5 was less than 50 percent. But when given 6 caterpillars, six test individuals moulted to the adult stage. However, when provided with 8 caterpillars survival increased and the stage durations were significantly reduced.

A similar situation occurred in the case of *C. nasalis*. None of the fifth stage females completed development on 8 or less caterpillars and only a few moulted when given 9 caterpillars. They required 10 caterpillars each to attain 50 percent survival with protracted stage durations. Two additional caterpillars increased their survival and led to significant reduction in stage durations. In males also a difference of one or two second instar caterpillars in the diet of the fifth stage predator changed sub-minimal diet to a marginal and optimal diet respectively.

4.8.3 Discussion:- Survival of *O. schellenbergii* and *C. nasalis* females, without food for such a long period may be explained in terms of their behavioural adaptations to prey shortages in nature. Such behavioural adaptation is likely to enhance their chances of survival in the absence of prey on the one hand and increase their chances of finding prey in the near future due to long survival without food on the other.

Kehat (1968) argued that capacity to survive for long periods without food or on a small amount of food and capacity to kill large numbers of prey when the prey are abundant are the basic characteristics of an efficient predator. Normal stage durations of second stage *O. schellenbergii* and *C. nasalis* when provided with one second instar caterpillar (3.5 mgs) suggest that one such caterpillar is sufficient to meet their basic food requirements. However, delayed moulting of later stages on small amounts of food is consistent with Kehat's (1968) observations. Dixon (1959) reported similar results on *Adalia decempunctata* (Coleoptera : Coccinellidae) and argued that the amount of food received had considerable effect on instar periods, survival rates and on the sizes of emerging predators. Glen (1973) observed a similar phenomenon in *Blepharidopterus angulatus* (Heteroptera : Miridae). He further argued that earlier stages of predators were able to compensate for inadequate diet by converting food into body tissue more efficiently.

There are several reports describing that predatory arthropods under conditions of food scarcity tend to moult to next stage, at significantly less body weight than when food is abundant (Fox, 1973; Hodek, 1973). As an exceptional case, spider, *Linyphia triangularis*, continues to moult without food and its successive stages become progressively smaller in size and weight until spider's death due to starvation (Turnbull, 1962).

4.9 ESTIMATE OF NUMBERS OF THIRD AND FOURTH INSTAR CATERPILLARS CONSUMED BY ADULT *O. SCHELLENBERGII* AND *C. NASALIS*

Adults of the two species readily attacked and captured third and fourth instar caterpillars (medium-sized prey). It was of interest to assess the number of medium-sized caterpillars the two species would eat during their adult life.

4.9.1 Methods:- Ten newly emerged males and females of each species were housed in 65 mm plastic petri dishes with lumps of artificial diet for caterpillars and a water source. Thereafter various numbers of caterpillars of particular stages as shown in Table 4.18 were introduced in each petri dish. Both species were provided with similar numbers of caterpillars per day. Adequate controls, with similar numbers of caterpillars but without predators were maintained to account for larval mortality due to cannibalism or any other natural cause. Predators were transferred to new petri dishes with a fresh complement of caterpillars, every day, and the numbers eaten in the old dishes were recorded.

Table 4.18. Number of caterpillars exposed to hemipterans per day.

Sex of the predator	n	Caterpillar	Caterpillars given/day
♀	10	third instar	12
♂	10		8
♀	10	fourth instar	3
♂	10		2

Record was maintained of the predator mortality and predators were paired once every week for mating, in order to keep the experimental situation comparable to field.

Data Analysis:- Due to small sample size and extremely large variability among the individual treatments, basic assumptions of the parametric tests that mean values were normally or approximately normally distributed could not be met, hence data were subjected to non-parametric test.

Data were analysed by Kruskal-Wallis one way analysis of variance for two species and two sexes (by treating them as four groups) when preying on third or fourth instar caterpillars to test the overall differences. Wherever overall differences were significant, mean values in those groups were further compared by the Mann-Whitney U test to ascertain which groups contributed to overall differences. Life spans of predators were also tested in a similar manner.

4.9.2 Results:- Female *C. nasalis* ate relatively more third instar caterpillars than males (Table 4.19); and more than either males or females of *O. schellenbergii*. However, overall differences in this group failed to reach the 5 percent significance level (Table 4.19).

When preying upon large caterpillars (fourth instars) overall differences between the two species were significant (Table 4.19). Female *C. nasalis* ate significantly more than *O. schellbergii* females or males. Nevertheless, differences between males of the two species were non-significant and differences between *C. nasalis* males and *O. schellenbergii* females were also non-significant.

4.10 ESTIMATION OF RATE OF PREDATION AND NUMBERS OF THIRD INSTAR CATERPILLARS REQUIRED FOR SATIATION BY THREE HEMIPTERANS

It has been demonstrated that the three species prey variously upon *H. punctiger* caterpillars (cf. 4.5.5). It was of interest to compare the predation rates of the three species and estimate the numbers of caterpillars required to reach satiation level.

Table 4.19. Numbers of third and fourth instar caterpillars eaten by two species in their life span at $28 + .2^{o}C$.

Species	n	Sex	Stage of caterpillar	Mean numbers eaten	Mean life span in days
O.schellenbergii	10	♀	Third instar	69.8	20.9
	10	o		50.9	29.5
C. nasalis	10	♀		83.2	25.2
	10	o		59.0	31.2
				$H=5.8$, $P > 0.05$	$H=2.9$, $P > 0.05$
O.schellenbergii	10	♀	Fourth instar	17.76	18.1
	10	o		10.1a	21.6
C. nasalis	10	♀		23.7c	23.5
	10	o		14.3ab	24.7
				$H=9.7$, $P < 0.05$	$H=2.2$, $P > 0.05$

Means followed by similar letters are not significantly different at 5 percent level, when compared by Mann-Whitney U test. But means followed by different letters are different at the above level.

4.10.1 Methods:- Ten males and females of each species 2-3 days old, first fed to satiation and then deprived of food for 36-48 hours at 27°C, were used as test animals. Tests were conducted in an insectary room at 16L:8D. The test period was divided into two eight-hour intervals in order to compare the initial predation rates with the later ones. Four third instar caterpillars were released in each 65 mm plastic petri dish and exposed to predators. When a caterpillar was captured in any treatment it was replaced by a new one. Observations were continued until each predator did not attack any caterpillar for more than two hours since its last capture. At this point predators were considered to have become satiated. Numbers of caterpillars consumed by each predator were recorded.

Analysis of data:- Differences within each species due to sex and differences between species and their predation rates in two intervals were compared by t test.

4.10.2 Results:- The numbers of third instar caterpillars required to reach satiation are illustrated in Figure 4.1. It is evident that the three species required vastly different numbers of caterpillars for satiation ($P < 0.001$). When differences between sexes within each species were compared, *T. nigrolineatus* failed to reach the 5 percent significance level ($t = 1.4$). Nonetheless, both *O. schellenbergii* and *C. nasalis* females required more food ($P < 0.001$).

Predation rates of the three species at two intervals were also vastly different (Figure 4.2) ($P < 0.001$). *T. nigrolineatus* males and females again had similar predation rates, and both captured

Fig. 4.1 The number of third instar caterpillars required by 3 hemipteran species for satiation.

A. = *T. nigrolineatus*
B. = *O. schellenbergii*
C. = *C. nasalis*

Fig. 4.2 Predation rates of three hemipteran species at two 8-hour intervals.

1 = First 8-hour period
2 = Second 8-hour period
A = *T. nigrolineatus*
B = *O. schellenbergii*
C = *C. nasalis*

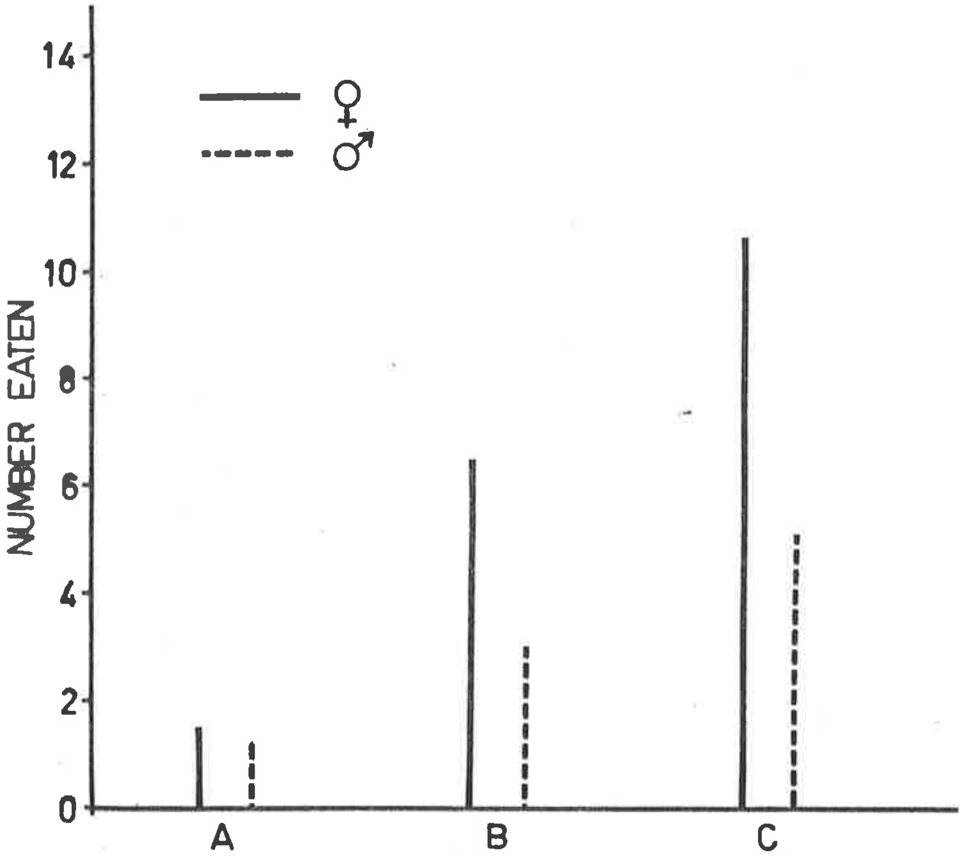

14
12
10
8
6
4
2
0
NUMBER EATEN
♀
♂
A
B
C

Fig. 4.1

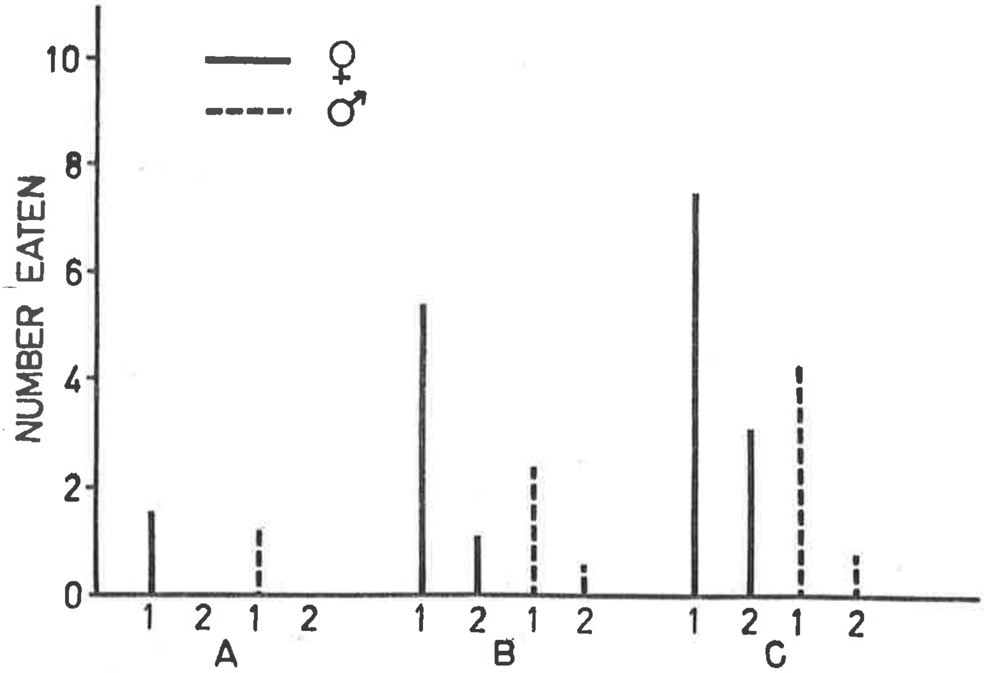

10
8
6
4
2
0
NUMBER EATEN
♀
♂
1
2
1
2
A
1
2
1
2
B
1
2
1
2
C

Fig. 4.2

the caterpillars after several attacks during the first eight-hour interval. There was no predation by *T. nigrolineatus* in the second eight-hour interval. Differences between the predation rates of *O. schellenbergii* and *C. nasalis* females and males were large and significant (Figure 4.2). Both sexes showed higher predation ($P < 0.01$) in the first eight-hour interval than the second.

4.10.3 Discussion:- Different food requirements of the three species to reach satiation may be explaiend in terms of their sizes. *C. nasalis* being the largest requires more caterpillars for satiation (Figure 4.1) and shows a higher predation rate as well (Figure 4.2). *O. schellenbergii* required less third instar caterpillars to attain satiation and *T. nigrolineatus,* the smallest of the three species required the least.

Differences between males and females of two pentatomids can also be explained in part on the basis of different sizes, since females are larger than males, and in part due to the greater energy demands of females for egg production (Kehat, 1968). Females of predacious insects have been shown to have higher predation rates than males (Kehat, 1968; Glen, 1973; Lopez *et al.*, 1976).

Adults of *T. nigrolineatus* were unable to overcome the strong resistance of third instar caterpillars as fast as the other two species and most of them captured only one caterpillar and either did not attack a second or failed to capture a second caterpillar. Only half of the females (Figure 4.2) were able to capture second caterpillar and only two males succeeded in doing so. Thus, the large number of attacks and their successive failures to capture large caterpillars in a simple universe, suggests that the probability of these predators capturing third instar caterpillars in nature is extremely low. It is noteworthy that this observation is inconsistent with Ashby's (1974) report that *Nabis capsiformis* (Hemiptera : Nabidae) preyed upon larger than third instar caterpillars of *Pieris rapae*. He also reported a different attack behaviour. "This predator stands to one side of the larva and feeds by inserting its mouthparts into an intersegmental membrane. In this position it is not discouraged when the larva throws the front of its body violently backwards when contacted by the predator."

4.11 EFFECT OF TEMPERATURE ON THE VORACITY OF *O. SCHELLENBERGII* JUVENILES UNDER SIMPLE AND COMPLEX SEARCHING CONDITIONS WHEN PROVIDED WITH SECOND INSTAR CATERPILLARS

4.11.1 Methods:- Same as already described (cf. 4.1.2).

Data Analysis:- There was little variability in the average numbers of caterpillars consumed in individual stadia. However, there were obvious differences due to sex in fifth stages. These differences were compared by Student's t test.

4.11.2 Results:- Figure 4.3 shows the results of predation under simple and complex searching conditions. Predators in each stage, on average, consumed similar numbers of caterpillars and their total feeding capacity was not affected by temperature. However, temperature had an over-riding influence upon the daily rate of food intake and the number of feeding days. The daily predation rate was low at 20°C in each stage (Table 4.20) and the number of feeding days was high. Nevertheless, daily food intake increased and number of feeding days decreased as the temperature increased.

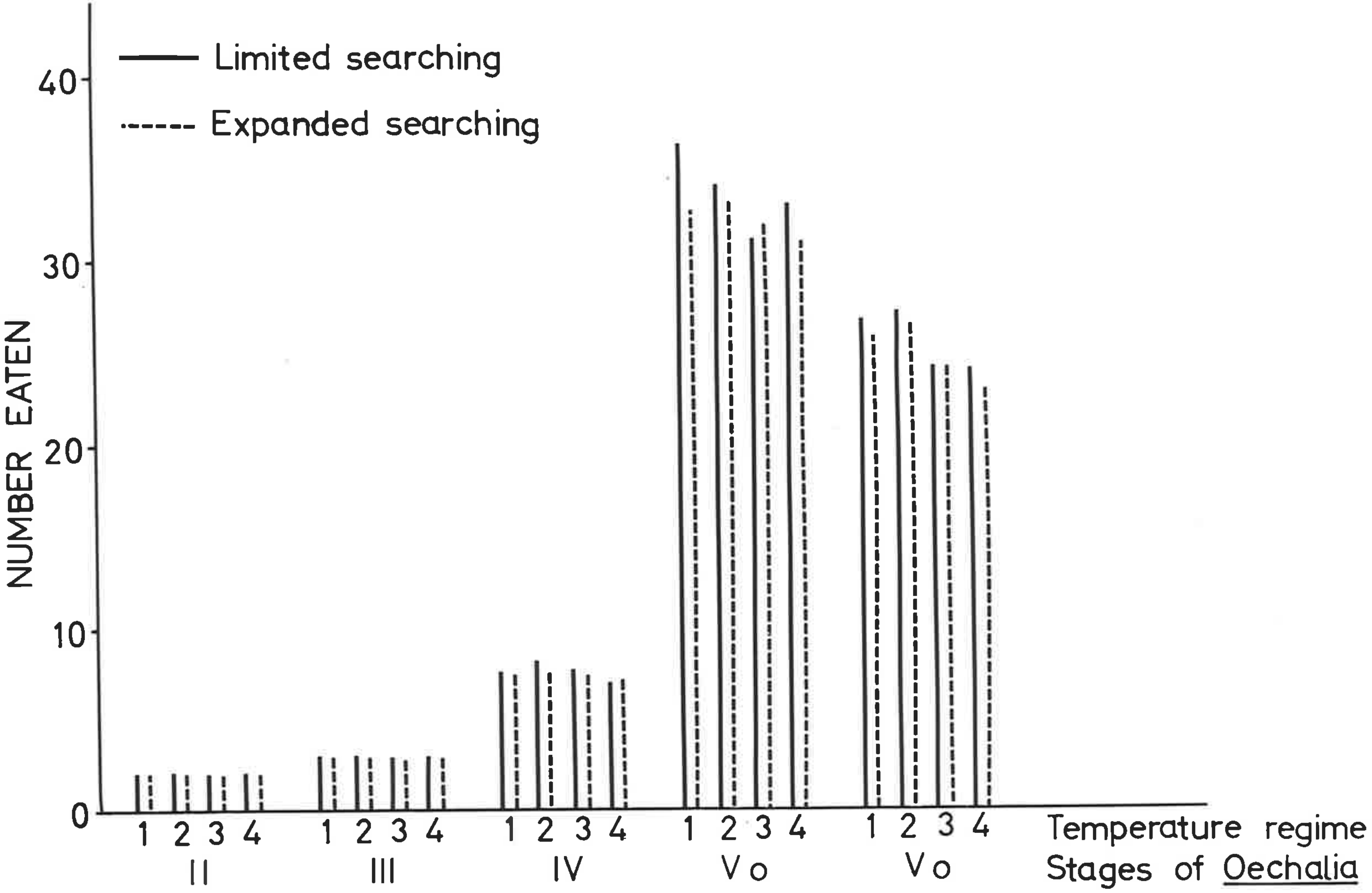
Table 4.20. Daily rate of predation of *O. schellenbergii* under limited searching at 4 constant temperature.

Predator Stages	II		III		IV		V♀		Vo	
Temp. ^oC	Average feeding days	Mean No. eaten/ day	Average feeding days	$\bar{x}$ no eaten	Average feeding days	$\bar{x}$ no. eaten	Average feeding days	$\bar{x}$ no. eaten	Average feeding days	$\bar{x}$ no. eaten/day
20	2.2	0.5	3.1	1.0	3.9	1.9	4.1	8.8	4.0	6.6
25	1.4	0.8	2.6	1.2	3.4	2.5	2.7	12.6	2.5	10.8
30	1.0	1.0	1.5	2.0	1.3	6.0	2.0	15.5	2.0	12.5
35	1.0	1.1	1.0	3.0	1.0	7.0	1.7	18.2	1.8	13.3

Table 4.21. Differential predation by *O. schellenbergii* in fith instar due to sex.

Predator Species	Temp. ^oC	Searching conditions	Mean Nos. Eaten by ♀ ± S.D.	Mean Nos. eaten by o ± S.D.	t value	P
O. schellenbergii	20	Simple	36.2 ± 4.0	26.7 ± 4.8	4.7	$P < .001$
	25		34.1 ± 3.6	27.1 ± 4.9	3.9	$P < .001$
	30		31.1 ± 4.0	25.2 ± 3.8	4.1	$P < .001$
	35		32.7 ± 4.4	24.0 ± 5.4	3.9	$P < .001$
O. schellenbergii	20	Complex	32.6 ± 4.8	25.7 ± 6.7	2.6	$P < .05$
	25		33.3 ± 5.8	26.5 ± 7.6	2.2	$P < .05$
	30		31.9 ± 8.6	25.1 ± 7.2	1.9	$P > .05$
	35		31.0 ± 6.0	22.9 ± 7.3	2.6	$P < .05$

Fig. 4.3 Voracity of *O. schellenbergii* against second instar *H. punctiger* caterpillars under limited (simple) and expanded (complex) searching conditions at four constant temperatures. (1 = 20°C, 2 = 25°C, 3 = 30°C and 4 = 35°C).


Limited searching
Expanded searching
NUMBER EATEN
0
10
20
30
40
1 2 3 4
II
1 2 3 4
III
1 2 3 4
IV
1 2 3 4
V o
1 2 3 4
V o
Temperature regime
Stages of Oechalia

Complexity of the searching universe was of little consequence as far as total feeding capacity was concerned (Figure 4.3). Predators on average consumed similar numbers under 'simple' and 'complex' searching conditions.

However, variability in feeding capacity of fifth stage predators due to sex was significant. Fifth stage females always consumed more caterpillars than males (Table 4.21) and these differences were significant irrespective of the temperature or searching conditions. Nonetheless slightly lower predation rates by both sexes under complex searching conditions resulted in lower level of significance. Thus females ate significantly more caterpillars ($P < 0.05$) than males except at 30°C, where the value just fell short of significance (Table 4.21).

4.11.3 Discussion:- Similar average numbers eaten per stage at each temperature may be explained in terms of large prey densities exposed to predation. This is consistent with the observations of previous workers (e.g. Kehat, 1968; Crocker *et al*., 1975). Nonetheless, Trpis (1972) reported that *Toxorhynchites brevipalpis* (Diptera : Culicidae) consumed more prey at higher temperatures than at lower ones.

Although *O. schellenbergii* consumed similar amounts of food per stage, nevertheless its daily food intake was high at higher temperatures. Other workers have also reported an increase in daily food consumption due to an increase in temperature (e.g. Kehat, 1968; Trpis, 1972; Brunner and Burts, 1975; Crocker *et al*., 1975; Lawrence and Watson, 1979). Thus, in nature temperature is likely to have a direct effect on daily predation rates and an indirect effect on predation potential.

Availability and density of the prey is probably likely to affect predation potential more directly. Dempster (1960) showed that predation potential of several general predators was limited by the numbers of broom beetle, *Phytodecta olivacia*. Brunner and Burts (1975) demonstrated that prey density not only altered total feeding capacity of *Anthocoris nemoralis* (Hemiptera : Anthocoridae) but it also reduced their daily food intake.

Complex searching conditions do not appear to affect *O. schellenbergii*'s predation rate and this is probably due to the large numbers of caterpillars used in the experiment. Nevertheless, a lucerne stem does not provide as much protection to larger caterpillars as to first instar caterpillars. (cf. 4.5.3). Reasons for differential predation due to the sex are discussed elsewhere (cf. 4.10.2).

4.12 ESTIMATE OF HANDLING TIME OF *O. SCHELLENBERGII* AND *C. NASALIS* AGAINST VARIOUS STAGES OF *H. PUNCTIGER*

O. schellenbergii and *C. nasalis* are different in size and have different predation rates (4.1.3). It was of interest to compare the handling times of the two species and to see its influence on the searching time.

4.12.1 Materials and Methods:- A random sample of ten newly emerged individuals of various stages of *O. schellenbergii* and *C. nasalis* was obtained from stock cultures and deprived of food for 24-36 hours at 27°C. *H. punctiger* instars in varying numbers as shown in Table 4.20 were exposed to these predators in simple petri dishes. The handling time was taken as the time interval between the initiation of attack and eventual release of the prey after feeding. Predators were given two hours to initiate the attacks and capture the prey. Predators that failed to perceive prey or capture the prey were considered as failures. Furthermore, predators that captured prey but failed to complete feeding in 4 hours were not watched any further. Notes were taken on the behavioural responses of predators to various prey sizes.

Table 4.22. The numbers of *H. punctiger* stages exposed to predators.

Species	Eggs	I	II	III	IV	V
O. schellenbergii	50	50	6	4	2	1
C. nasalis	50	50	6	4	2	1

4.12.2 Results:- Results are presented in Figure 4.4.

All the stages of *C. nasalis* tested failed to respond to the presence of eggs within two hours. This is consistent with earlier observations (cf. 4.2.3). However, the second to fourth juvenile stages of this predator attacked and captured first instar caterpillars. On the other hand, fifth and adult stages of *C. nasalis*, despite their responsiveness and several attacks, failed to capture first instar larvae. This was largely due to their inability to insert their stylets into very small caterpillars; by the time the predator stretched its proboscis, the caterpillar moved away and the proboscis touched the petri dish instead of the caterpillar. After some futile probing attempts, predators stopped further attacks. But caterpillars from the second instar onwards were all attacked and most of them were captured by large predators, except the fifth instar caterpillars. Handling times of various stages of predators were related to the size of the prey. Against any one stage of prey, handling times tended to decrease with the age of predator (see Figure 4.4).

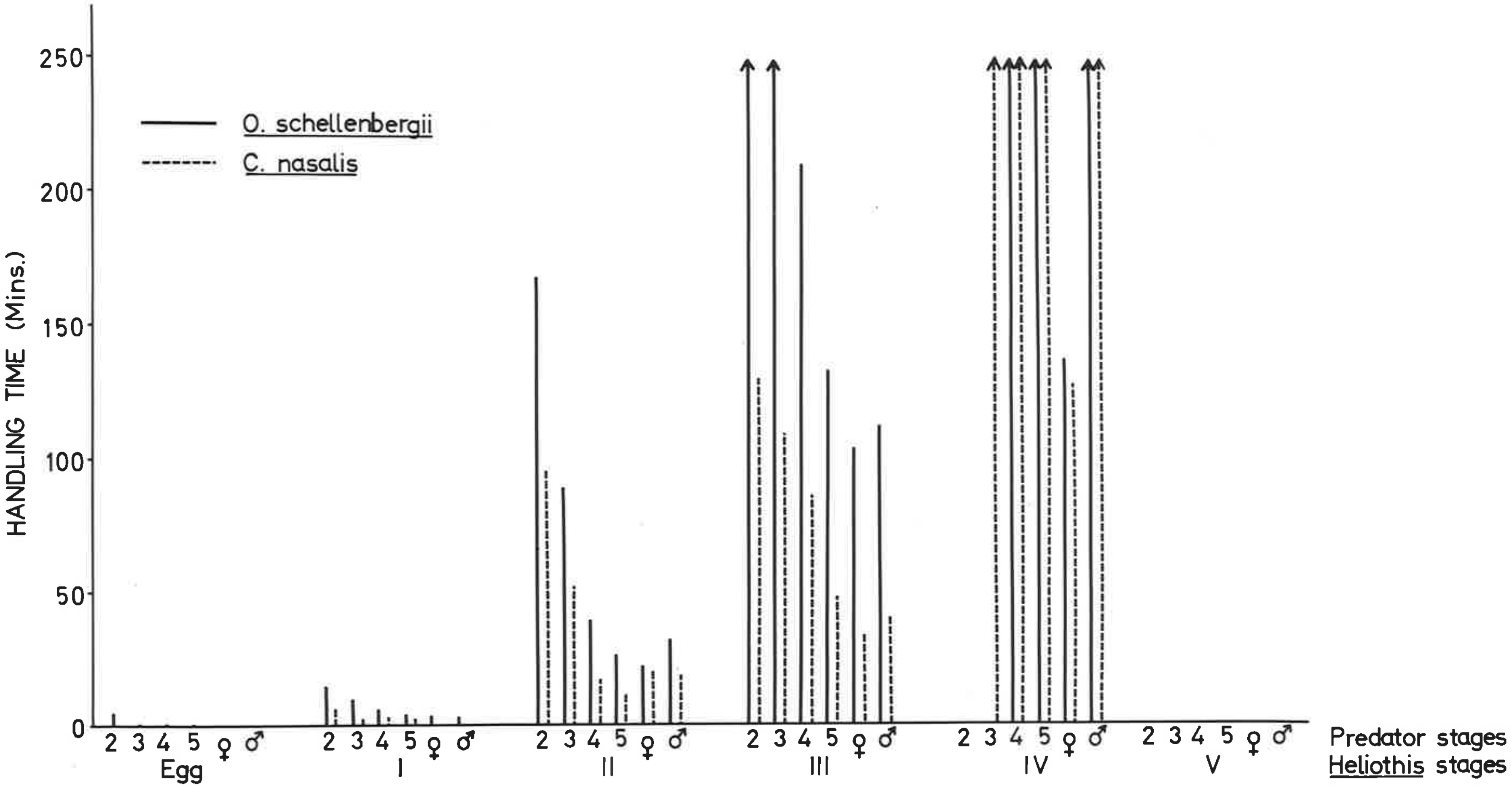
Of the two predators *O. schellenbergii* was more responsive to eggs of *H. punctiger* and in that all juveniles responded to eggs (Figure 4.4) even though the adults did not respond to eggs. Both juveniles and adults preyed upon first instar caterpillars, however, thus indicating that their behavioural adaptation to small *H. punctiger* caterpillars is relatively better than *C. nasalis*. *O. schellenbergii* attacked and captured eggs to fourth instar caterpillars and showed handling times as indicated in Figure 4.4. In this species too, handling time decreased as the size of predators increased but it increased as the size of prey increased.

O. schellenbergii had relatively long handling times against instars of *H. punctiger* than *C. nasalis*. *C. nasalis* handled a wider range of caterpillars than *O. schellenbergii* (Figure 4.4).

4.12.3 Discussion:- *O. schellenbergii* and *C. nasalis* showed vastly different handling times against various stages of *H. punctiger*. The unresponsiveness of *C. nasalis* to *H. punctiger* eggs further strengthens the evidence already gathered that this species is not an egg predator (cf. 4.1.3). Shorter handling times of *C. nasalis* for caterpillars can be explained in terms of their larger sizes relative to *O. schellenbergii*. Furthermore, *C. nasalis* probably discards the caterpillars when the net energy return from continued

Fig. 4.4 Handling time of two pentatomids (*O. schellenbergii* and *C. nasalis*) against various stages of *Heliothis punctiger*.

(Arrows indicate that the prey were captured but the handling time exceeded the 4 hour time limit).


HANDLING TIME (Mins.)
250
200
150
100
50
0
O. schellenbergii
C. nasalis
2 3 4 5 ♀ ♂
Egg
2 3 4 5 ♀ ♂
I
2 3 4 5 ♀ ♂
II
2 3 4 5 ♀ ♂
III
2 3 4 5 ♀ ♂
IV
2 3 4 5 ♀ ♂
V
Predator stages
Heliothis stages

feeding is likely to be less than the return from pursuit and capture of another prey; thus caterpillars are abandoned rather incompletely sucked out compared with *O. schellenbergii*. Zalom (1978) noted this in *Notonecta* spp. and argued that differences in handling times and complete or partial consumptions of prey could be attributed to different sizes of the predators.

Furthermore, long handling times and more efficient utilisation of food by *O. schellenbergii* are probably due to the high relative cost of attacking and capturing a new caterpillar due to the small size of this hemipteran, i.e. the long handling times of this species would mean less time available for searching (Holling, 1963) and this would lead to reduced predation.

5. EVIDENCE OF SIZE RELATED DIFFERENTIAL PREDATION BY *O. SCHELLENBERGII* AND *C. NASALIS* ADULTS ON *H. PUNCTIGER* CATERPILLARS

5.1 INTRODUCTION

In nature predators are often faced with a variety of potential prey that vary in size, 'catchability' and nutritive value to the predator (Cody, 1974; Cornell, 1976). Efficient exploitation of food is the basic requirement of every organism; and study of animal food preferences is thus vital to the field of ecology (Emlen, 1966).

Predators that detect prey at a distance by visual or olfactory cues, and that are generally required to handle prey before consumption are thought to develop a 'search image' for a particular prey and hence prey upon it selectively (Murdoch, 1969). Tinbergen (1960) evoked 'special search' image formation in forest birds to explain the changing proportions of prey in their diets. However, Royama (1970, 1971) argued that concentration of searching activity in temporally profitable micro-habitats can lead to similar results. Croze (1970) provided evidence for both food and habitat-related learning in crows.

However, predators that cannot detect prey at a distance (cf. Chapter 6) such as coccinellids, tend to grasp and capture any prey that is encountered. In such interaction prey detection and capture takes place simultaneously; hence there is no time for the predator to make a choice (Murdoch and Marks, 1973).

Several authors have emphasized the importance of relative size in predator-prey relations. In many cases the predators' size determines the size of prey it can pursue, capture and ingest (Hespenheide, 1973;

Enders, 1975; Wilson, 1975; Paine, 1976). Studies on insect predators, including the sphecid, *Philanthus bicinctus* (Mason, 1965), some species of genus *Tachysphex* (Evans, 1970), many species of pompilid wasps (Kurczewski and Kurczewski, 1968) and Chaoborus larvae (Fedorenko, 1975) have shown that prey size is an important parameter that limits the range of prey regularly captured. Shape or form (Hespenheide, 1973) and bright or contrasting colours (Brower, 1969; Dennis *et al.*, 1975) have also been shown to influence the choice of prey. Planktivorous fish selectively prey upon large-sized prey and the number of large prey consumed is much more than would be the case if the feeding were at random (Brooks and Dodson, 1965; Galbraith, 1967; Wells, 1970).

In the last few years, feeding habits of animals in general have received considerable attention. These studies have provided background information for the theory of 'optimal diets' on which there is now a great deal of experimental information and much theoretical discussion (e.g. Emlen, 1966, 1968; McArthur and Pianka, 1966; Manly *et al.*, 1972; Estabrook and Dunham, 1976). A large number of recent models make predictions about foraging behaviour of animals based on the assumption that animals tend to maximise their rate of energy intake per unit effort (see Pyke *et al.*, 1977, for review).

Observations on the handling time $\underline{Th}$ of *O. schellenbergii* and *C. nasalis* (Chapter 4) against various stages of *H. punctiger* indicated that large predators either failed to respond or took a relatively long time to respond to the presence of small prey. Nevertheless, when exposed to medium sized or large prey their response was immediate. The aim of this experiment was to determine: (1) which stage or stages of *H. punctiger* caterpillars would be taken by large predators when given a choice between various sizes, (2) what happens to the caterpillars that are attacked but escape capture, and (3) does the predator attack similar caterpillar in subsequent attacks, or has the caterpillar first captured no influence on later attacks.

5.2 METHODS

Lucerne stems of similar height and prepared in a similar way as described before (cf. Chapter 4) were used in these observations.

Three caterpillars, second, third and fourth instars representing three size categories, small, medium and large respectively, were obtained from stock cultures and randomly released on lucerne stem in equal numbers (8 caterpillars of each size/stem). The caterpillars were given ten minutes to settle and commence feeding.

Adults of *O. schellenbergii* and *C. nasalis* 3-4 days old, fed to satiation and then deprived of food for 24-36 hours were used as test animals. After the fasting period, the predators were released individually at a marked site on the lucerne stem. Records were made of the encounters (cf. Chapter 8 for definition of encounter) with each prey, the number of attacks and successful capture against each size class. Sites on the large caterpillar probed by predators were also recorded.

5.2.1 Estimate of the injury-induced mortality in fourth instar caterpillars

Large caterpillars, when attacked and held for a while, avoided capture by defense ploys and dropped off the plant. These caterpillars were collected in clean, autoclaved vials with artificial diet and their further development was monitored. Adequate controls were maintained to check for the natural mortality among the caterpillars.

5.2.2 Effect of probe-site and size of predator on time of immobilisation

Effects of probe site and predator size on immobilisation were ascertained in a separate experiment in which male and female *O. schellenbergii* deprived of food as mentioned before (cf. Section 5.2) were released in 65 mm plastic petri dishes with second, third and fourth instar caterpillars respectively.

5.2.3 Influence of caterpillar first captured on second capture

Ten *O. schellenbergii* females that captured small caterpillars (second or third instar) were allowed to consume them on plants and score second captures. The caterpillar captured in the second attempt was recorded.

However, when the predators captured the large prey (fourth instar caterpillars), both predator and prey were taken off the plant (in view of the long Th see Chapter 4). Prey densities were kept constant by adding new prey, as and when they were captured.

5.3 RESULTS

During the initial settling period, all caterpillars moved towards the top of the lucerne stem. *H. punctiger* larvae are known to have marked preference for lucerne buds, flowers and fruit (Cullen, 1969). Nevertheless, small (second instar caterpillars) and medium sized prey (third instars) were pushed and driven away from preferred food sites by large prey (fourth instar caterpillars) which accomplished this by waving their heads at the small caterpillars. However, some small prey (second instar caterpillars) managed to hide themselves in the flowers and fruit. Other small and medium sized prey dispersed and settled on the leaves of lucerne stem.

Predators also moved towards the top of the lucerne stem and they showed an uneven encounter rate for various prey (Table 5.1). Predators encountered fourth instar caterpillars more often ($P < 0.001$) than any of the other size classes. Furthermore, encounters were not evenly distributed between the other two prey sizes for any of the predators tested (Table 5.2).

Females of *O. schellenbergii* and *C. nasalis* probed and attacked large prey (fourth instar caterpillars) more frequently (Table 5.3) despite the fierce resistance and powerful defense ploys of the large caterpillars. Although several attacks proved futile, nonetheless some eventually resulted in successful captures of fourth instar caterpillars (5.4). Thus, female *O. schellenbergii* captured significantly more ($P < 0.001$) fourth instar caterpillars. While *C. nasalis* females preyed mainly on medium (third instar) and large (fourth instar) caterpillars, difference between the numbers of two size classes eaten were not significant ($P > 0.05$).

Males of both species encountered and attacked significantly more large prey (fourth instar) than the other two size classes. Nevertheless, males of *O. schellenbergii* captured significantly more ($P < 0.001$) medium sized caterpillars (third instars). But *C. nasalis* males showed only a weak preference for the medium size prey and the

Table 5.1. Size related differential predation by O. *schellenbergii* and *C. nasalis*.

Species	Sex	n	Second instar caterpillar (small prey)			Third instar caterpillar (medium)			Fourth instar caterpillar (large)		
			Encounters	Probes	Captures	Encounters	Probes	Captures	Encounters	Probes	Captures
O. schellenbergii	♀	50	16	2 .13	2 .13	45	12 .27	12 .27	148	84 .57	36 .24
	♂	50	37	11 .30	11 .30	67	24 .36	24 .36	211	99 .47	15 .07
C. nasalis	♀	23	15	-	-	42	10 .24	10 .24	106	38 .36	13 .12
	♂	29	29	5 .17	5 .17	47	13 .28	13 .28	140	69 .49	11 .08

Table 5.2 Number of encounters of *C. nasalis* and *O. schellenbergii* adults against various prey sizes.

Predator	Size of Prey			Chi-square value
	Small	Medium	Large	
C. nasalis ♀	15	42	106	$\chi^2_2 = 80.4$***
C. nasalis ♂	29	47	140	" = 98.5***
O. schellenbergii ♀	16	45	148	" = 138***
O. schellenbergii ♂	37	67	211	" = 164***

Table 5.3. Number of probes against various sized prey by adult predators.

Predator	Size of Prey			Chi-square value
	Small	Medium	Large	
C. nasalis ♀	0	10	38	$\chi^2_1 = 16.3$***
C. nasalis ♂	5	13	69	$\chi^2_2 = 83.8$***
O. schellenbergii ♀	2	12	82	$\chi^2_2 = 122.7$***
O. schellenbergii ♂	11	24	99	$\chi^2_2 = 97.0$***

* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

Table 5.4. Number of successful captures of *C. nasalis* and *O. schellenbergii* against three prey sizes.

Predator Species	Size of Prey Small	 Medium	 Large	Chi-square	Probability
C. nasalis ♀	0	10	13	$\chi^2_1 = 0.39$	n.s.
C. nasalis ♂	5	13	11	$\chi^2_2 = 3.6$	n.s.
O. schellenbergii ♀	2	12	36	$\chi^2_2 = 36.7$	***
O. schellenbergii ♂	11	24	15	$\chi^2_2 = 11.2$	***

Table 5.5 Attack strategy of *O. schellenbergii* and *C. nasalis* females against larger prey (fourth instar caterpillar).

Predator Species	Captures	Distribution of Probes Near head	 Middle	 Posterior	Chi-square	Probability
O. schellenbergii ♀	36	21	5	10	$\chi^2_2 = 11.1$	***
C. nasalis ♀	13	9	0	4	$\chi^2_1 = 1.9$	n.s.

* - $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$ n.s. non significant

numbers captured from each size class were not statistically significant ($P > 0.05$). However, this may be due to relatively small sample size.

Furthermore, males of two species were relatively incapable of handling large prey mainly due to the latter's strong retaliation. After many unsuccessful attacks, they started to avoid large prey and to turn towards medium sized prey. Nevertheless, head-waving movement of large prey (fourth instar caterpillar) was a continuous source of distraction and disturbance to predators that were about to probe and capture small prey. This distraction often resulted in the escape of small prey which may otherwise have been captured. Mori and Chant (1966) noted a similar phenomenon with the predatory mite, *Phytoseiulus persimilis*, which gave up even captured prey when other prey bumped into the predator.

5.3.1 Injury induced mortality

A large percentage of large prey (fourth instar caterpillars) that were successful in avoiding captures after they were attacked nevertheless died within 48 hours. Mortality was higher among the larvae attacked by females of two species than the males (Table 5.6).

Table 5.6. Injury induced mortality in escaped large prey (fourth instar caterpillars).

Species	Sex	n	No. died	% mortality	n	Control death
O. schellenbergii	♀	20	12	60.0	20	-
	♂	20	4	20.0	20	-
			$\chi^2_1=4, P=0.05$			
C. nasalis	♀	20	15	75.0	20	-
	♂	20	9	45.0	20	-
			$\chi^2_1=1.5, P>0.05$			

However, mortality due to sex was only significantly different in the case of *O. schellenbergii* ($P = 0.05$) and not so, for *C. nasalis* (Table 5.6). There was no mortality among the controls. Dying larvae showed characteristic signs and displayed certain behaviour patterns seldom observed in normal larvae. The area around the probe site turned bluish green, larvae appeared restless and showed violent movements such as head-waving, squirming and occasional scratching of the probed area with mandibles. This violent activity gradually subsided into a state of paralysis followed by death. The larvae that died seldom took any food. However, the ones that were able to withstand predator attacks started feeding in a few hours time. Marston *et al.* (1978) observed a similar pattern of morbidity among several lepidopterous larvae that were attacked by *Podisus maculiventris* (Hemiptera : Pentatomidae) but escaped.

Both species of pentatomid predator appeared to pursue the escaped prey for some distance and reattack. This behaviour may be related to the weakened physiological condition of the prey and hence the less energetic resistance it offers or it may be no more than a response to the rapid and violent movements of the prey that make it more conspicuous among its conspecifics.

5.3.2 Influence of caterpillar first captured on second capture

The females of *O. schellenbergii* that captured small or medium sized caterpillars tended to capture any type of prey encountered in the subsequent captures (Table 5.7). Thus the prey first captured and eaten did not appear to influence the second capture.

Females tended to attack large prey almost every time after eating the medium sized prey.

Table 5.7. Type of prey captured in second captures after feeding on small or medium sized prey by female *O. schellenbergii*.

n	Small	Medium	Large	
10	0	4	6	$\chi^2_1 = 0.4$, n.s.

5.3.3 Effects of the probe site and predator size on immobilisation time

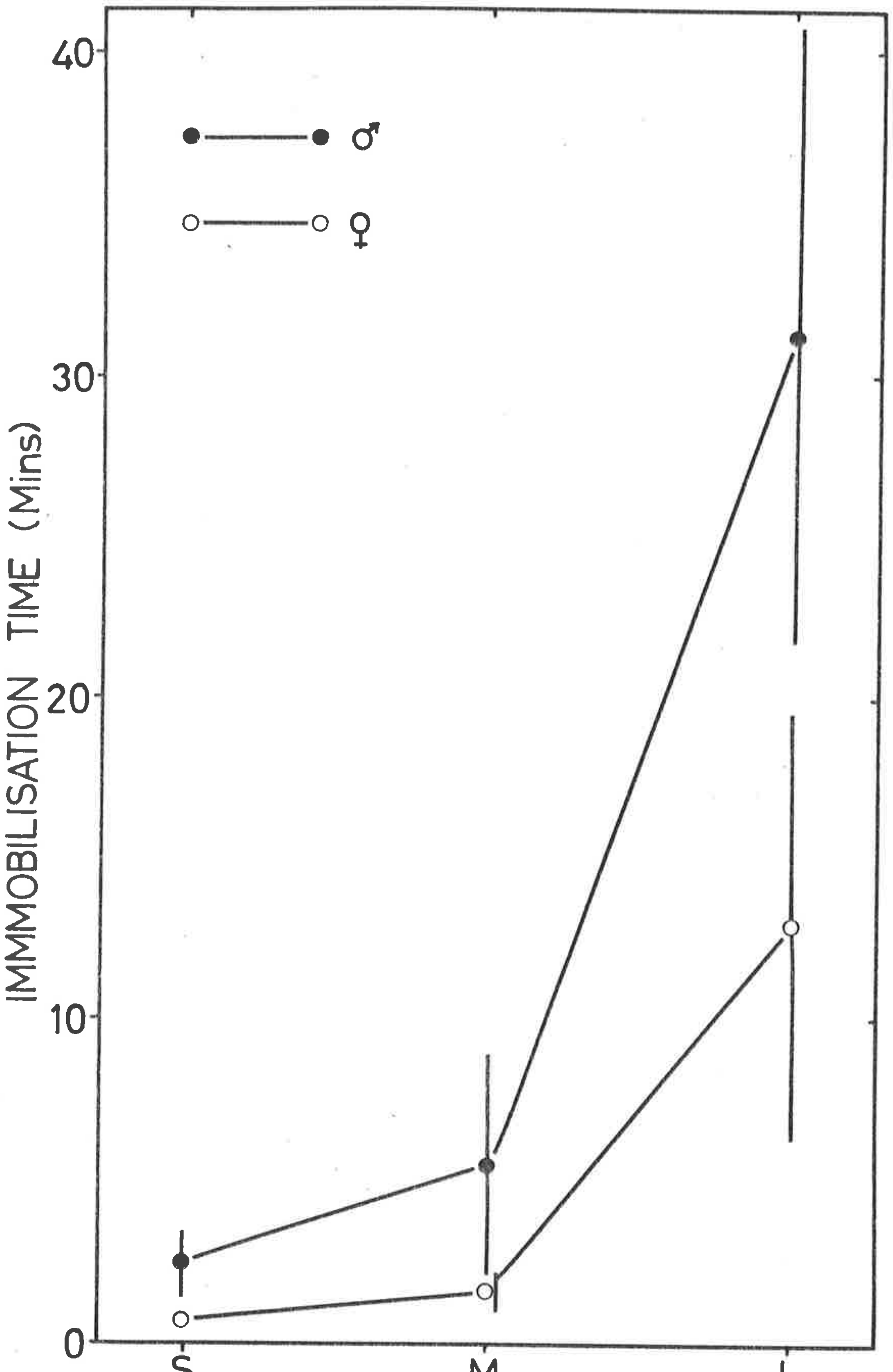
Probe site appeared to have a significant influence on the immobilisation of fourth instar caterpillar (Table 5.8).

Table 5.8. Interaction between probe site and immobilisation time of adult *O. schellenbergii* against fourth instar caterpillars.

Species	Sex	n	Probed close to head	$\bar{x}$ immobilisation time in mins ± S.D.	Probed at rear	$\bar{x}$ immobilisation time ± S.D.
O. schellenbergii	♀	25	18	9.2 ± 1.5	7	22.6 ± 5.0
	♂	25	9	20.0 ± 2.7	16	37.8 ± 4.7
				t=8.3, P<0.01		t=7.0, P<0.01

Caterpillars probed near the head were rapidly immobilised by males and females as compared to the ones attacked at the rear. Females took significantly less time ($P < 0.01$) than males in immobilising fourth instar caterpillars whether attacked near head or attacked at the rear end.

Fig. 5.1 Immobilisation time (mean ± S.D.) of adult male and female *O. schellenbergii* against small, medium and large *H. punctiger* larvae. (S = second instar, M = third instar and L = Fourth instar caterpillars).



♂
♀
IMMMOBILISATION TIME (Mins)
40
30
20
10
0
S
M
L
CATERPILLAR STAGE

Moreover, females' immobilisation time was significantly less ($P < 0.01$) against caterpillars of each size class than males (Figure 5.1).

5.4 DISCUSSION

Two factors appear to influence the capture of prey by *O. schellenbergii* and *C. nasalis* adults: (1) the size relationship between predator and prey, and (2) prey distribution. Predator-prey size interactions determine 'catchability' of the prey by *O. schellenbergii* and *C. nasalis*. Any study of the food preferences of predators, unless it considers prey 'catchability' (Ivlev, 1961; Emlen, 1968) does not represent actual field conditions. Rapport (1971) argued that such studies must take into account the basic parameters of prey 'catchability', the attack strategy of the predator, and the availability of the protective cover to the prey.

A greater number of attacks on large prey (Table 5.1) following representation of medium-sized prey, is in agreement with the postulates of the theory of 'optimal diets', according to which organisms tend to maximise energy intake/unit effort. This is the common argument advanced by several authors (e.g. Schoener, 1969; MacArthur, 1972; Charnov, 1973; Timin, 1973; Pearson, 1974; Pulliam, 1974; Werner and Hall, 1974). Some studies have also demonstrated that animals select their prey on the basis of their profit ability (e.g. Kear, 1962; Menge and Menge, 1977).

The capture of small and medium-sized prey may in part be due to an inability of predators to capture large prey as a consequence of the energetic defenses of the latter (Morris, 1963); in other words, when predators failed to overcome strong retaliation of large prey they turned towards small prey that were more 'catchable'. Thus, differences in prey defenses can make predators selectively prey on species with less powerful defenses.

Murdoch and Marks (1973) noted that *Coccinella 7-punctata* (Coleoptera : Coccinellidae) preyed mainly on *Aphis fabae* when given choice between *A. fabae* and *Acyrthosiphon pisum*, not because of any real preferences or because of differences in the prey availability, but simply because of the latter's greater ability to escape. Bass and Shepard (1974) demonstrated that selective predation by *Sycanus indagator* (Hemiptera : Reduviidae) on *Galleria mellonella* as compared with *Spodoptera frugiperda* was due mainly to the latter's ability to avoid captures by using potent defense ploys and the former's inability to do so.

Furthermore, prey 'catchability' is perhaps also responsible for Cooper's (1979) observations. He reported *O. schellenbergii* and *Nabis tasmanicus* (now known as *T. nigrolineatus*) feeding on large virus-killed caterpillars of *H. punctiger*. My field observations support his contention. Often several second stage *O. schellenbergii* and *C. nasalis* were found feeding on large sick or virus-killed prey, of a size that the predators at such an early stage would have been unable to capture had the prey been healthy. This particular behaviour pattern brings them close to Slobodkin's (1968) concept of prudent predator, although it is very doubtful that they actually seek out the sick, old or enfeebled prey as some vertebrate predators do. Nevertheless, Glen

(1973) reported *Blepharidopterus angulatus* (Hemiptera : Miridae) preying upon parasitised aphids when healthy prey were scarce, and Dixon and Russel (1972) observed a similar phenomenon in *Anthocoris confusus* (Hemiptera : Anthocoridae).

Since the large prey occupied positions on top of lucerne stems, where most of the predators did their searching, this spatial distribution of the prey on plants may, in part, be responsible for greater frequency of contact and hence greater number of attacks on large prey. Furthermore, the head movement of large prey may attract predators from a greater distance. It has been demonstrated that *O. schellenbergii* respond to the movements of the caterpillars (Chapter 6).

Mortality among the large caterpillars that escaped an attack after its initiation may be due to the neurotoxins or salivary secretions that were injected into prey's body. The differential mortality observed may be due to different amounts of secretions poured into prey by female and male predators (cr. 5.3.3) or possibly due to their different attack strategies. This injury-induced mortality is an important factor that contributes significantly to prey mortality, apart from actual consumption of prey by predators. Tothill *et al.* (1930), Prebble (1933), Mukerji and LeRoux (1965), suggested that hemipterous predators probably inject poisons into prey when they attack them, and some larvae that escaped after attacks died subsequently, indicating that some toxin was involved. Anderson (1961) (in Evans, 1976) provided supportive evidence and showed that salivary secretions of predatory bugs had a paralysing effect on prey. He demonstrated that an aphid once attacked but separated quickly from an anthocorid did not survive, but an aphid wounded by a fine pin continued to live and feed.

The total absence of small prey (second instars) in the captures of *C. nasalis* females and the poor representation of small caterpillars in the captures of other predators may be a behavioural adaptation related to the fact that small prey are unprofitable to predators. For small prey sizes, the order of the rank of profitability may be the same as the order of the size of the prey (Werner & Hall, 1974; Elner and Hughes, 1978). Many authors have reported a total or near total lack of prey below a certain size from the diets of birds, lizards and fish (Root, 1967; Andrews, 1971 Sexton *et al*., 1972).

Results of this study are in general agreement with previous observations reported by several authors (e.g. Dixon, 1958; Dixon and Russel, 1972; Glen, 1973, 1975; Wratten, 1973; Evans, 1976). However, present observations do not agree with some of the Tostowaryk's (1971) observations on *P. modestus* (Hemiptera : Pentatomidae). He noted that adult predators retreated after one unsuccessful attack and they attacked any part of the prey body. This did not occur in *O. schellenbergii* and *C. nasalis,* which continued attacking large prey several times, and females of both species selectively attacked the anterior part of the prey.

CONCLUSION

Present observations support the results obtained in previous experiments and demonstrate that adults of *O. schellenbergii* and *C. nasalis* tend to prey selectively upon medium-sized prey. Prey 'catchability' is the main constraint that prevents them feeding on large prey and large prey infected with a viral pathogen may be attacked if their defensive strategies are attenuated.

6. SEARCHING BEHAVIOUR OF *O. SCHELLENBERGII*

6.1 INTRODUCTION

Searching behaviour of entomophagous insects has been the subject of many investigations and, as a result, many mathematical models have been proposed (e.g. Nicholson, 1933; Holling, 1959; Watt, 1959; Hassell and Varley, 1969; Rogers, 1972; Hassell and May, 1974). These models assumed, directly or indirectly, that entomophagous insects encounter their hosts or prey at random. Nevertheless, experimental evidence indicates that this is not true in many cases.

Studies in the last decade or two have shown that many entomophagous insects are attracted towards hosts or prey from considerable distance and that they use very sophisticated means to achieve this. Some entomophages search for habitats where they are most likely to find their hosts or prey.

(1) Search for habitat:- Location of suitable habitat is accomplished either by (i) vision or (ii) olfaction.

(i) Vision:- There are few reported cases of entomophages locating suitable habitats by visual cues; for example syrphid and chrysopid adults have been shown to be attracted to different colours and respond to flowers visually (Ickert, 1968; Schneider, 1969).

(ii) Olfaction:- Olfaction appears to be the main means of habitat location (from a distance) by many entomophages. For instance, predators of barkbeetles respond to the aggregation pheromone of their prey (Camors and Payne, 1973). The aphidophagous coccinellid, *Anatis ocellata* is attracted towards the aromatic substances emanating from pine needles (Kesten, 1969). *Chrysopa carnea* is attracted towards honeydew, and locates it by anemotaxis (by flying upwind towards the source (Hagen *et al.*, 1971)). Furthermore, artificial honeydew has not only proved successful in attracting chrysopids to fields, but also in retaining them there (Hagen *et al.*, 1971; Hagen and Tassan, 1972).

This is also true for several insect parasites. For instance, *Nemeritis canescens* responds to the aggregation pheromone of its host, *Ephistia cautella* (Corbet, 1971), so does the parasite *Aphitis melinus* to its hosts coccids (Sternlicht, 1973). Ullyett (1953) demonstrated that the parasite *Pimpa bicolor* reacted strongly to the damaged cocoons of its host *Euproctes terminalia*.

Once in a suitable habitat, entomophagous insects must find their hosts or prey and this is accomplished in a variety of ways. Some use vision, as *Vespula germanica* (Kartsev, 1979). Movement is known to be an important cue to searching entomophages. Thus, *Bracon hebetor* discovered and attacked wandering hosts, *Ephistia cautella* larvae, ten times more often than the stationary ones (Hagstrum and Smittle, 1977). Some rely on olfaction, as *Lixophaga distraeae* which follows the odours of its host's larval frass (Bennett, 1969). So does the parasite *Orgilus lepidus*, when finding its host, *Phthorimaea operculella* (Hendry *et al.*, 1973). Some use vision and olfaction as *Stomoxys calcitrans* (Gatehouse and Lewis, 1973). Others use physical characteristics of hosts or prey or their artefacts, in order to locate them. For example, the parasite *Apanteles melanoscelus* follows the silk webbing of its host *Lymantria dispar* (Weseloh, 1976), and *Solenotus begini* follows the leaf mine of its host, *Phytomyza atricornis* (Doutt, 1957).

Searching behaviour of predacious pentatomids has received little attention and reports in the literature are mainly based on qualitative observations. In this Chapter searching behaviour of *O. schellenbergii* was investigated to ascertain (i) what leads them to their prey (what cues are involved in prey finding) and (ii) what role is played by their sensory organs in the process of prey finding, and finally (iii) an estimate of their searching activity on plants and their searching capacity at very low prey density.

6.1.2 Materials and Methods:- Observations were made in a simple arena (20 cm x 20 cm). Forty adult female *O. schellenbergii*, 3-4 days old, were fed to satiation and then deprived of food for 36-48 hours. They were then divided into two lots of 20 each, and tested. The first lot was tested against a wandering fourth instar caterpillar and the second lot against stationary caterpillars. Caterpillars used in the latter part were deprived of food for 24 hours and released on lumps of artificial diet. The times predators took to locate and attack the caterpillars were recorded. Each test animal was allowed a maximum of 15 mins. searching time; predators that failed to find and attack caterpillars in this time were removed from the arena. The ones that found prey in less than the allotted time were also removed and not used again. A caterpillar was considered attacked when predators oriented and stretched their proboscides to probe it. The average time required to attack wandering caterpillars, as against stationary ones, was compared by Student's t-test. Unless indicated otherwise, tests were conducted at 28±2°C.

6.1.3 Results:- Wandering caterpillars were more susceptible to perception ($P < 0.01$) than stationary ones (Table 6.1).

Table 6.1. Time taken by adult *O. schellenbergii* to find and attack wandering and stationary caterpillars.

n	Mean time taken to attack wandering prey ± S.D.	n	Mean time taken to attack stationary prey ± S.D.
20	3.8 ± 0.8	20	8.7 ± 2.7
	$t = 7.3$		$P < 0.01$

Actual observations indicated that predators responded to the movements of the caterpillars at a short distance, oriented and moved towards them to attack them. Furthermore, wandering larvae were seldom touched by the antennae prior to attack, an indication that probably predators were perceiving the prey movement. Moreover, some caterpillars walked straight into the path of a searching predator, in which case they were readily perceived and attacked.

But in the case of stationary caterpillars, some predators appeared to perceive them after antennal contact, others perceived them at a close range without antennal contact.

6.2 INFLUENCE OF ARTIFICIAL CATERPILLAR MOVEMENT ON PREDATORS' RESPONSE

Previous experiment showed that wandering larvae were more readily perceived (cf. 6.1.3). Nevertheless, the fact that some larvae walked into a predator's path may have contributed to significant results. This experiment was designed to avoid such an interference.

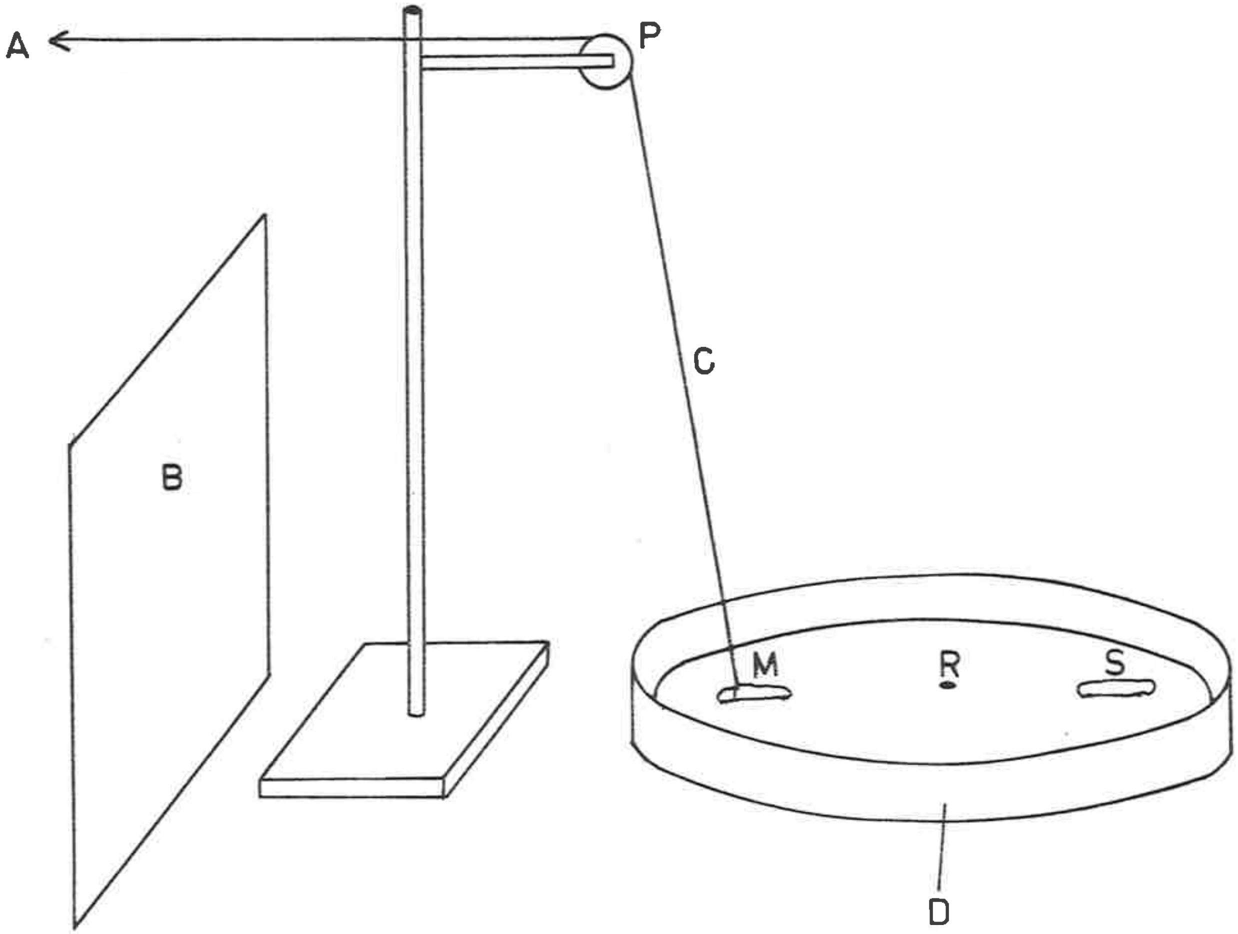
6.2.1 Methods:- Test procedure was the same as described before (6.1.2), except that caterpillars used in the tests were dead (killed in hot water). A release site was marked in the centre of the arena (R) and at an equal distance on either side two sites (M) for moving and (S) for stationary caterpillars were marked and caterpillars placed on them. The caterpillar placed on M site was tied by the neck to a thread passed over a pulley (Figure 6.1). A wooden sheet wrapped in aluminium foil was placed between the arena and operator. One predator was released at point R and a caterpillar at point M was pulled up and down to simulate the head lifting movement of the caterpillars. Numbers successful in finding either prey were compared by chi-square (χ^2) test, while average times required to attack were compared by t test.

6.2.2 Results:- Larger numbers of predators oriented and attacked the moving caterpillars ($P < 0.05$) and they took significantly less time ($P < 0.01$) to perceive them than the stationary ones (Table 6.2).

Dead caterpillars were perceived, but average perception times were a little longer than those observed in Experiment 1. This may have been because of larger number of replicates, or restrained prey

Fig. 6.1 Predatory response of *O. schellenbergii* to artificial prey movements.

A = Operator.
B = Wooden sheet.
C = Cotton thread.
D = Arena (simple petri dish).
M = Moving Caterpillar.
P = Pulley.
R = Predator release site.
S = Stationary caterpillar.


A
P
B
C
M
R
S
D

movement, or possibly because dead caterpillars were less attractive to predators, or artificial movement was not similar to natural movement. Despite this, a significant response (Table 6.2) to artificially moved caterpillar demonstrates that prey movement is important in prey perception.

Furthermore, it appeared that within a certain distance, even stationary caterpillars were vulnerable to attacks and as observed before (cf. 6.1.3), some predators perceived them without antennal touch. Thus, the possibility of involvement of olfaction in prey location by *O. schellenbergii* exists and needs further investigation.

Table 6.2. Influence of artificial movement on predator's response.

n	Predators responding to moving prey	Responding to stationary prey	Mean time taken to attack	
			Moving prey	Stationary prey
50	33	17	5.0 ± 1.7	9.3 ± 3.7
	$\chi^2_1 = 5.1$, $P < 0.05$			($t = 5.5$, ($P < 0.01$

6.3 RESPONSE OF *O. SCHELLENBERGII* TO LARVAL FRASS

6.3.1 Methods:- The test procedure was same as described above (6.1.2), except that the size of the arena was reduced (65 mm plastic petri dish) and searching time was reduced to 5 mins. per predator. One lot of 20 predators were individually exposed to larval frass. In controls, predators were exposed to artificial diet granules. Numbers in the two groups that contacted frass and diet granules and the numbers that probed these materials were compared by chi-square test.

6.3.2 Results:- Almost similar numbers of predators encountered the frass and diet granules ($P > 0.05$). However, significantly large numbers of predators probed the frass (Table 6.3), while none probed the artificial diet granules.

Table 6.3. Predators' response to larval frass.

n	Contacted frass	Probed frass	n	Probed artificial diet	Probed diet
20	17	13	20	15	0

$\chi^2_1 = 4.7, \quad P < 0.05$

Predators showed normal predatory behaviour on encountering frass and repeatedly probed it. Furthermore, they showed increased turning movements and searched the adjacent area more intensively before walking away from the frass. This did not occur in controls. Predators that contacted artificial diet pellets palpated them with the antennae and turned away.

6.4 INFLUENCE OF THE COMPLEXITY OF THE SEARCHING UNIVERSE ON THE PREY-FINDING CAPACITY OF *O. SCHELLENBERGII*

6.4.1 Methods:- A honeycomb-like structure of plastic material (Figure 6.2) with 84 individually numbered cells was placed in a

Fig. 6.2 Honeycomb like complex arena (with individually numbered cells(1-84) used in tests to evaluate the effects of complex searching conditions on the searching ability of adult *O. schellenbergii*.

simple arena. The empty space around the edges of the honeycomb was filled with wax. One 24 hour fasted fourth instar caterpillar was placed on a lump of artificial diet in a cell chosen at random and a predator was released in another. Predators were allowed a maximum of 1 hour to find and attack the caterpillar. Tests were replicated 30 times.

6.4.2 Results:- Results of this experiment are presented in Table 6.4. Complexity of the searching arena had a great deal of effect on a predator's average time to find prey (Table 6.4), as compared with predators searching in a similar but simple arena (cf. 6.1.3). However, the numbers that found prey and the ones that failed to find them were not significantly different ($P > 0.05$)

Table 6.4. Effect of complex arena on searching capacity of predators.

n	Predators successful	Failures	Average time taken by successful predators to find prey
30	19	11	43.5 min

$\chi^2_1 = 2.1, \quad P > 0.05$

Search pattern of *O. schellenbergii* appeared undirected, until they reached the edge of the cell containing the caterpillar, or the cell adjacent to it; from there on searching activity tended to be directed and intense. Furthermore, searching predators that came within one cell of a caterpillar seldom failed in locating it. This substantiates the results of previous experiment that *O. schellenbergii* also uses olfactory cues in locating its prey and that this signal is perceptible at a close range.

6.5 ASSESSMENT OF ROLE OF EYES AND ANTENNAE IN PREY PERCEPTION OF *O. SCHELLENBERGII*

6.5.1 Methods:- Test procedure was similar to that described in 6.1.2, except that test animals used had their sense organs impaired. After satiation, predators were placed on ice cubes, anesthetized and treated as described by Storch (1976), that is eyes and ocelli were painted with gloss enamel paint and antennae with a nail polish. Animals with one eye and ocelus painted, one antenna painted were compared with normal predators. Data were analysed by analysis of variance.

6.5.2 Results:- Predators' searching ability was impaired by the treatments and they took significantly more time ($P < 0.05$) to locate and attack prey than normal predators (Table 6.5). But the difference between normal predators and those with one eye painted did not appear to be significant (Appendix 9). This indicates that loss of an antenna appeared to impair prey finding capacity more than the loss of vision on one side.

Table 6.5. Prey perception by predators with one eye and one antenna obstructed.

Predators with one eye and ocelus painted			Predators with one antenna painted			Normal		
n	successful	Mean time in mins	n	successful	Mean time in mins	n	successful	Mean time in mins
10	10	7.6	10	10	11.6	10	10	4.5

$F = 8.83$, $P<0.05$

6.6 ASSESSMENT OF INFLUENCE OF OBSTRUCTION OF BOTH EYES AND BOTH ANTENNAE ON PREY FINDING CAPACITY OF *O. SCHELLENBERGII*

6.6.1 Methods:- The methods were the same as described before (6.1.2), except that records were also maintained of the probing sites of predators.

6.6.2 Results:- Results of this experiment are presented in Table 6.6.

Predators' searching ability was impaired in that although they captured similar numbers of caterpillars, their average attack times were increased.

Furthermore, observations on probe sites indicated that predators with both eyes painted failed to differentiate between the anterior and posterior end of caterpillar and hence their probes were evenly distributed ($P > 0.05$). But predators with both antennae impaired, like normal predators, attacked the anterior end of caterpillars ($P < 0.05$). Moreover, several observations on the attack behaviour of predators with painted eyes showed that their proboscides often missed the prey and passed above the latter's body. This seldom occurred in predators with painted antennae or normal ones. Hence vision is not only important in detecting prey movement at a distance, but it is also important in the final act of probing at close range.

6.7 ASSESSMENT OF THE PREY-FINDING CAPACITY OF PREDATORS WITH OCELLI, BOTH EYES, AND BOTH ANTENNAE OBSTRUCTED

6.7.1 Methods:- The methods were the same as described before (6.1.2), except that predators were allowed 30 minutes searching time.

Table 6.6. Prey finding ability of predators with impaired sense organs and distribution of their probe sites against the body of prey.

Predators with both eyes obstructed						Predators with both antennae impaired						Normal predators					
n	Success-full	Distribution of probes			$\bar{x}$ time	n	Success-full	Distribution of probes			$\bar{x}$ time	n	Success-full	Distribution of probes			$\bar{x}$ time
		Ant.	Mid	Post				Ant.	Mid	Post				Ant.	Mid	Post	
30	26	9	5	11	10.4	30	26	16	1	8	14.1	15	15	11	-	4	5.4
	$\chi^2_2 = 2.1$	$P > 0.05$					$\chi^2_2 = 13.1$	$P < 0.01$					$\chi^2_2 = 4.0$	$P < 0.05$			

6.7.2 <u>Results</u>:- Searching capacity of predators was dramatically reduced (Table 6.7). Only two predators attacked caterpillars and on average they took longer to do so. Furthermore, treated predators showed an unusual search pattern not observed before; they moved about with the proboscis extended, stroking it along the floor of the petri dish, and on one occasion the proboscis accidentally touched the caterpillar which was attacked and captured. But this searching activity was sporadic and did not last for long. Moreover, on one occasion a caterpillar walked into the predator, which touched the caterpillar with its front tarsi, then stretched out the proboscis and attacked it.

Table 6.7. Prey perception by predators with both eyes and antennae obstructed.

n	Predator's condition	Successful	Mean time (min)
10	impaired	2	24.5
10	normal	10	4.9
		$\chi^2_1 = 5.3$, $P < 0.05$	$\chi^2_1 = 13.0$, $P < 0.01$

This indicates that receptors on the proboscis and tarsi can partially compensate for loss of the antennae.

6.8 ASSESSMENT OF THE IMPORTANCE OF SPEED OF PREY IN PREY PERCEPTION BY *O. SCHELLENBERGII*

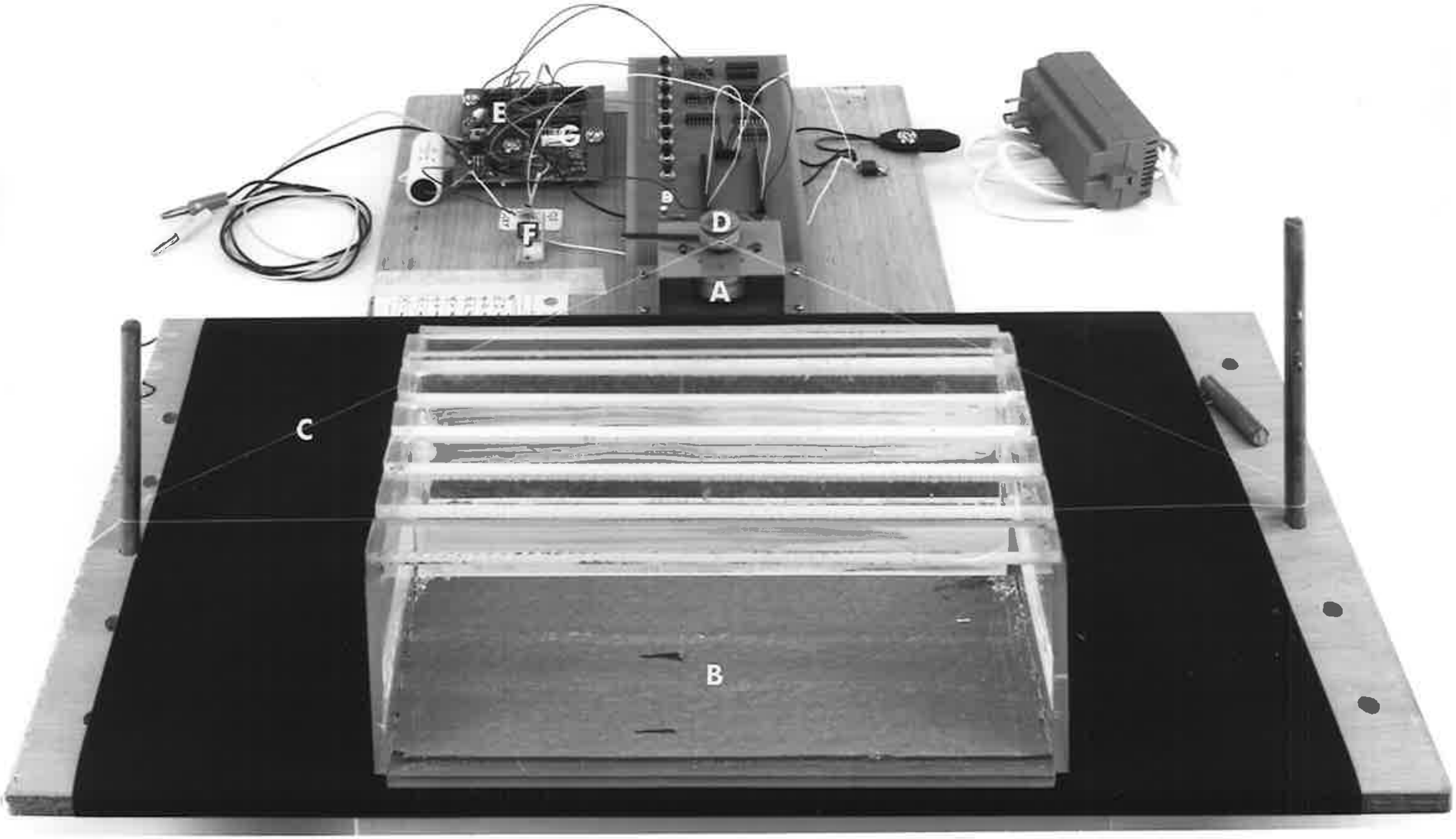
6.8.1 <u>Methods</u>:- Female *O. schellenbergii* were prepared for tests as described before (6.1.2). The speed of movement of the caterpillar was controlled and manipulated by a reversible stepping motor (with a wide range of pulses from 1-255) connected to a pulse generator (Figure 6.3).

A simple box-like arena (26 cm x 14 cm) made of perspex sheets was used in the tests. The box was left open at the front and its top was lined with 1.5 cm wide and 14 cm long perspex bars, with a small gap between the two adjacent bars. Thus, when a vertical sheet was passed through these gaps the size or width of the arena could be reduced to 2, 4, 6 and 8 cms (Figure 6.3). An endless cotton thread was passed around the poles and through the side walls of the arena near the base. A freshly killed fourth instar caterpillar was attached to the thread. Side walls of the arena were coated with a strip of "fluon" in order to prevent predators climbing the walls of the arena. Position of the caterpillar was adjusted so that it moved forward and backward in the centre of the arena and covered a distance of 20.6 cms either way; thereafter one unfed predator was released at a common marked site and a vertical sheet lowered after it. Preliminary observations indicated that predators responded to prey movement at short range 2-3.5 cms, hence the smallest size (2 cms) of the arena was chosen for the experiment, and thereby the maximum possible response was expected. The caterpillar was moved forward, back and then forward again and the predator's response to its speed was tested. Thus, a batch of 10 predators was tested at various speeds, starting with 0, 0.12 cms/sec, 0.25 cms/sec, 0.39 cms/sec, 0.51 cms/sec, 0.64 cms/sec and 0.7 cms/sec (0.12 was the lowest possible speed).

Data were analysed by regression analysis and a line plotted according to regression equation.

Fig. 6.3 Stepping motor with electric gadget and box-like arena used in evaluating the predatory response of *O. schellenbergii* to caterpillars moving at different speeds.

A = Stepping motor.
B = Box-like arena.
C = Cotton thread.
D = Pulley.
E = Electric gadget.
F = Reversible switch.
G = Micro-switchboard (to increase or decrease the number of pluses).


E
G
F
D
A
C
B

6.8.2 Results:- Predators showed a maximum response to the slowest-moving caterpillars (i.e. at a speed of 0.12 cms/sec) and displayed their normal predatory behaviour. But, as the speed of caterpillar increased the predator's response decreased, until a point was reached where predators failed to respond at all (Figure 6.4).

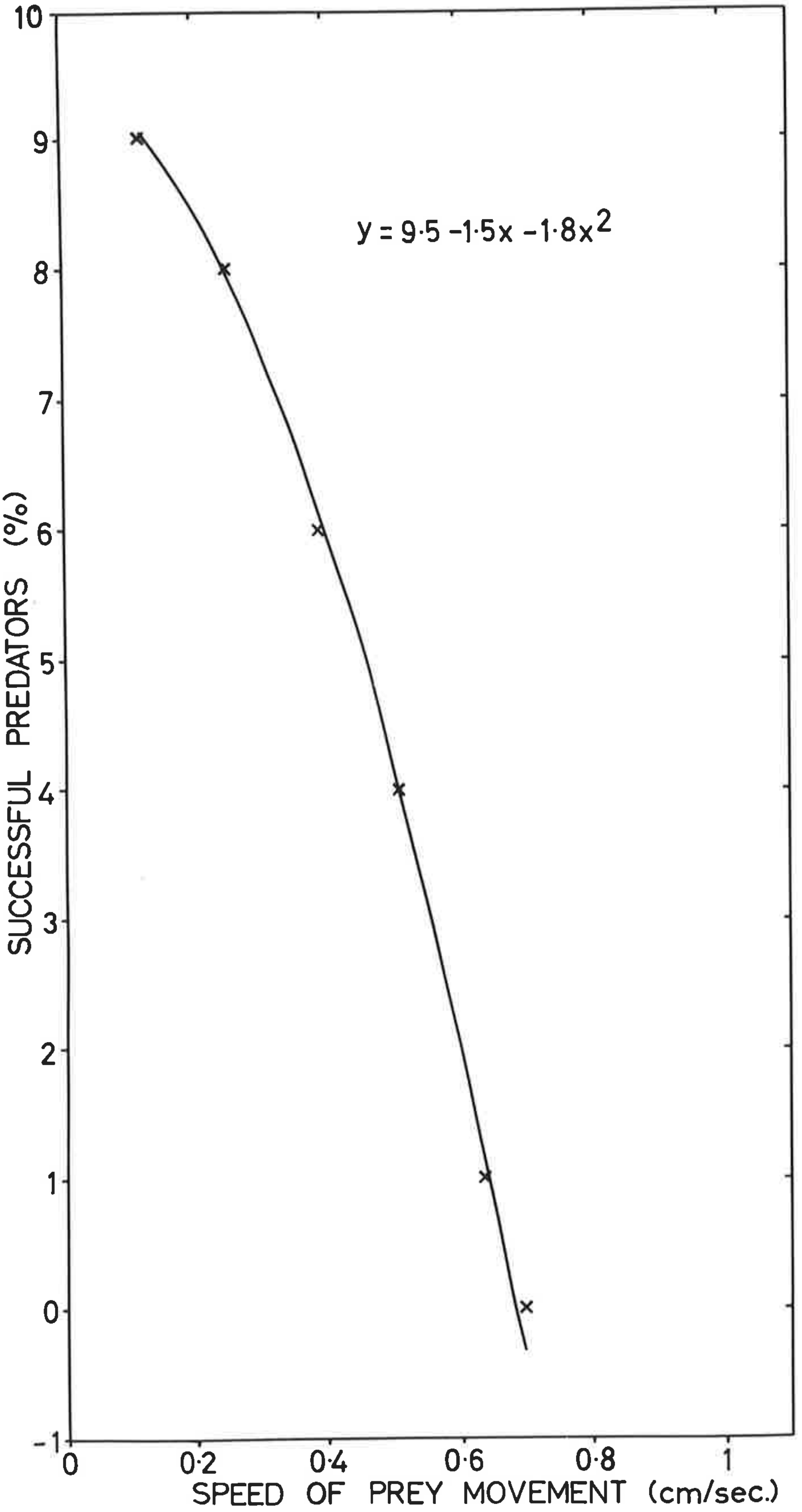
Furthermore, a predator's behavioural response changed as the caterpillars became fast-moving (0.7 cms/sec). Predators often oriented towards the caterpillar, raised their antennae but seldom approached closer to attack the prey.

Conclusion:- By integrating the results of experiments on normal predators and on predators with impaired sense organs, it is concluded that *O. schellenbergii* perceives its prey by olfaction as well as vision. Olfaction works at a distance and so does vision, especially when the prey is moving at a slow speed. Furthermore, vision also plays an important part, at close range, in the final act of probing prior to attacks.

6.9 DISCUSSION

O. schellenbergii appeared to be using olfaction and vision in prey detection. Their searching behaviour was similar to *Podisus modestus* (Morris, 1963) and *P. maculiventris* (Tostowaryk, 1971). Like these predacious pentatomids, *O. schellenbergii* were engaged in active search and mainly stalked their prey, but occasionally showed a behavioural response that was similar to 'ambush'. It is the general conclusion of several authors that ambush and true-hunting predators

Fig. 6.4 Predatory response of female *O. schellenbergii* to dead but artificially moved fourth instar caterpillar at different speeds.


y = 9·5 −1·5x −1·8x²
SUCCESSFUL PREDATORS (%)
SPEED OF PREY MOVEMENT (cm/sec.)
10
9
8
7
6
5
4
3
2
1
0
−1
0
0·2
0·4
0·6
0·8
1

mainly rely on vision in prey location, e.g. Mantids (Mittlestaedt, 1957; Holling, 1966); Odonata (Corbet, 1962); Heteroptera like *Zelus* (Edwards, 1966; Ables, 1978), Hemiptera like *Podisus* (Morris, 1963) and *Notonecta* which are also responsive to vibrations (Ellis and Borden, 1970); many aculeate wasps (Evans and Eberhard, 1970) asilids (Lavigne and Holland, 1969); cicendelids (Balduf, 1935); dyticids (Young, 1967); and spiders (Turnbull, 1973); likethomicids (Haynes and Sisojevic, 1966); lycosids (Anderson, 1974) and salticids (Horner and Starks, 1972).

Prey movement, natural or artificial, appeared to induce predatory behaviour in *O. schellenbergii*. Prey movement has been demonstrated to be the source of prey perception by many predators like *Zelus exsanguis* (Edwards, 1966); *Platymerus rhadamanthus* (Edwards, 1962b); *Rhinocoris bicolor* and *R. tropicus* (Parker, 1969); *Vestula lineaticeps* (Parker, 1971); *Z. renardii* (Ables, 1978); *P. maculiventris* (Iwao and Wellington, 1970; Marston *et al.*, 1978) and the robberfly, *Proctacanthella leucopogon* (Shelly and Pearson, 1980).

Inability of blinded predators to probe the caterpillar in the first attempt (e.g. passing of the proboscis above the caterpillar's body), and the random nature of their probe sites in contrast to bugs with unobstructed eyes, demonstrates the involvement of vision at close range in the act of probing. The visual predator *Z. renardi* also tends to attack large caterpillars close to the head (Ables, 1978).

Detection of prey by treated predators through physical contact with the protarsi indicates a role for tarsal mechano-receptors. Several coccinellids are known to perceive their prey by mechanoreception, by touching the prey either with their legs or their mouth parts (Fleschner, 1950; Banks, 1955, 1957; Dixon, 1959, 1970; Kaddou, 1960; Murdoch and Marks, 1973; Storch, 1976). However, Allen *et al.* (1970) and Mary Stubbs (1980) have demonstrated that some occinellids are able to perceive their prey by olfaction and vision prior to physical contact.

Undirected and unusual search pattern of some treated predators in which the proboscis was stretched and tapped against the floor of the arena, and the occasional accidental contact between proboscis and prey that resulted in capture, indicates employment of mechanoreceptors at the tip of the proboscis. Some anthocorids have been reported to find their prey either by contact with antennae or by rostrum (e.g. Dixon and Russel, 1972; Madsen, 1961; Evans, 1976). This is also true of the mirid predator, *Blepharidopterus angulatus* (Glen, 1973; 1975).

The similar way of approaching prey employed by predators either with both eyes impaired or without treatment, and the display of frequent turning movements and intensive searching close to a hidden caterpillar in the complex arena, points to the presence of a chemical signal that works at close range. Predators are known to make use of such chemical signals. For instance, airborne kairomones of *Heliothis zea* stimulate searching in *Chrysopa carnea* larvae (Lewis *et al.*, 1977).

Nordlund *et al.* (1977) demonstrated the presence of another kairomone in egg deposition material that stimulated feeding in *C. carnea*.

Furthermore, investigation and repeated probes against larval frass strengthens the evidence already gathered in support of a chemical signal being involved in prey perception by *O. schellenbergii*. Predators' responsiveness to larval frass and subsequent heightened activity in that general area may have important ecological consequences, and may lead predators to caterpillars partially or completely buried in lucerne fruits, flowers and buds. McLain (1979) in a recent study demonstrated that predacious pentatomids, *Euthyrhynchus floridanus*, *Alcaeorrhynchus grandis* and *P. maculiventris*, when given a choice between frass, hemolymph and water trails, showed greater response to frass trails followed by hemolymph trails and no response to water trails. On encounters with frass and hemolymph trails predators tapped them with antennae and probed them.

Results of the present study are in general agreement with the results of earlier workers (e.g. Morris, 1963; Mukerji and LeRoux, 1965; Tostowaryk, 1971; Marston *et al.*, 1978).

6.10 ASSESSMENT OF DISTRIBUTION OF WITHIN PLANT SEARCHING ACTIVITY OF *O. SCHELLENBERGII*

6.10.1 Introduction:- Some predators and parasites are known to search particular parts or areas of plants more vigorously than others, presumably in relation to the spatial location of their hosts or prey. Such localised searching activity brings them close to their hosts or prey and enhances their chances of finding them. Thus, the parasite *Trichogramma nubilale* concentrates its search in the middle of the corn plant, a site preferred by its host, *Ostrinia nubilalis* (Burbutis *et al.*, 1977). Similarly, the damsel bug, *Reduviolus roseipennis* (Hemiptera : Nabidae) spends most of its searching time in the upper third of the cotton plant (Donahoe and Pitre, 1977), and this corresponds with egg placement sites of *Heliothis* moths (Galindo-Toro, 1975) and their subsequent larval activity (Kincade *et al.*, 1967).

Orius tristicolor (Hemiptera : Anthocoridae) spends most of its searching time on inflorescences, a site where it not only finds its prey, but also pollen, which serves as a supplementary food (Aguilar and Ehler, 1977). Dixon and Russel (1972) found that immature stages of *Anthocoris confusus* spent 34 percent of their time on the veins rather than on the interveinal areas of the leaves; since 78 percent of the sycamore aphids were found on the veins, the tendency of juvenile anthocordis to search on veins enhanced their chances of finding prey.

However, Wilson and Gutierrez (1980) studied the within plant distribution of predators, *Geocoris pallens* and *G. punctipes*, *Nabis americoferous* and *Chrysopa carnea* on cotton, and concluded that adult predators were generally found higher on plants than their juveniles. This was in contrast to the activity of their prey, which usually occurred on lower parts of the plant.

Plant topography reportedly influences the searching behaviour of some predators. Some spend relatively more time searching edges and veins, and return to search them more than once (Dixon, 1959, 1970;

Bansch, 1966; Dixon and Russel, 1972). Nevertheless, Murdoch and Marks (1973) demonstrated that *Coccinella septempunctata* larvae, although they made thorough searches of most leaves and stems, largely avoided repeated visits to the same area. Marks (1977) suggested that this was due to a chemical marker, secreted through the anal disc and specific to each *C. septempunctata* larva, that helped them to recognise the areas already searched, and hence prevented waste of searching time. Dixon (1959) showed that coccinellids exhibited a negative geotaxis, and hence tended to move upwards on the plants. However, this response tended to weaken gradually with fasting and eventually predators moved off the plants.

Field observations indicated that female *O. schellenbergii* laid their eggs in the upper part of the lucerne plants, and first and second stage juveniles were also seen in that general area. Searching behaviour of predacious pentatomids on plants has not been investigated before, and so observations were made on their within plant searching behaviour.

6.10.2 Materials and Methods:- Lucerne stems 10-12 cms high prepared as described earlier (4.2.2, voracity experiment) were marked into three sections of equal length and designated as base, middle and top.

Fourth stage *O. schellengergii* were obtained from the stock culture immediately after moulting and deprived of food for 24-36 hours at 28 ± 2°C. They were released on stems near the base and allowed to search the plants until they walked off. The amount of time they spent in each section and the number of visits to each before abandoning the plants were recorded.

6.10.3 Results and Discussion:- Predators searched every part of the stem and spent about the same amount of time in each section (Table 6.8). Furthermore, the number of visits to each section was similar ($P > 0.05$). It was observed that predators searched the greatest area of the plant during their first exploration of it; and they spent less time in each part on subsequent visits. Dixon (1958) reported similar searching behaviour of *Adalia bipunctata* (Coleoptera : Coccinellidae).

Table 6.8. Within plant searching activity of fourth instar stage *O. schellenbergii* at 27°C.

	Base		Middle		Top	
n	Mean time in mins ± S.E.	Visits	Mean time in mins ± S.E.	Visits	Mean time in mins ± S.E.	Visits
10	15.8±5.2	25	13.2±6.4	29	19.2±5.8	32

$\chi^2_2 = 0.9$, $P > 0.05$ for number of visits to different sections

6.11 ASSESSMENT OF THE PREY FINDING CAPACITY OF FOURTH STAGE *O. SCHELLENBERGII* AT VERY LOW PREY DENSITY UNDER RELATIVELY SIMPLE SEARCHING CONDITIONS

6.11.1 Methods:- Ten lucerne stems 16-18 cms long were prepared as mentioned above (4.2.2). Some of their leaves were then removed at random so that each stem had a predetermined number of large leaves, namely 75, 78, 86, 89, 91, 95, 97, 105, 110 and 115, together with a few terminal smaller leaves. One second instar caterpillar was released at the top of each stem and allowed 10 minutes to settle. Then one unfed predator was released near the base of the stem and allowed one hour searching time. If it failed to find the caterpillar within this time, the predator was recorded as scoring a failure and taken off the plant; a predator that did not encounter the caterpillar and walked off the plant in less than one hour's time was also recorded as failing. The number of successful predators was noted and the time they spent searching was recorded. Their behavioural changes after encounters with caterpillars were observed. Tests were replicated 60 times at 28 ± 2°C and the data subjected to χ^2 analysis.

6.11.2 Results:- A large number of predators were able to find and capture prey ($P < 0.01$) but some failed to locate prey and some walked off the plant (Table 6.9).

Observations on the searching behaviour showed that the predators searched plants at random until they had approached a caterpillar, to within approximately twice the length of their antennae. At this range, the predator oriented towards the caterpillar and moved to attack and capture it.

Table 6.9. Prey finding capacity of fourth stage *O. schellenbergii* at very low prey density under simple plant foliage.

n	No. successful	No. walked off	No. failed	Mean time ±S.E. taken by successful predators	Mean time taken by predators to walk off the plant
60	38	13	9	27.6 ± 2.3	41.8 ± 3.5

$\chi^2_2 = 24.7, \quad P < 0.01$

On five occasions caterpillars dropped on silken threads, but predators remained near the point of contact and were able to capture caterpillars when they climbed back. On a few occasions predators were seen probing the silken threads and once a partially buried caterpillar was pulled out of a lucerne bud. Thus, *O. schellenbergii* appeared efficient in finding caterpillars at very low densities, albeit under simple conditions.

6.12 EVALUATION OF THE PREY FINDING CAPACITY OF FOURTH STAGE *O. SCHELLENBERGII* AT VERY LOW PREY DENSITY AND RELATIVELY COMPLEX SEARCHING CONDITIONS

6.12.1 Methods:- In this experiment searching conditions were made complex by increasing the amount of plant foliage and stem heights to double that used in previous experiments. The rest of the test procedure was the same, and tests were replicated 40 times.

6.12.2 Results and Discussion:- The increased complexity of searching conditions led to reduced number of captures (Table 6.10, cf. Table 6.9). Nevertheless, quite a large number of predators still found and captured caterpillars. Significantly less ($P < 0.01$) predators walked off the plants, indicating that the larger amount of foliage and height of plants occupied more searching time. Even so, when numbers of successes were compared with failures these proved to be similar ($\chi_1^2 = 0.6$, $P > 0.05$). This indicates that plant foliage and stem height would limit prey finding capacity of *O. schellenbergii*, especially at very low prey densities. Donahoe and Pitre (1977) argued that larger plants with more foliage provide cover and protection to the prey on one hand and increase the searching area of the predator on the other, and this reduces a predator's efficiency.

Table 6.10. Prey finding capacity of fourth *O. schellenbergii* at very low prey density and complex searching conditions.

n	Successful predators	Predators walked off the plant	Predators failed	Mean time taken by successful predators ± S.E.	Mean time to walk off ± S.E.
40	21	3	16	39.5 ± 2.8	43.0 ± 9.2

χ^2_2 = 12.9, $P < 0.01$

7. EFFECT OF TEMPERATURE ON THE FUNCTIONAL RESPONSE OF *O. SCHELLENBERGII*

7.1 INTRODUCTION

Solomon (1949) proposed the terms functional and numerical response to describe the increase in the number of prey killed per predator per unit time in relation to increase in prey density and the subsequent increase in predator numbers (numerical response). Since the numerical response is a by-product of the functional response and arises from the effects of the consumption of prey on reproduction, immigration, emigration and mortality of the predators, so the functional response is more important in terms of predator-prey interactions (Holling, 1966).

Holling (1959a,b, 1963, 1965, 1966) gave a great deal of thought to predation and the functional response of predators, and reviewed the literature on the subject. As a consequence of this he described three basic types of functional response curves observed in a wide variety of predators. A curve with a linear rise to a plateau was designated as Type I, a curve with a decelerating rise to a plateau as Type II and an S-shaped rise to a plateau as Type III. He further argued that invertebrate predators generally show Type II response curves or, in other words, increase in the number of prey killed is inversely density dependent.

Furthermore, Holling (1965) identified and divided the components of the functional response into two categories. Those that are part of every predator-prey interaction, such as rate of successful search, the time for which predator and prey are exposed to each other, and handling time, are basic components; whilst those that occur in some situations and not in others, like hunger, learning by predators, social facilitation, and avoidance learning by prey, are subsidiary components.

Several authors have demonstrated the present of Type II response curves in many insect predators (DeBach and Smith, 1941; Burnett, 1951; Miller, 1960; Messenger, 1968; Ables, 1978; LeCato and Arbogast, 1979). Chant (1961) found a linearly rising curve to a plateau for a predatory mite. However, Mori and Chant (1966) demonstrated a domed curve for another species of predator mite. Mansour *et al.* (1980) noted a sigmoid curve for the spider, *Chiracanthium mildei.*

Predacious pentatomids are known to show Type II curves to prey density. Previous authors have looked at many parameters affecting the functional response of pentatomid predators, such as age (Mukerji and LeRoux, 1969), prey size, and density (Hokyo and Kawauchi, 1975) and prey defense (Morris, 1963). But no one has looked at the effects of changes in the ecological setting and their impact on the functional response of a predacious pentatomid. Predator's behaviour and performance in a particular habitat may depend on conditions of the habitat (Real, 1979). Variables like the number of prey refuges, alternate prey species, and ambient temperature, may influence a predator's efficiency. Ables *et al.* (1978) demonstrated that the presence or absence of aphids had a dramatic effect on the functional response of *Hippodamia convergens* (Coleoptera : Coccinellidae) to *Heliothis virescens* eggs. In the absence of aphids response was super-proportional (directly density-dependent) but in their presence it was sub-proportional (inversely density-dependent).

The aim of the present experiment was to look at the effects of changes in ecological settings on a predator's functional response. Temperature appears to be one such variable that has largely been ignored and thus merits consideration. Furthermore, an effective predator should consume a large proportion of the prey as the prey density increases (Solomon, 1949; Hassell, 1966). It would be of interest to know if the number of prey killed remained unaffected by changes in the temperature.

7.2 MATERIALS AND METHODS

Newly emerged *O. schellenbergii* females 1-2 days old, were held individually and fed to satiation at 28°C, then divided into 5 batches of equal numbers and transferred to 5 test temperatures (15, 20, 25, 30, 35°C) where they were deprived of food for 36-48 hours.

Two small prey stages were chosen for the experiment in order to avoid the effects of inhibition on the predator by energetic prey defenses (Morris, 1963; Holling, 1966). These prey stages, when probed, are always captured by females. Prey stages were designated as Prey I and Prey II, according to their sizes (see Table 7.1).

Table 7.1. Particulars of prey types used in the functional response experiment.

Prey class	n	Mean length in cms ± S.D.	Range	n	Mean weight in mgs ± S.D.	Range
I	25	0.6 ± .08	0.6-0.8	100	3.7 ± 0.4	3.0-5.1
II	25	1.24 ± .08	1.2-1.4	100	20.2 ± 2.2	15.2-25.0

Fig. 7.1 Predation chamber used in the functional response experiments.

Prey in required densities were released on lucerne stems 10-12 cms long, held in water-filled vials and placed in large cylindrical containers (Figure 7.1), with ventilated lids. The containers were then moved to the test temperature cabinets and rooms and given one hour to settle and acclimatize at each temperature. Then predators (one to each container) were released on the stems. After 24 hours, predators were transferred to new containers with fresh lucerne stems and a full complement of new prey (same density). The number of prey killed in the previous containers was ascertained in two ways, (i) by counting the number of live prey in each container and (ii) by counting the number of head capsules and body remains of the eaten prey, whether left on plants or at the base of containers. Moreover, prey found dead and partially consumed were recorded as killed by predators. The experiment lasted for 72 hours. Prey densities used were 2, 4, 8, 16, 24, 32 and 40 for Prey I and 2, 4, 8, 16 and 24 for Prey II. Tests were replicated 5 times for Prey I and 10-12 times for Prey II.

Previous studies have demonstrated that *H. punctiger* larvae do not become cannibalistic until they reach the fourth instar (Kirkpatrick, 1961; Cullen, 1969), a stage far bigger than the two prey stages used in this experiment. Nevertheless, adequate controls were maintained to check mortality due to cannibalism or any other natural cause. Relative humidities inside the containers were high with a range of 75-95 percent at the two extreme temperatures.

7.2.1 Handling Time

The aim of this experiment was to determine the effects of temperature on the handling time of predators. Thus, 20 females of the same age and treated in the same way as in the functional response experiment, were given 6-8 Prey I in 65 mm petri dishes and their handling time was recorded from the moment they attacked the prey until they abandoned it at each test temperature. Data obtained in this experiment and the functional response experiment were used to calculate attack rate, a, of predators. Attack rate, a, was calculated from the random predator equation of Rogers (1972) for one predator.

$$Na = N \ 1 - \exp - a(T - ThNa)$$

where

Na = Number of prey eaten,

N = Prey density,

T = Total time prey are exposed to predation,

a = Attack rate, and

Th = Handling time.

7.3 RESULTS

Functional response curves obtained in the experiment against two prey stages are illustrated in Figures 7.2 and 7.3. Curves are based on the average number of prey consumed per predator in 72 hours at various temperature regimes and appear similar to Holling's (1965) Type II response curves.

Fig. 7.2 Effect of temperature on the functional response of *O. schellenbergii* female, when preying upon second instar *Heliothis punctiger* larvae.

Closed circles = 15°C.
Open circles = 20°C.
Closed triangles = 25°C.
Open triangles = 30°C.
Squares = 35°C.

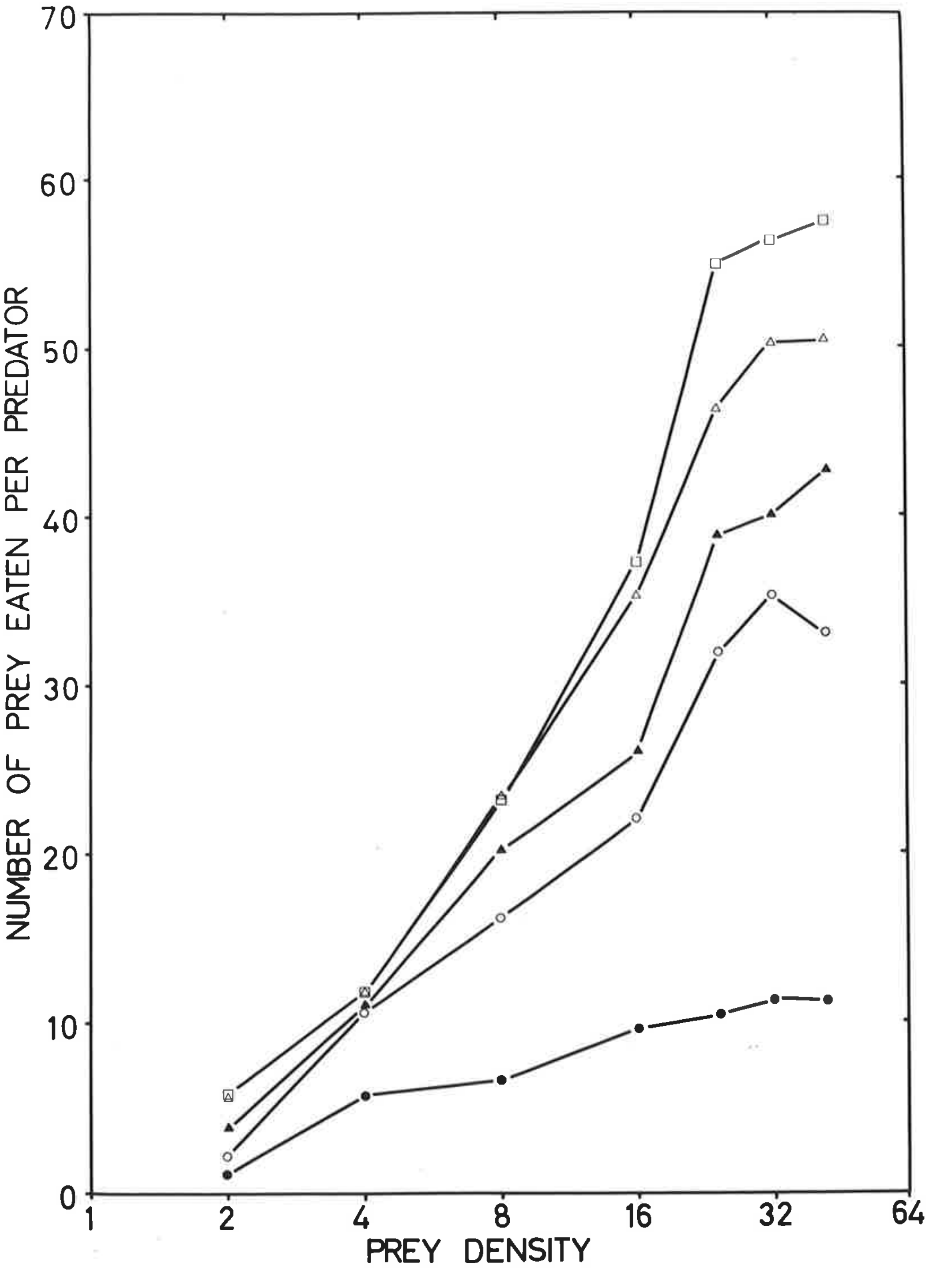

NUMBER OF PREY EATEN PER PREDATOR
0
10
20
30
40
50
60
70
PREY DENSITY
1
2
4
8
16
32
64

Fig. 7.3 Effect of temperature on the functional response of *O. schellenbergii* females when preying upon third instar *H. punctiger* larvae.

Closed circles = 15°C.
Open circles = 20°C.
Closed triangles = 25°C.
Open triangles = 30°C.
Open squares = 35°C.

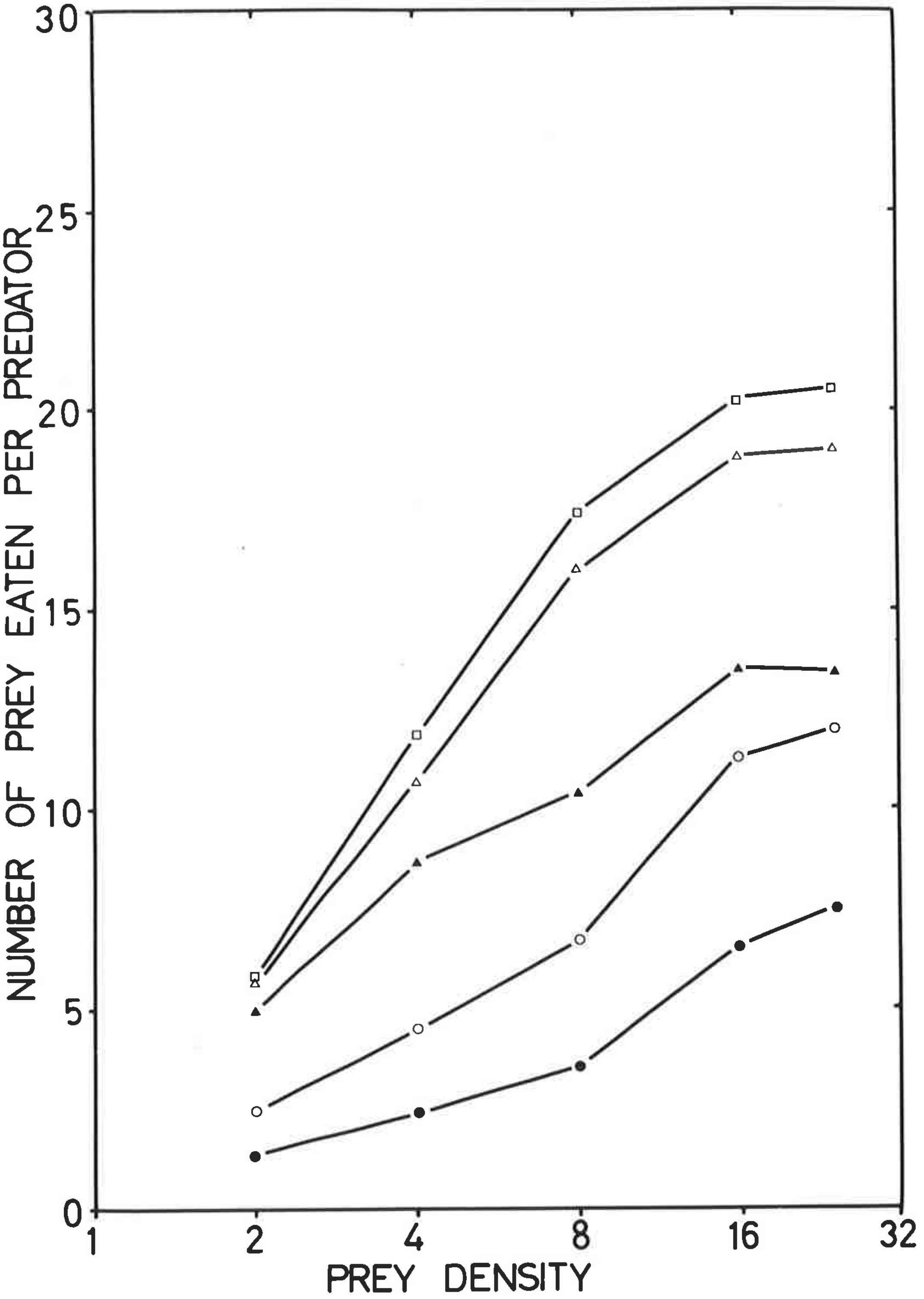
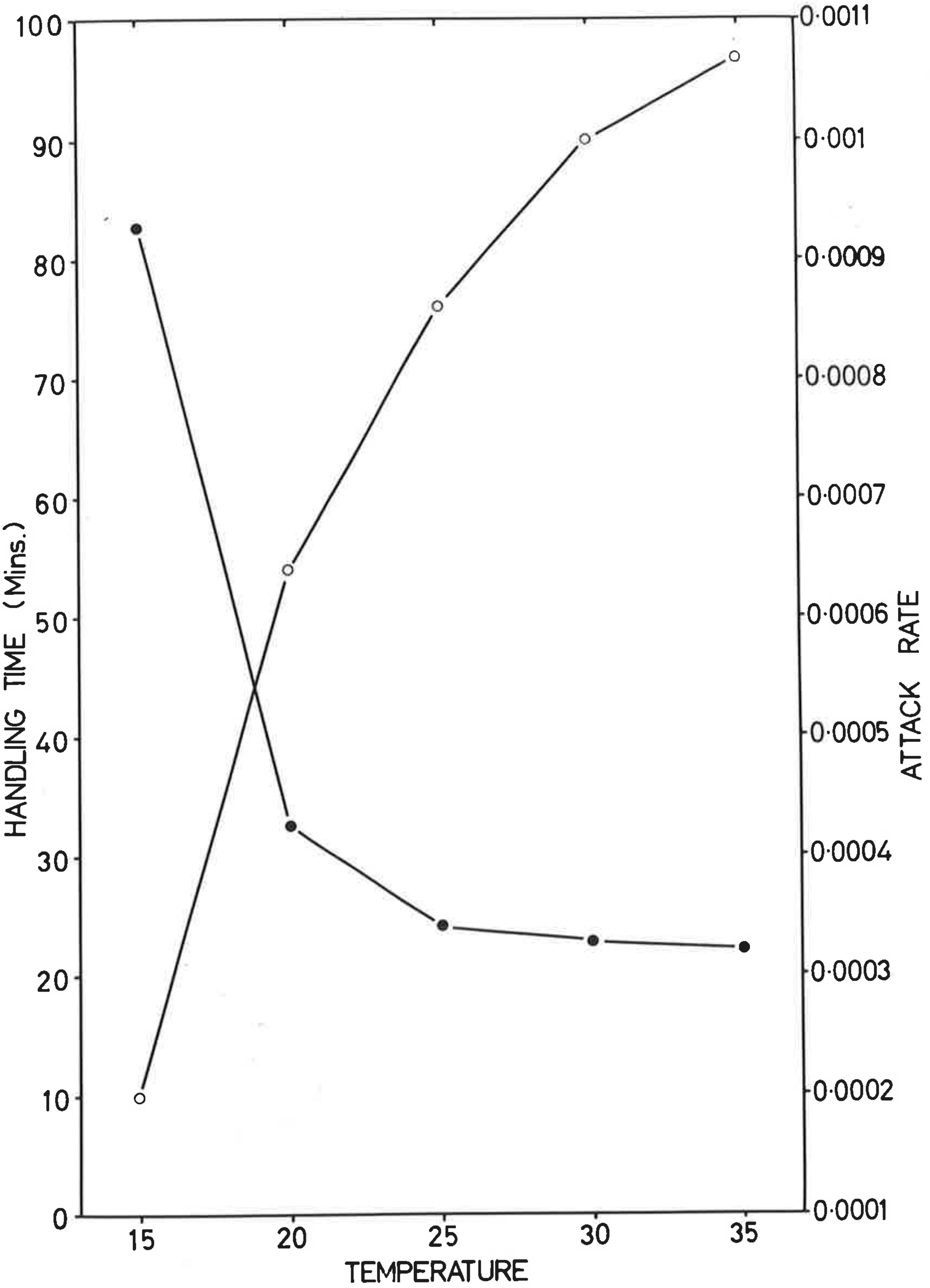

NUMBER OF PREY EATEN PER PREDATOR
0
5
10
15
20
25
30
1
2
4
8
16
32
PREY DENSITY

Fig. 7.4 Effect of temperature on attack rate and handling time of *O. schellenbergii* females against second instar *H. punctiger*.

● = Closed circles = Handling time.

O = Open circles = Attack rate.


HANDLING TIME (Mins.)
100
90
80
70
60
50
40
30
20
10
0
ATTACK RATE
0·0011
0·001
0·0009
0·0008
0·0007
0·0006
0·0005
0·0004
0·0003
0·0002
0·0001
15
20
25
30
35
TEMPERATURE

Response curves against Prey I tend to show a rather linear rise to a plateau, in particular at higher temperatures. This was mainly due to predators' ability to find and capture almost all the prey at lower prey densities. However, this did not occur at 15°C where the number of prey consumed increased in a decelerating manner before levelling off (Figure 7.2). The total number of prey eaten was less for both prey stages at 15 and 20°C than at the higher temperatures. Thus, response curves levelled off at lower numbers at these two temperatures, indicating that temperature exerted a strong influence on the individual performance of the predators and thus affected their overall response.

Only a few (4, Prey II) partially consumed or dead but unconsumed prey were found throughout the experiment. This happened mainly at higher temperatures and at high prey densities. These larvae probably were attacked but escaped capture and died afterwards. There was no prey mortality among the controls.

Temperature had considerable effect on predators' handling time (Th). It was significantly longer at 15 and 20°C but assumed a constant value at other test temperatures (Figure 7.4).

Direct estimates of the predator and prey activity were not made. However, temperature appeared to affect their activities. At lower temperatures predators and prey were less active and *vice versa*. Observations on predators' speed of movement (Chapter 8) demonstrated that predators moved much more slowly at 15°C than at other temperatures. However, predators moved at similar speeds at 27 and 30°C.

7.4 DISCUSSION

Functional response consists of a complex of components (Holling, 1959, 1963, 1965, 1966) and each component is further divisible into several sub-components. Changes in one or many sub-components with temperature would alter the overall predator response. Temperature appeared to affect handling time (Th) and attack rate (a) of *O. schellenbergii* (see Figure 7.4). Temperature also affected predators' hunger level which interacted with some of the sub-components of Th and a to limit their response.

Handling time (Holling, 1966) is a function of time spent (a) pursuing, (b) subduing, (c) eating, and (d) digesting prey. Pursuing time in *O. schellenbergii* was probably limiting only at lower prey densities. Subduing times were similar at all test temperatures. The two sub-components of Th that significantly changed handling times at lower temperatures were (c) and (d). Eating (prey consumption) and times spent in pauses, presumably while stomach contents were being digested, were longer at 15 and 20°C. However, a near constant handling time between 25 and 35°C (Figure 7.4) indicated that predators were feeding at their maximum rates, and this was especially true at higher prey densities. Handling time of *O. schellenbergii* against Prey I decreased exponentially as temperature rose to 25°C, and assumed near constant value at 25, 30 and 35°C. Burnett's (1951, 1954) data on the functional response of the chalcid parasite, *Dahlbominus fucipennis* indicate a similar decrease in Th with temperature. Lawton (1971) noted that food consumption and gut clearance times were dramatically affected by temperature in damselfly larvae. There was dramatic increase between 5-15°C but beyond this temperature the rate of increase was minimal. Fedorenko (1975) demonstrated that temperature affected the functional response of two chaoborid species, *Chaoborus americanus* and *C. trivittatus* preying upon *Diaptomus tyrelli* and *D. kenai*. Thompson (1978) calculated Th values from Fedorenko's functional response data and discovered similar trends in Th as shown by Burnett (1951, 1954), Thompson (1978) and Everson (1980). Ford (1975) provided more precise information on the handling time of two spiders, the lycosid, *Paradosa amentata*, and the linyphiid, *Lepthyphantes zimmermanii*, at different temperatures. In his studies Th of both predators decreased with temperature. Higher handling time at 5°C was the main factor that limited the spider's response.

Thompson's (1978) data on the functional response of damselfly larvae, *Ischnura elegans* also demonstrate that Th decreased with temperature up to 16°C and then assumed a near constant value at 20, 24 and 28°C. He argued that constant Th at higher temperatures was probably due to the maximum feeding rates of predators. Nonetheless, Everson (1980) noted that Th in predatory mites decreased with temperature but never attained a constant value. This, he argued, indicated that mites were not feeding at maximum rates.

The second key parameter that limited *O. schellenbergii*'s response was their lower attack rate at lower temperatures. Attack rate (Holling, 1963, 1966) is a function of (a) reactive distance of a predator, (b) speed of movement of prey, (c) speed of a predator and (d) predator's capture success. Temperature affected the general behaviour of predators and prey. Both were less active at 15°C. Lower activity levels of the two may lead to fewer contacts and hence fewer captures. Everson (1980) speculated that, while feeding, mites or other small insects like aphids remain mostly non-locomotory. This probably would make speed of prey movement negligible at all temperatures. But *H. punctiger* larvae do not remain inactive on lucerne plants (cf. Chapter 5). Their head-waving behaviour was found to attract *O. schellenbergii* (cf. Chapter 5). *H. punctiger* larvae were less active at 15°C and this is likely to affect the predator's reactive distance to the prey and consequently limit its capture success.

Response curves levelled off at higher prey densities due to predators becoming satiated. Predators with full guts entered what may be assumed to be a 'digestive pause' and did not capture more prey for some time. Thus, satiation lowers the attack rate a. Unfed *O. schellenbergii* moved faster than satiated ones and were more successful in capturing prey (cf. Chapter 8). Sandness and McMurtry (1970) and Glen (1975) noted that speed of predators increased with fasting, in other words the longer they were deprived of food the faster they moved and the more successful they were in capturing prey.

The attack rate a of *O. schellenbergii* increased non-linearly with temperature and levelled off at 30°C (Figure 7.4). Thompson (1978) reported a sigmoid initial increase in a, which then levelled off at 20°C in *Ischnura elegans*, indicating that some physical or physiological factor had become limiting. Everson (1980) observed a linear increase in a with temperature and argued that increase in attack rate may be due to increased energy demands of predators at higher temperature.

Thompson (1978) calculated attack rates of two chaoborid predators from Fedorenko's (1975) data and noted that a increased in a non-linear way with temperature in her studies as well.

CONCLUSION

Temperature had a dramatic effect on the functional response of *O. schellenbergii*. It limits their response at lower temperatures by affecting two key parameters a and Th of the functional response. The functional response of *O. schellenbergii* is inversely density-dependent (Type II curve) like many other predators.

8. EFFICIENCY OF CAPTURE OF *O. SCHELLENBERGII* AT 27°C AGAINST LARVAE OF *H. PUNCTIGER* AND EFFECT OF TEMPERATURE ON THE EFFICIENCY OF CAPTURE OF FOURTH STAGE AND ADULT FEMALE OF *O. SCHELLENBERGII*

8.1 INTRODUCTION

Dixon (1959) defined efficiency of capture as a measure of the proportion of prey actually captured in a series of encounters between predator and prey. Present pest control methods involving effective use of natural enemies are fraught with lack of basic knowledge about them (van den Bosch and Stren, 1962). This is even true for the relatively well studied predacious coccinellids (Brown, 1972). Previous authors have shown that efficiency of capture (Dixon, 1959; Dixon and Russel, 1972; Evans, 1976), functional response (Holling, 1959; 1966) and behavioural changes to prey distribution (Banks, 1957; Dixon, 1958) are some of the parameters that would determine the outcome of predator prey interaction. Despite this, very few studies have dealt with the efficiency of capture of predators.

Furthermore, studies concerned with this aspect of predation have largely been restricted to coccinellids (Banks, 1957; Dixon, 1958; 1959; Fleschner, 1950; Brown, 1972; Wratten, 1973) and anthocorids (Dixon and Russel, 1972; Evans, 1976) that mainly prey upon aphids. These predators are known to find their prey by physical contact (cf. Chapter 6). *O. schellenbergii*, however, locates its prey by olfaction and vision. The larvae, unlike aphids, are patchy in distribution. The efficiency of predacious pentatomids in capturing prey does not seem to have been investigated before. Moreover, little is known of the effects of temperature on a predator's efficiency of capture despite the likelihood that temperature will affect behaviours of both predator and prey.

The present observations describe the efficiency of capture of *O. schellenbergii* at one temperature and they go on to study the efficiency of capture of two predator stages (fourth stage and adult females) against one prey stage (third instar caterpillar) at 15, 20, 25, 27 and 30°C.

8.2 MATERIAL AND METHODS

Experimental stages of *O. schellenbergii* were obtained from stock cultures, just after each moult, and deprived of food for 24-36 hours at 28±2°C before the tests. Twenty *H. punctiger* larvae of a particular instar, one day old if first instar larvae and in their mid-instars in the other stages, were released on washed lucerne stems 10-12 cm high with flowers and fruits, held in water-filled plastic vials. Caterpillars were allowed 10-15 minutes to settle on plants and commence feeding. Then, one test animal was released on a marked site in the middle of the stem. Each predator was given a maximum of 20 encounters to capture the prey or two hours, which ever occurred first; thereafter the predator was taken off the plant. In other words, if a predator scored a capture in less than 20 encounters, it was taken off the plant or if it failed to complete 20 encounters in two hours it was also removed from the plant.

Encounter in this study differs significantly from Dixon's (1958) definition. *O. schellenbergii* responds to its prey in a typical way and its response consists of three consistent events that always appear in sequence: (1) raising the antennae towards the prey, (2) moving closer and stretching out its proboscis, (3) probing and attacking the prey. An encounter was considered to have taken place when the second event was observed.

No animal, once used in the test, was used again until it had moulted to the next stage and was deprived of food again. The predators' approach to prey of different sizes, the number of encounters and the number of attacks before a successful capture were recorded for every predator prey combination. Prey that escaped attacks or captures and dropped off the plant were replaced by new ones, so were the ones that were captured. A capture was recorded when prey stopped struggling and was completely immobilised.

8.2.1 Speed of predators at various temperatures

Each individual in a randomly selected sample of 10 newly moulted fourth instar *O. schellenbergii* was placed in a separate container and deprived of food, at various temperatures for 36-48 hours. These unfed predators were released on a pre-marked horizontal rod one at a time, and the time they took to cover a distance of 15 cms at each temperature was measured.

8.2.2 Effects of fasting (deprivation of food) on the readiness of predators to subdue and capture the prey

From a large number of newly moulted fourth instar *O. schellenbergii*, two lots of 25 were selected at random, one lot for each of the test temperatures (15 and 20°C). These lots were further divided into five replicate batches of 5 predators and individual batches, one to five were then transferred to constant temperature rooms with 12L:12D photoperiod. At the end of each 24 hour period, one batch of predators was tested against third instar *H. punctiger* caterpillars at the same temperature by the standard procedure described above (cf. 8.2). During fasting, all predators were provided with drinking water.

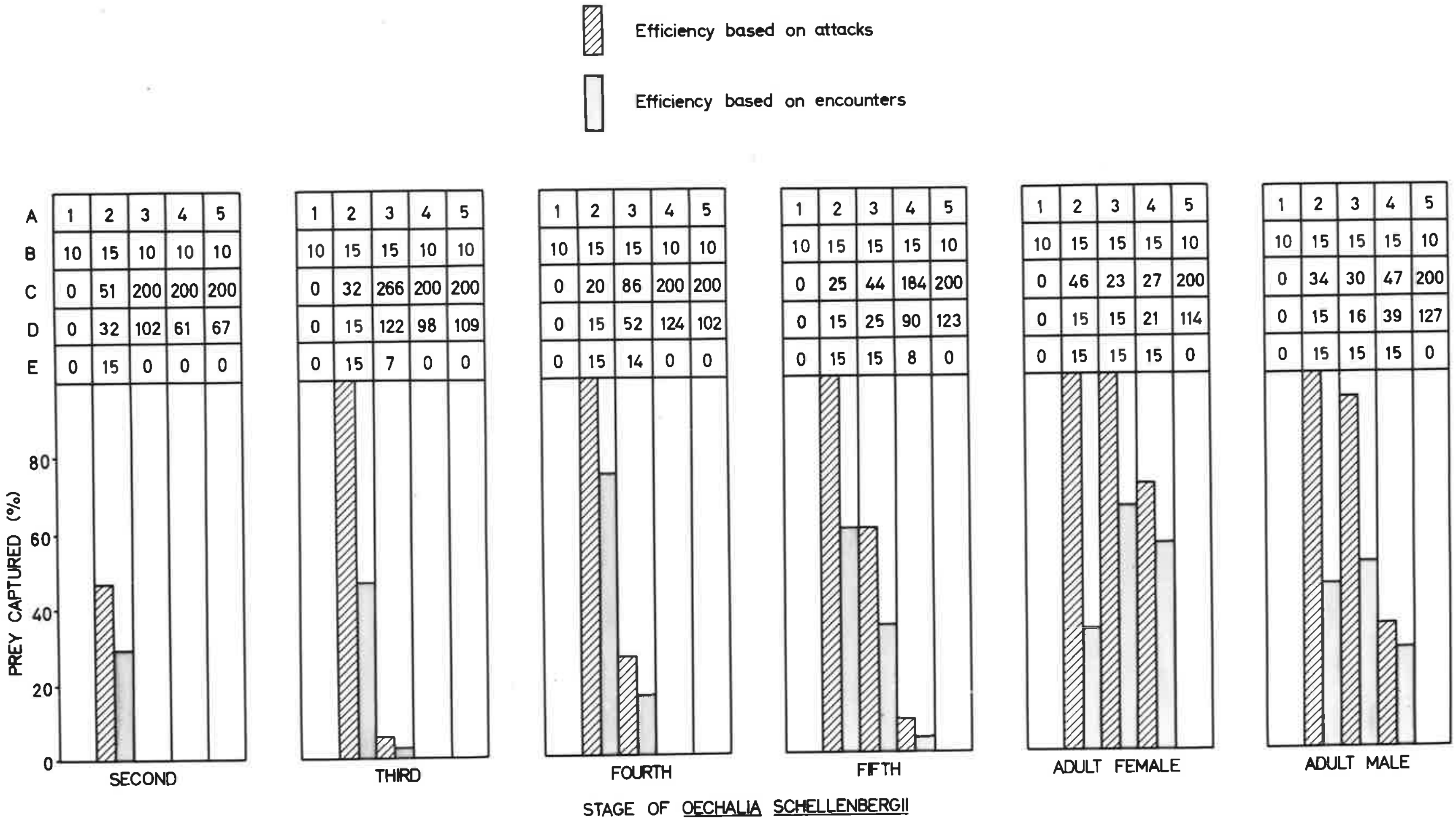
8.3 RESULTS

H. punctiger larvae dispersed rapidly on lucerne stems during the initial settling in period. As indicated before (Chapter 5), almost all the larvae moved towards the top of the lucerne stem. First instar *H. punctiger* larvae were apt in hiding themselves in flowers, buds and fruits of lucerne and at the end of 10-15 minutes none of them was visible. This boring into plant terminals provided them with protection against predation. Donahoe and Pitre (1977) noted this in *H. armigera* (Lepidoptera : Noctuidae) larvae on cotton bolls and squares.

Predators frequently encountered and attacked other than those of the first instar *H. punctiger* larvae with varying degree of success (Figure 8.1). Second stage predators were able to capture second instar caterpillars but failed to capture large caterpillars despite several attacks. Dixon (1970) observed this in coccinellids. He noted that small predators were restricted to feeding on small (first instar) aphids. Third stage *O. schellenbergii* were successful against second instar prey and to a very small extent (cf. Chapter 4) against third instar prey. However, they were more efficient in handling second instar prey than the second stage predators. Fourth stage predators showed highest efficiency in capturing second instar prey (75 percent) and they were slightly more efficient than fifth stage and adult predators. Fifth stage predators were able to capture few fourth instar larvae. Adults were able to capture fourth instar caterpillars along with small prey (second and third instars). Females were usually more efficient than males. However, fifth instar caterpillars were immune to captures by all predators (Figure 8.1).

Fig. 8.1 Efficiency of capture of various stage of *O. schellenbergii* against various instars of *H. punctiger* at 27°C, based on encounters and on attacks.

A = *Heliothis* instars.
B = Number of predators.
C = Number of encounters.
D = Number of attacks.
E = Number of captures.

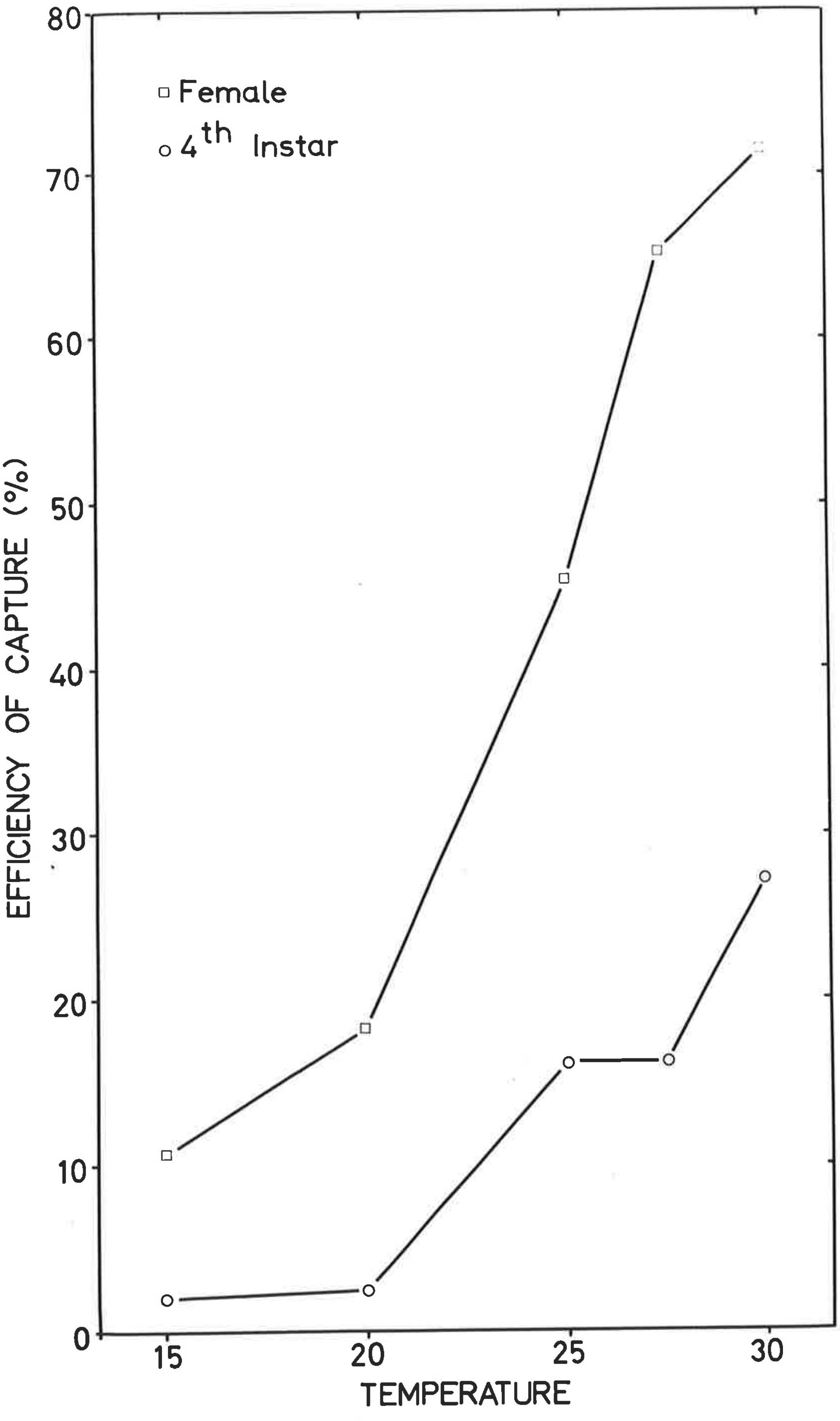

Efficiency based on attacks
Efficiency based on encounters
PREY CAPTURED (%)
0
20
40
60
80
A 1 2 3 4 5
B 10 15 10 10 10
C 0 51 200 200 200
D 0 32 102 61 67
E 0 15 0 0 0
SECOND
1 2 3 4 5
10 15 15 10 10
0 32 266 200 200
0 15 122 98 109
0 15 7 0 0
THIRD
1 2 3 4 5
10 15 15 10 10
0 20 86 200 200
0 15 52 124 102
0 15 14 0 0
FOURTH
1 2 3 4 5
10 15 15 15 10
0 25 44 184 200
0 15 25 90 123
0 15 15 8 0
FIFTH
1 2 3 4 5
10 15 15 15 10
0 46 23 27 200
0 15 15 21 114
0 15 15 15 0
ADULT FEMALE
1 2 3 4 5
10 15 15 15 10
0 34 30 47 200
0 15 16 39 127
0 15 15 15 0
ADULT MALE
STAGE OF OECHALIA SCHELLENBERGII

Efficiency of capture of *O. schellenbergii* increased with age, and within each stage was high when preying upon small larvae in the case of juvenile predators. Adult predators' efficiency was higher when preying on small to medium sized prey. Evans (1976) demonstrated this in *Anthocoris nemorum* preying upon pea aphids *Acyrthosiphon pisum*. Brown (1972) noted that efficiency of capture of *Lioadalia flavomaculata, Scymnus morelleti, Exochomus concavus* and *Cheilomenes lunata* (Coleoptera : Coccinellidae) increased with their age. Dixon and Russel (1972) found that *Anthocoris nemorum* was restricted to feeding on first instars of sycamore aphid, *Drepanosiphum plantoides* but the efficiency of capture increased as the predators became older.

8.3.1 Temperature effect on efficiency of capture

The fourth stage and adult female *O. schellenbergii* showed similar changes in behaviour with change in temperature. But females were more efficient at subduing the probed prey at each temperature and thus scored more captures than fourth stage predators. At 15°C the fourth stage predators required more encounters than adult females to capture prey. Some failed to score captures and some even failed to complete twenty encounters in two hours. They seldom struggled with the prey once they had probed it, and were quick to abandon it if it reacted violently. They did not seem to undertake an active search, but any prey that came close enough was either probed or an attempt was made at probing. Nevertheless, missed prey were seldom pursued. At 20°C, movement of the predators was still slow. The efficiency of female predators was nearly twice as high as at 15°C. But fourth instar predators showed a minor

Fig. 8.2 Effect of temperature on the efficiency of capture of fourth stage and female *O. schellenbergii* against third instar *H. punctiger*.


80
70
60
50
40
30
20
10
0
□ Female
○ 4th Instar
EFFICIENCY OF CAPTURE (%)
15
20
25
30
TEMPERATURE

increase in the efficiency of capture (Figure 8.2). The efficiency of the latter was similar at 25°C and 27°C but reached a higher value at 30°C. However, efficiency of capture of females continued to increase with each increase in temperature.

8.3.2 Effect of temperature on predators' speed

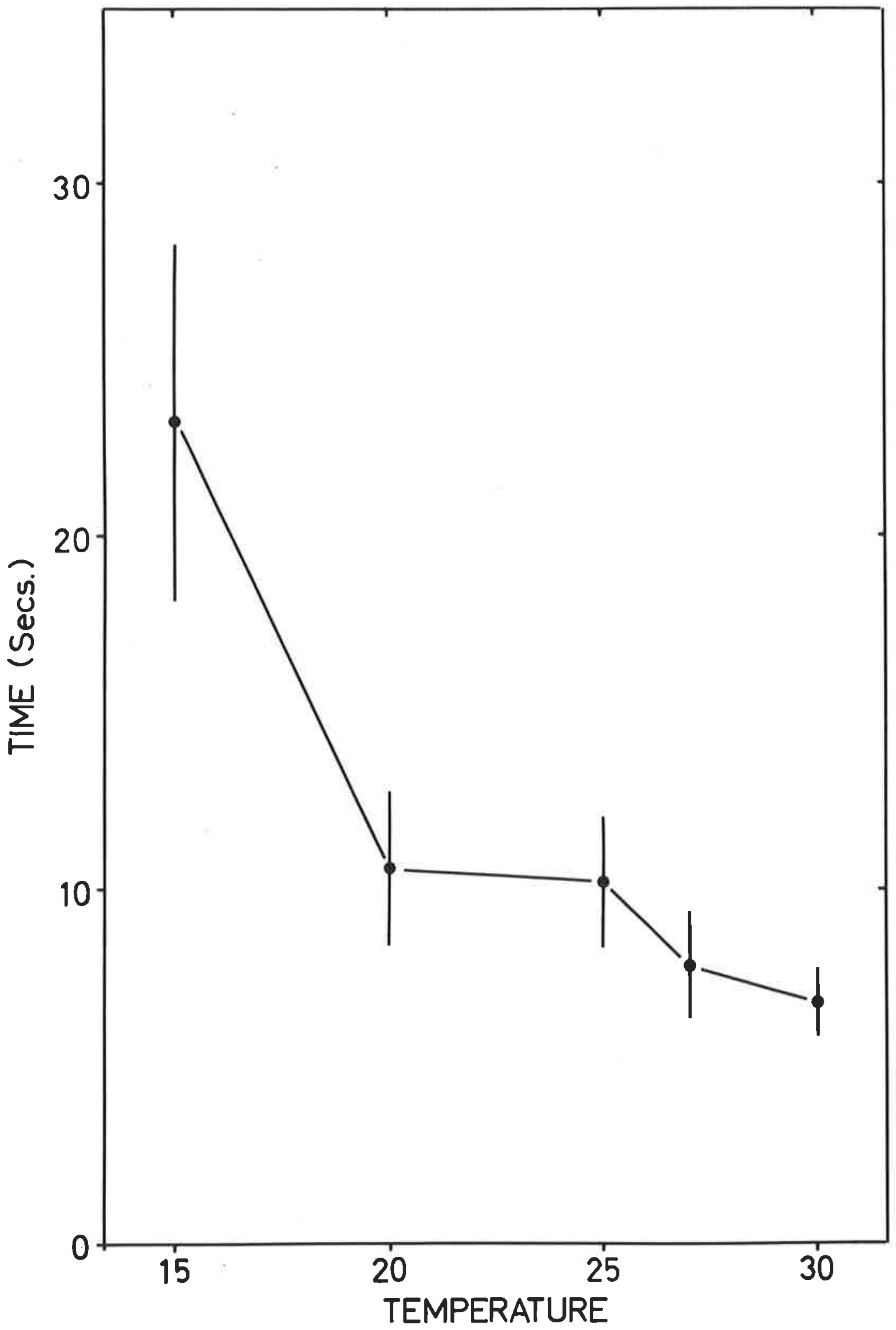
Temperature had a great deal of influence on predators' general activity. They moved more slowly at 15 and 20°C and faster at higher test temperatures, where their speed appeared similar (Figure 8.3).

8.3.3 Effects of fasting (deprivation of food)

Observations on fasting indicate that it caused an increase in the readiness of predators to attack and capture prey. When predators were recently fed they appeared to be non-responsive to the prey. The ones that probed and attacked prey tended to release them quickly if the prey reacted.

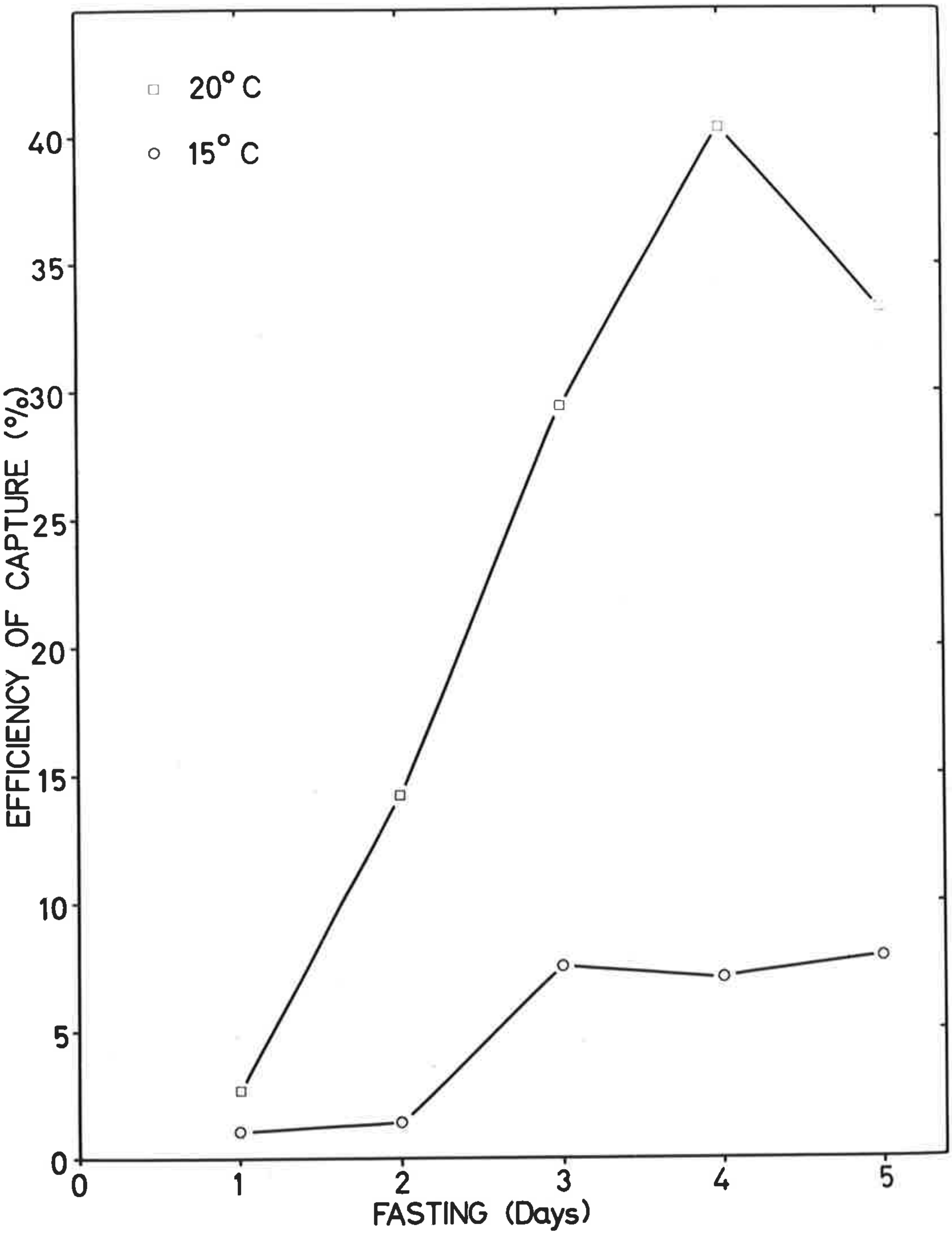
The predators' efficiency increased with increase in fasting time. At 15°C, efficiency reached a maximum value after three days fasting and then levelled off. At 20°C efficiency reached its highest value on the fourth day, but then declined gradually (Figure 8.4). Dixon (1970) noted that one day old and unfed larvae of *Adalia bipunctata* (Coleoptera : Coccinellidae) were inefficient in capturing first instars of sycamore aphids, but their efficiency increased four-fold on the third day and then fell off.

Fig. 8.3 Effect of temperature on speed of fourth stage *O. schellenbergii* (mean ± S.D.) at 5 constant temperatures.



TIME (Secs.)
30
20
10
0
15
20
25
30
TEMPERATURE

Fig. 8.4 Effects of fasting on the effiency of capture of fourth stage *O. schellenbergii* at 15 and 20°C.


□ 20° C
○ 15° C
EFFICIENCY OF CAPTURE (%)
0
5
10
15
20
25
30
35
40
FASTING (Days)
0
1
2
3
4
5

8.4 DISCUSSION

O. schellenbergii is a polyphagous predator but mainly preys upon lepidopterous larvae. It is one of the main causes of mortality of *H. punctiger* larvae (Cullen, 1969). Laboratory observations on second stage *O. schellenbergii* indicate that its effectiveness as a predator of *H. punctiger* larvae was likely to be affected by the availability of small stages of its prey in the field. It is capable of feeding on eggs, first instar larvae (cf. Chapter 4) and, to a limited extent, on second instar (see Figure 8.1) *H. punctiger* larvae. First instar prey were able to avoid capture by hiding, but in voracity experiments second stage predators proved apt at finding and capturing first instar *H. punctiger* larvae if the density of prey was large enough. Cullen (1969) reported that even large *H. punctiger* larvae were able to bore into tomatoes, bean and pea pods and this 'refuge-seeking' may be of survival value against visual predators. But larvae older than second stage cannot hide in the lucerne plant terminals.

Unlike coccinellids (Banks, 1957; Dixon, 1958, 1959, 1970; Brown, 1972; Wratten, 1973) and anthocorids (Dixon and Russel, 1972; Evans, 1976) immature predacious pentatomids (Iwao and Wellington, 1970; Mukerji and LeRoux, 1965; Tostowaryk, 1971) are capable of attacking prey larger than themselves. Often several second stage predators would be attracted to the struggle between a second stage predator and a large caterpillar and their joint attack would result in the death of the prey (Tostowaryk, 1971). The ability to obtain food from large prey (cf. Chapter 4), and to prey upon aphids and other small insects may help them to overcome shortages of prey of more suitable size.

Female *O. schellenbergii* lay eggs in the upper quarter of lucerne stems as do the females of *H. punctiger*. Thus, spatial location of predator eggs coincides with the eggs of their prey. This spatial coincidence may enhance the chances of small predators in finding the small prey in the later part of the season. But initial non-synchronisation between the predator and prey life cycles allows *H. punctiger* to build its numbers. *H. punctiger* moths appear in early spring (cf. Chapter 3), whereas overwintered adults of *O. schellenbergii* seldom appear before October. This time lag between the two, on the one hand hampers the predators' ability to regulate *H. punctiger* numbers, but on the other hand ensures the availability of a variety of prey stages for the first generation of predators.

O. schellenbergii females show a high reproductive potential in the laboratory (cf. Chapter 3). However, their inability to capture large prey and their total dependence on small to medium sized prey is likely to affect their egg production. Dempster (1968) suggested that egg production in *Anthocoris sarothamni* (Hemiptera : Anthocoridae) preying upon the psylid, *Arytania* spp. is often limited by the availability of food. *A. confusus* and *A. memorum* are known to move from one plant species to another in search of higher prey densities (Anderson, 1962). There is circumstantial evidence that adults of *O. schellenbergii* leave lucerne patches at low prey densities and search for *Ectropis excursaria* (Lepidoptera : Geometridae) on adjacent hedges of pine trees (Mariath, 1980). Furthermore, alternate prey may not be suitable for maximum egg production. Waddill and Shepard (1975) noted that *Stiretrus anchorago* (Hemiptera : Pentatomidae) produced few eggs when fed on *Galleria* *mellonella*. This may well be the reason for lower predator populations in lucerne patches, together with mortality due to parasitism by the egg parasite *Trissolcus* spp. (see Appendix II).

Previous studies on the efficiency of capture of predators have been based on encounters (Dixon, 1958; Dixon and Russel, 1972), contacts (Evans, 1976) and attacks (Brown, 1972). Efficiency of capture, when based on number of attacks leads to over-estimation of predators' efficiency in certain predator-prey combinations (Figure 8.1). For instance, large *O. schellenbergii* were 100 percent efficient in capturing any small larvae they attacked. But their efficiency was less when based on encounters. In laboratory studies encounters and contacts give a more realistic picture, in relation to field conditions, since they do not preclude the use of evasive reactions by prey before the initiation of attacks.

Lower predator efficiency at lower temperatures is not surprising, since capture success is a sub-component of attack rate $\underline{a}$ of predators (Holling, 1966) among other sub-components (reactive distance, speed of predator and prey movement). Any change in one sub-component is likely to affect the whole interaction. Temperature has been shown to affect the predators' speed of movement (cf. 8.3.2) and it is further discussed and commented upon in Chapter 7.

Furthermore, fasting may affect predators to a different extent at different temperatures. Gut clearance may be faster at higher temperatures and extremely low at lower ones. Thus a predator with a full or nearly full gut may be slow in attacks or it may not attack prey at all. Holling (1966) demonstrated a positive relationship between the pursuit distance and time of food deprivation of mantids. Fasting also affects predators' efficiency of capture (8.3.3).

8.5 CONCLUSION

Present observations indicate that *O. schellenbergii* is restricted in its ability to feed on or kill *H. punctiger* larvae. Immature predators attack almost all prey stages but seldom capture or kill the large ones. They are mainly restricted to feeding on small prey. Adult predators prey almost entirely upon small to medium sized larvae, with a preference for medium sized prey.

9. ANTI-PREDATOR PLOYS OF CATERPILLARS OF *H. PUNCTIGER* AGAINST THEIR PREDATOR *O. SCHELLENBERGII* AND FORAGING TACTICS OF THE LATTER TO COUNTER THESE PLOYS

9.1 INTRODUCTION

Insects, like other animals, show a wide range of predator-avoidance tactics, which may broadly be classified as primary and secondary defense systems (Robinson, 1969; Edmunds, 1974). The primary defense of many insects comprises anachoresis, crypsis, mimicry and aposematism, whilst their secondary defense is based on deimatic behaviour, thanatosis, retaliation, chemical defense and the formation of defensive groups (Edmunds, 1974). For review on animal defense see Edmunds (1974), Curio (1976).

There is no reported case of complete anachoresis in lepidopterous insects. However, final instar caterpillars of convolvulus hawkmoth, *Herse convolvuli* remain buried in the ground during the day and forage at night and hence appear to avoid predation by partial anachoresis (Edmunds, 1974).

Many lepidopterous insects are not only cryptic but are also polymorphic and choose habitats where they are most invisible to predators (cf. Poulton, 1888; Bell and Scott, 1937; Pinhey, 1960). The black and yellow caterpillars of Cinnabar moth, *Callimorpha jacobaeae* appear to be aposematic to many predators (Ford, 1955; Dempster, 1971).

Mimicry is by far the most common means of primary defense in lepidopterous insects (cf. Brower, 1958; Brower *et al.*, 1960; Brower and Brower, 1962; Edmunds, 1969a).

Among the reported secondary defense systems that lead to reduced predation in leipdopterous insects are deimatic behaviours (cf. Hinton, 1948; Blest, 1957, 1963, 1964; Blest *et al.*, 1963; Bedford and Chinnick, 1966; Robinson, 1968); thanatosis (Heinrich, 1979) and aggressive retaliation (Marston *et al.*, 1978).

Aim of the present experiment was to ascertain the primary and secondary defense strategies of *H. punctiger* caterpillars and to relate them to predator prey size ratios, and to evaluate their overall impact on the ability of juvenile and adult predators to capture them. Furthermore, observations were also made on foraging tactics of predators that appeared to show behavioural adaptations to counter the caterpillars' defense systems.

9.2 METHODS

The experimental procedure was the same as mentioned before (cf. 8.2) except that predators' probe sites and escape responses of prey before and after probes were also recorded.

9.3 RESULTS

As mentioned previously (cf. Chapter 8) none of the predators encountered first instar *H. punctiger* caterpillars. Various instars of caterpillars reacted differently and showed a variety of predator avoidance strategies such as walking away, head waving, head flicking, dropping off the plant, spitting, biting, rolling over and tail wagging. These kinds of activity occurred either on their own or in various combinations (Table 9.1). The escape responses, that were observed can broadly be divided into two categories: (a) pre-probe and (b) post-probe responses.

(a) Pre-probe responses: These are the responses that occurred before initiation of attacks, in other words, they were primary defenses of caterpillars.

Walking: When a predator approached, a caterpillar usually stopped feeding and ceased all movement momentarily. But if this did not deter the advancing predator, the caterpillar tended to walk quickly out of the predator's path. This was the most frequent response used by each caterpillar against all predators (Figure 9.1).

Head waving: This was the second most common defense response. Larvae lifted their heads up and waved them at the approaching predator. This action by large caterpillars was an effective deterrent against small predators and often resulted in their retreat. However, it failed to provide any protection to small caterpillars against large predators. Furthermore, it often appeared to make them more vulnerable to attacks.

Dropping off the plant: Small caterpillars second and third instars, when encountered by large predators dropped off the plant either on the silken thread or on the ground. Caterpillars that dropped on silken threads remained suspended in air for a while and then climbed back to the plant on the thread by twisting and turning their bodies.

Table 9.1. Actual number of secondary escape responses observed in *H. punctiger* caterpillars.

Predator stage	Caterpillar instar	n	Occurrence of various responses																	
			Single				Double						Triple						Quadruple	
			WA	HF	BB	TW	HF+ WA	HF+ BB	BB+ WA	BB+ DG	HF+ DG	TW+ WA	HF+RO +DG	BB+RO +DG	HF+RO +DT	HF+BB +WA	HF+RO +WA	HF+BB ±DG	HF+BB RO+DG	HF+BB RO+DT
II	II	17					11						6							
	III	102	31	44	1	3	10	5	2							2		4		
	IV	61	23	12	10		5	11												
	V	67	32	14	5	16														
III	II																			
	III	115	27	33	2		1		6	3				15	11		1		13	3
	IV	98	17	24			14	21	16				6							
	V	109	54	34	4	11		3			2	1								
IV	II																			
	III	38	6	8						1	1		13	1	4		3		1	
	IV	124	39	17	33	1		1	2	6	4		2	18				1		
	V	102	59	17	14	3	1			1	2	5								
V	II																			
	III	10					2						8					12		
	IV	82		8	7		8		23	5				19						
	V	123	36	56	8	14					7		1			1				
♀	II																			
	III																			
	IV	6									1			3			1			
	V	114	22	33	18	3	3	16	4	4	2		9							
♂	II																			
	III	1											1							
	IV	24	2						3		1		8	10						
	V	127	37	83	3			1			2			1						

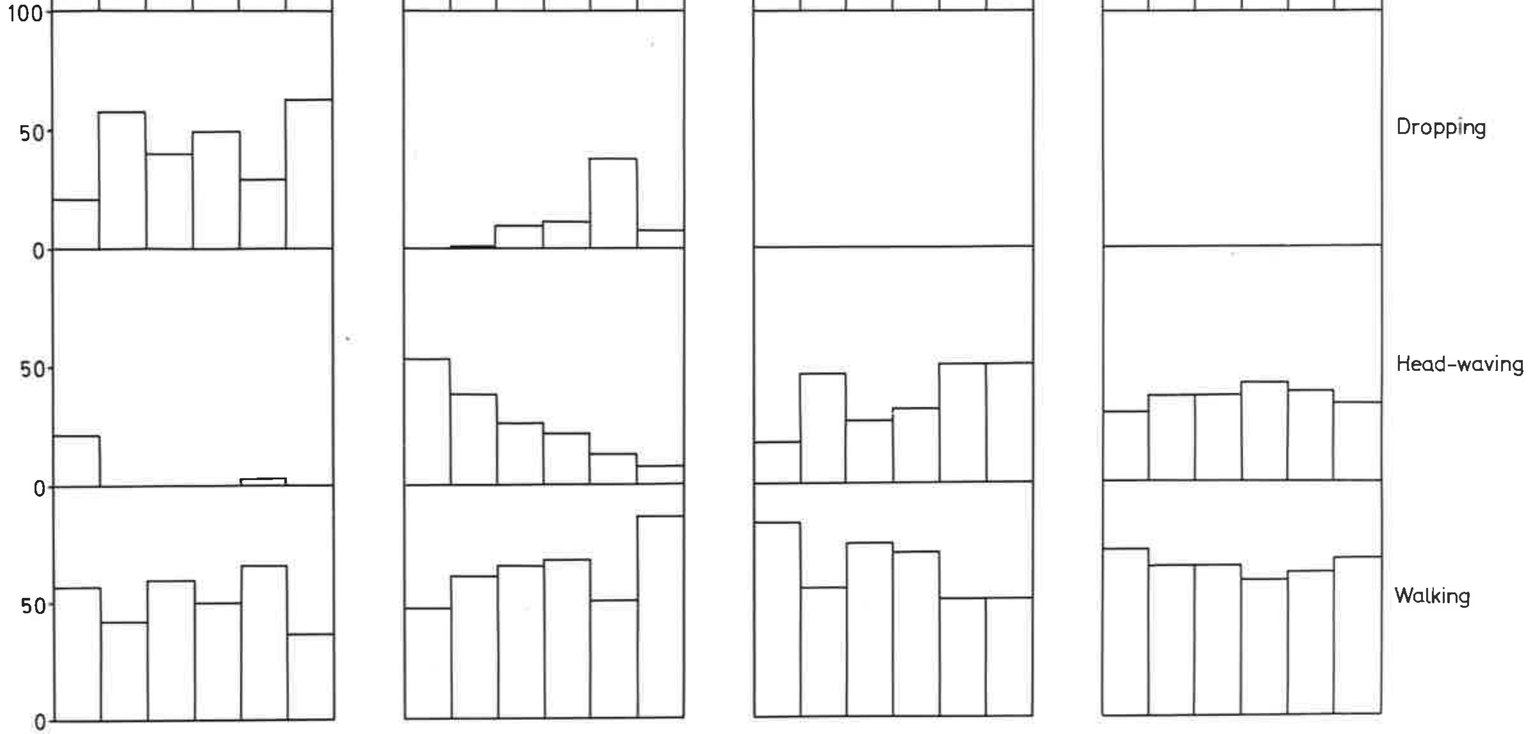
WA - Walked Away : HF = Head Flicked : BB = Bit Back : TW = Tail Wagged.

Fig. 9.1 Pre-probe escape responses - (primary defense-ploys) of *H. punctiger* larvae against various stages of *O. schellenbergii*.

A = Predator stages.
B = Number of predators tested.
C = Number of encounters.
D = Number of captures.
E = Number of prey escaped by primary defense.
F = Number of prey escaped by secondary defense.

<u>HELIOTHIS</u> INSTARS

II						III						IV						V						
2	3	4	5	♀	♂	2	3	4	5	♀	♂	2	3	4	5	♀	♂	2	3	4	5	♀	♂	A
15	15	15	15	15	15	10	15	15	15	15	15	10	10	10	15	15	15	10	10	10	10	10	10	B
51	32	20	25	46	34	200	266	82	44	23	30	200	200	200	184	27	47	200	200	200	200	200	200	C
15	15	15	15	15	15	0	7	14	15	15	15	0	0	0	8	15	15	0	0	0	0	0	0	D
19	17	5	10	19	19	98	144	34	19	8	14	139	102	76	94	6	8	133	91	98	77	86	73	E
17	0	0	0	0	0	102	115	38	10	0	1	61	98	124	82	6	24	67	109	102	123	114	127	F



This was the most common and effective primary defense of small caterpillars (Figure 9.1).

(b) Post-probe responses. Observations in this category were based on the responses of caterpillars that were attacked by predators but managed to avoid capture. In other words, these were the secondary defense strategies of caterpillars.

Walking. Walking was also used as part of secondary defense by caterpillars. Attacked caterpillars pulled their bodies forward and tended to move away from predators. This was most effective ploy used against second, third and fourth stage predators by fourth and fifth instar caterpillars (Table 9.1).

Head flicking: Large caterpillars (fourth and fifth instars) when attacked by small predators reacted by violent head flicking. They lifted their heads up and banged them against the predator's body. This thumping proved effective deterrent against all predator stages and in particular against small ones, that had already been beaten off. Occasionally, oral spitting accompanied this thumping, after which predators spent considerable time in cleaning their antennae and probosces.

Biting: Some attacked caterpillars turned their heads back and charged at the proboscis or head of the predator with mandibles. Biting was always accompanied by oral spitting and this was an often effective ploy that made small predators release the caterpillar.

Tail Wagging: This response appeared only when small predators (second, third and fourth stages) interacted with much larger caterpillars (fifth instars). Caterpillars simply lifted or moved their rear end and this action was sufficient to dislodge the predators that had initiated the attack.

These individual responses some times failed to dislodge predators and were backed up by one or two other responses. The number of responses occurring together increased as the sizes of predators and prey became more evenly matched (Table 9.1).

9.4 DISCUSSION

Defense strategies of *H. punctiger* caterpillars are diverse and are of course directed against several predators and not just *O. schellenbergii*. Earlier instars of caterpillars are green and hence cryptic, when resting on lucerne leaves. Crypsis is a major form of primary defense of many insects such as grasshoppers (Ergene, 1950a), mantids (Beljajeff, 1927) and bark inhabiting bugs, *Certozygum horridum* (Silberglied and Aiello (1980). Heinrich (1979) demonstrated that palatable lepidopterous larvae restricted themselves to the lower side of the leaf surface (where they were most concealed), foraged at night, often moved away from a feeding site, and returned to feed on the same leaf and usually snipped off partially eaten leaves after feeding. Unpalatable larvae, on the other hand, rested on the leaf surfaces and did not snip off an unfinished leaf. Heinrich argued that these behaviour patterns were due to selective predation pressure exerted by visual predators on the two kinds of larvae.

Furthermore, in their fifth instars, *H. punctiger* larvae become polymorphic. Polymorphism in cryptic animals is of greater survival value since it enables them to be cryptic in many habitats (Allen, 1972); moreover, caterpillars of different colours have been reported to select habitats similar to their own colours. For instance, caterpillars of the hawkmoth, *Errinyis ello* are green in earlier instars and rest upside down on green leaves but its last three instars appear in three morphs, green, brown and grey. Whilst green larvae continue to rest on green leaves, the brown and grey tend to rest dorsal side uppermost, on brown twigs (Curio, 1965).

Final instar larvae of *H. punctiger* bury themselves in the ground where they pupate, and first instar caterpillars of *H. punctiger* bore into plant materials and hence avoid predation (cf. Chapter 8). This may be considered as partial anachoresis. Furthermore, small caterpillars (second and third instars) on plants are very sensitive to a predator's approach; they first assume characteristic motionless position, with body pressed against the leaf and if this fails to deter the approaching predator the caterpillars tend either to walk away or simply to jump off the plant, either remaining suspended on silken threads or falling all the way to the ground. Marston *et al.* (1978) noted that several lepidopterous larvae such as *Heliothis zea*, *Trichoplusia ni*, *Pseudoplusia includens*, *Anticarsia gemmatalis* and *Plathypena scabra* adopted motionless or 'alarm' postures in the face of predation, with the anterior parts of their bodies rigidly elevated. However, *H. punctiger* larvae, although they ceased moving were seldom seen motionless with anterior parts of the body lifted. Besides large caterpillars (fourth instar and onwards) when poked gently rolled into a ball and remained motionless or apparently feigned death. This was also observed in large caterpillars (fourth and fifth instars) that came off the plant. Thanatosis or 'playing dead' is part of the defense of many other insects (cf. Capinera, 1976; Wilson and Clark, 1977).

Dropping off the plants to escape predators is common in aphids (Dixon, 1958; Dixon and Russel, 1972; Russel, 1972). But at times it can be hazardous, especially in summer when ground temperatures are high or the vegetation is sparse. Furthermore, it interrupts feeding. Thus, in areas where ground temperatures are high, aphids defend themselves by back-up tactics and do not drop off the plant (Roitberg and Myers, 1979). Similarly, it may be disadvantageous for small *H. punctiger* caterpillars to drop to the ground. Thus, many of them drop on silken threads and climb back on them when danger is passed.

Large caterpillars (fourth instar and onwards) do not drop off the plant but defend themselves by aggressive retaliation. The weapons used in retaliation include 'head-flicking', oral spitting and biting. Head flicking was effective deterrent against many predator stages which drove them off. Myers and Smith (1978) noted head flicking in tent caterpillars in response to the flight sounds of their tachinid parasite, *Tachinomyia similis*. Furthermore, Sullivan and Green (1950) reported an interesting observation on the retaliatory/aggressive behaviour of the web-worm "web-worm larvae of the last instar were more discrete in their reaction. During one episode a larva encountered a bug on the lower outside surface of the web. It grapsed the bug by a leg with its mandibles, lifted it off the web, and hanging head downwards, and whipped the forepart of its body to and fro. Thus when the bug was finally released, it was thrown away from the web".

Biting as a means of defense has been reported for caterpillars and other insects. For instance, Hays and Vinson (1971) noted *H. virescens* caterpillars biting at their parasite *Cardiochiles nigriceps* and Morris (1963) observed *Hyphantria cunea* larvae chewing at the legs and antennae of *P. maculiventris*.

Oral spitting of *H. punctiger* caterpillars that usually goes with biting and occasionally with head flicking is probable of defensive nature, as predators are often seen cleaning their antennae and probosces after being bitten off. Eisner *et al.* (1974) demonstrated that 'oral effluent' of sawfly, *Neodiprion sertifer* larvae was deterrent to its predators. 'Oral effluent' of other insects has been proved to be of a defensive nature. For instance, regurgitate of many orthoptera (Freeman, 1968; Eisner, 1970; Lambery and Baily, 1980) acts as deterrent to predators.

9.5 FORAGING BEHAVIOUR OF *O. SCHELLENBERGII*

9.5.1 Introduction:-

Animal predators show a wide range of prey capturing strategies. For example, there are filter feeding predators (blue whales), predators that trap their prey (web-spinning spiders), others that rely mainly on ambush (leopard and mantids); or on stealth (chameleons) or on speed, such as cheetahs and birds of prey (Hassell, 1976).

Insect predators also use diverse tactics to capture their prey. Some resort to ambush, others search actively and stalk their prey. Also the attack strategy of a predator may be influenced by several factors such as attractiveness or position of the prey; fasting level or reproductive state of the predator (Rilling *et al.*, 1959; Holling, 1966).

There are few published reports on the foraging tactics of predacious pentatomids and they are not only sketchy but are also based on few observations. These observations were made on the attack behaviour of juvenile and adult predators to determine whether predation tactics change as the relative sizes of predator and prey change.

9.5.2 Methods:- Observations on foraging tactics and escape responses were made simultaneously.

9.5.3 Results:- Foraging tactics of *O. schellenbergii* are related to the size of the caterpillar encountered. When caterpillars were small compared with the predator, any part of the caterpillar that was exposed to predators or came within their reactive distance (Holling, 1966) was attacked (Table 9.2). However, attack strategy changed dramatically when predators and prey of equal sizes interacted. In this event predators tended to attack the caterpillar close to head and they did this persistently (Table 9.3). It has already been demonstrated for adult *O. schellenbergii* (cf. Chapter 5 and 6). Moreover, a caterpillar attacked closer to the head was more susceptible to captures (cf. Chapter 5).

Predators are known to use different tactics to handle different sized prey. For instance, *Zelus exsanguis* ensnares small prey in sticky hairs on fore and mid tibiae (Edwards, 1962), but mainly pounces on the large prey. *Tropiconabis* spp. also use different methods to cope with different kinds of prey (cf. Chapter 4).

By attacking large or evenly matched caterpillar close to the head, *O. schellenbergii* can block the occurrence of two very potent defense ploys, such as head waving and biting back.

Table 9.2. Distribution of probe sites of large predators against small caterpillars.

Predator Stage	Prey instar	Total probes observed	Distribution of probes			
			Anterior	Middle	Posterior	
Fifth (15)	Second	15	5	3	7	$\chi^2_2=1.6$ P>0.05
Adult ♀ (15)	"	15	4	4	4	$\chi^2_2=1.2$ P>0.05
Adult ♂ (15)	"	15	5	5	4	$\chi^2_2=0.2$ P>0.05

Number in parenthesis shows number of predators tested.

Table 9.3. Distribution of probes against evenly matched caterpillars by O. schellenbergii.

Predator	*n*	Prey instar	Total probes observed	Distribution of probes			
				Anterior	Middle	Posterior	
Second	15	Second	32	18	3	11	$\chi^2_2=10.3$ P<0.01
Fourth	15	Third	52	28	9	15	$\chi^2_2=10.9$ P<0.01
Adult ♀	15	Fourth	21	15	3	3	$\chi^2_2=13.7$ P<0.01

Table 9.4. Probing attempts of small predators against large caterpillars.

Predator	*n*	Prey instar	Total probes observed	Distribution of probes			
				Anterior	Middle	Posterior	
Second	10	Fifth	67	6	11	50	$\chi^2_2=52.0$ P<0.001
Third	10	"	109	23	11	75	$\chi^2_2=63.7$ P<0.001
Fourth	10	"	102	19	12	71	$\chi^2_2=61.1$ P<0.001

Furthermore, attack behaviour changed when small predators (second, third and fourth stages) interacted with large caterpillars (fifth instars). In the first few encounters, predators attacked any part of the caterpillar that was exposed to them, but after being beaten off once or twice, they appeared to start avoiding going close to the head. Instead, they persistently attacked the posterior part of the caterpillar, in particular the posterior prolegs became the targets of attacks (Table 9.4). Small predators attack prolegs with the appearance of skilled marksmanship (cf. Chapter 4).

9.5.4 Discussion:- *O. schellenbergii* appeared to be an opportunistic predator and is not restricted in diet as is another pentatomid predator, *Stiretrus anchorago* (Hemiptera : Pentatomidae), which accepted *Galleria melonella* larvae only reluctantly (Waddill and Shepard, 1975). The foraging tactics of *O. schellenbergii* are related to the size of its prey. Small caterpillars, that drop off the plant when disturbed are approached cautiously and surreptitiously, the stylets are inserted at any part of the caterpillar that comes within the predator's reactive distance. Tostowaryk (1971) noted similar behaviour pattern in *P. modestus* attacking sawfly larvae, *Neodiprion swainei*.

However, when the predator and prey are evenly matched in size, the predators tend to attack close to the head. This may be due to the prey's normal movement, during which the anterior part of the head is conspicuous and possibly attracts the predator's attention. Iwao and Wellington (1970) demonstrated that the attack strategy of *P. maculiventris* was correlated with prey movement. However, the fact that persistent attacks by *O. schellenbergii* occurred at the anterior end of *H. punctiger* caterpillars only in certain combinations of predator-prey sizes and not in others, negates Iwao and Wellington's view. Furthermore, in evenly matched predator and prey interactions predators tended to adopt a 'backup' behaviour. They pulled back a little and appeared to pull the caterpillar off the plant and keep it suspended in the air. Marston *et al.* (1978) noted this backup behaviour in *P. maculiventris*. Other authors have also observed similar behaviour in predacious pentatomids (e.g. Sullivan and Green, 1950; Morris, 1963; Mukerji and LeRoux, 1969). Furthermore, Mukerji and LeRoux also observed *P. maculiventris* using its forelegs to hold the prey. This was seldom observed in the present study.

Ables (1978) reported that *Z. renardii* predominantly attacked the tobacco budworm larvae close to the head and that in case of vigorous struggle, the proboscis was withdrawn and stylets reinserted in another region. *O. schellenbergii* never does this while attacking small caterpillars. But it does use the re-insertion behaviour in evenly matched interactions, where, during the struggle, predators are forced to release the caterpillar temporarily. The predators then tend to probe again near the head.

Attacks by juvenile predators directed at the prolegs may probably be due to their less sensitivity compared with the rest of the body. This strategy of small predators against large caterpillars does not appear to have been reported before and it is an advantageous adaptation of survival value (cf. Chapter 4).

CONCLUSION

Observations on escape reactions of *H. punctiger* caterpillars demonstrate that only a proportion of caterpillars encountered are actually captured by *O. schellenbergii*. Large caterpillars (fifth instar and onwards) are immune to predation due mainly to their massive sizes and effective defense ploys. Even fourth instar caterpillars were able to deter most of the juveniles by their defense ploys.

Observations on foraging tactics of *O. schellenbergii* indicated that they were geared to break the defenses of *H. punctiger* caterpillars. But in interactions where they cannot counter their ploys, they may be able to feed off the host without totally subduing it.

GENERAL DISCUSSION

Tropiconabis nigrolineatus, Oechalia schellenbergii and *C. nasalis* are endemic general predators that prey upon a wide variety of prey species including the native budworm, *Heliothis punctiger*. There has been a great deal of discussion on the relative importance of predators and parasites as biological control agents of agricultural pests. Although opinions still vary, there is a general consensus among entomologists that parasites are more efficient control agents than predators. Most parasites are host specific, their life cycles are often well synchronised with their hosts and the fact that their juveniles do not search for hosts increases their efficiency as bio-control agents (Doutt and DeBach, 1964).

The poor searching ability of many predacious insects, especially in their early stages is their greatest disadvantage (Dixon, 1958; Dixon and Russel, 1972; Brown, 1972; Glen, 1973, 1975; Wratten, 1973, 1976) and compared with parasites they require a higher prey density for survival of first stage juveniles. *O. schellenbergii, C. nasalis* and other predacious pentatomids (Muckerji and LeRoux, 1965; Tostowaryk, 1971) have to some extent overcome the problem of inefficient early search by having non-feeding (non-predacious) first stages (cf. Chapter 3); nevertheless, the searching ability of second stage *O. schellenbergii* and *C. nasalis* is low (cf. Chapter 4) and these species do not appear to have obtained a great deal of advantage from avoiding earlier predation. Doutt and DeBach (1964) have argued that each predator must be judged on its own merits and their importance should not be deprecated simply because they are not host specific.

Furthermore, some spectacular successes in biological control have been achieved with predators alone, e.g. the biological control of spider mites throughout the world (Huffaker *et al.* 1969).

There has been some discussion on the subject of 'specialists versus generalists' and it appears that on the basis of recorded successes in biological control programmes 'specialists' have won the contest; i.e. specialists (oligophagous predators or parasites) are considered to be more reliable bio-control agents than 'generalists' (polyphagous predators or parasites). This is particularly true in stable habitats (Huffaker *et al.*, 1971). Nonetheless, Doutt and DeBach (1964) argued that in annual crops (unstable conditions) where host species are much depressed by other factors (Ehler *et al.*, 1973) the 'specialists' would be at a greater disadvantage than 'generalists' which would prey upon alternate species and switch over to the main prey species when it increased again. Switching from one species to another, according to their relative abundance, is common in general predators (Murdoch, 1969). Although experiments on 'switching' among the hemipterans studied were not conducted, there is circumstantial evidence suggesting that *O. schellenbergii* and *C. nasalis* adults switch over to caterpillars of *Ectropis excursaria* (Mariath, 1980; unpublished data) and vine moth, *Phalaenoides glycine* (Cordingly, 1977) at times when *H. punctiger* larvae are low in lucerne patches.

The relative importance of exotic (introduced) versus indigenous (local) predators has generated a great deal of comment in recent years. The role of indigenous predators in suppressing pest populations has largely been considered as minor, and the statements about the impact of indigenous predators based on the correlations of predator abundance and changes in pest populations are viewed with scepticism, due mainly to the fact that such data represent the cumulative impact of parasites, predators and pathogens. Most reviews (Hagen and van den Bosch, 1968; Hodek, 1973; van Emden, 1972) discuss the overall impact of natural enemies rather than predators alone, and this perhaps is partly due to the inseparable nature of the impact of natural enemies in nature.

However, some workers were able to separate this action. For instance, Smith and Hagen (1966) studied the impact of indigenous predators on spotted alfalfa aphids in California (prior to the introduction of parasites and use of resistant varieties) and found that local coccinellids effectively controlled aphids in spring and fall. *Neuenschwander et al.* (1975) corroborated Smith and Hagen's findings and showed that the numbers of coccinellids and hemerobiids were closely related to the aphid populations and showed a density-dependent relationship in the abundances of predators and aphids. These authors further argued that polyphagous predators such as chrysopids and hemipterans became important when the dominant coccinellids became either inactive due to diapause or when lower aphid numbers prompted their migration to other places.

Several studies of interactions between aphids and their local predators in different agro-ecosystems have substantiated the importance of native predators (cf. Tamaki *et al.*, 1967; Shands *et al.*, 1972; Tamaki, 1973). General predators appear to be responsible for preventing some pest outbreaks, especially in monocultures. According to DeBach (1951) "general predators act as a sort of a balance wheel in the pest/natural enemy complex", tending to prey opportunistically upon whatever prey is present in abundance". Thus, there is need to evaluate the effectiveness of native predators before contemplating foreign introduction (Tamaki *et al.*, 1974).

Furthermore, general predators have been shown to be effective bio-control agents of noctuids such as *Spodoptera exigua* and *Trichoplusia ni* in annual monoculture crops like cotton, but these pests become abundant after insecticide applications against *Lygus* buggs (van den Bosch *et al.*, 1971). Eveleen *et al.* (1973) and Ehler and van den Bosch (1974) considered this was due to the destruction of the general predators, *Geocoris* spp., *Orius* spp., *Nabis* spp. and *Chrysopa* spp. that led to increase in numbers of noctuids. Insecticides are perilous to many predator species (Clausen, 1956; McMurtry *et al.*, 1970).

Moreover, the plant-feeding habits of hemipterans (cf. Chapter 3) make them susceptible even to systemic poisons (Ridgway and Jones, 1968). Although systemic insecticides are not used against *H. punctiger* in Australia, nevertheless strong formulations and frequent applications of DDT and other organochlorines exterminate the predators.

Ehler and van den Bosch (1974) noted that most hemipterans and chrysopids acted in a density-independent fashion relative to the intrageneration abundance of their lepidopterous prey in cotton. In their view these predators are r-strategists, a strategy of expected value in unstable situations. I agree with them; none of the hemipterans studied are likely to act in a density-dependent manner and they conform to the characteristics of r-strategists.

Furthermore, hemipterans have higher egg and nymphal development thresholds (cf. Chapter 3) relative to *H. punctiger*. This, and the time lag between the two allows *H. punctiger* populations to build up in numbers and

H. punctiger's relatively high reproductive potential (Cullen, 1969) further reduces the chances of predators catching up with the pest populations. But when the pest populations crash (Cullen, 1969; Cooper, 1979) due to virus epizootics in mid or late summer, predators may keep the populations at lower levels thereafter and there is evidence that predators may help spread virus infections from one population to another or even from one paddock to the other (Cooper, 1979).

Experiments on voracity at various constant temperatures indicated that temperature did not affect the overall feeding capacity of predators, albeit it affected their daily food consumption to a great extent (cf. Chapter 4). I agree with Frazer and Gilbert (1976) when they argue that temperature has a single effect on prey or host species but a double effect on predators. Temperature affected predators' rate of development and daily food intake and, above all, it affected their efficiency of capture (cf. Chapter 8). Many ecologists (Frazer and Gilbert,1976) insist that laboratory studies must be followed up and supplemented by field trials. If not, extreme caution must be exercised in relating them to field situations. I fully subscribe to this view and suggest that present results should be used as background information for further field studies.

Data on fecundity of the three species, collected at different temperatures shows a high reproductive potential for each species; and, as indicated by Lawton, Hassell and Beddington (1975) an increase in predator numbers is a function of (i) duration of each instar, (ii) survival rates within each instar, and (iii) the fecundity of adults, and all these components are dependent on the availability of prey (Beddington *et al.*, 1976). Hence my data on the survival rate of juveniles and on fecundity must be viewed with caution as they were gathered in a situation where animals were feeding at their maximum rates, a condition different from real field conditions.

Results on searching behaviour (cf. Chapter 6) indicated that *O. schellenbergii* located its prey by visual and olfactory cues. Two previous reports on predacious pentatomids, *Podisus modestus* (Morris, 1963) and *P. maculiventris* (Mukerji and LeRoux, 1965) have suggested the involvement of vision in prey-finding by these predators. I have taken this aspect of pentatomid's searching one step further and demonstrated their responsiveness to larval movement and quantified the speed of prey movement that was most attractive to them. At fast speeds caterpillars were either imperceptible or failed to elicit predatory response in *O. schellenbergii.* What was it so?. And what could be the plausable explanation for this behaviour?. The explanation probably lies in the structure and physiology of the insect compound eyes, which provide poor image formation but are excellent at detecting movements. Predators are known to respond to a moving stimulus (Edwards, 1966; Ables, 1978), but this does not explain the non-responsiveness to fast-moving caterpillars observed in this investigation. The best explanation that I can think of and that conforms to general concepts about predators is that the fast-moving caterpillars probably move out of predators' reactive distance and because of this fail to elicit predatory response.

In addition to responsiveness to prey movement, *O. schellenbergii* is also capable of responding to *H. punctiger* larvae by olfaction at a short distance and search the adjacent area more intensively, coupled with turning behaviour (Klinokinessis), as reported in several insect predators (e.g. Fleschner, 1950; Banks, 1957; Wylie, 1958; Hafez, 1961; Bansch, 1966; Murdie and Hassell, 1973; Brunner and Burts, 1975; Storch, 1976; Stubbs, 1980). This may keep *O. schellenbergii* longer in areas of relatively high prey density and may lead to the discovery of small and hidden prey in the lucerne fruits, buds and flowers.

Observations on the defense strategies of *H. punctiger* (cf. Chapter 9) indicate that prey 'catchability' is a major factor that limits the effectiveness of hemipterans in preying upon *H. punctiger*. Large caterpillars (fifth and sixth instars) are immune to all predators and this is due to their effective use of defense ploys against juveniles and adults.

Despite the high reproductive potential of two pentatomid species under laboratory conditions their numbers were low in the field. This was mainly due to a scelionid parasite *Trissolcus* spp., which was originally introduced in the biological control of *Nezara viridula*, a cosmopolitan vegetable pest. The parasite has controlled the vegetable bug and has turned to other pentatomid eggs as well. This could well be a case of an unfortunate decision with regard to a foreign introduction of a biological control agent.

This parasite is more perilous to *C. nasalis* than *O. schellenbergii* and its degree of parasitism reaches its maximum level in January-February, a period when the last generation eggs are laid. Heavy mortality at this stage results in fewer overwintering adults and hence lower numbers to start the next population the following spring. The differential mortality in the two species of pentatomids caused by the parasite was not followed up (due to lack of time); it may well be related to differences in the sizes of the egg batches of the two species. Alternatively, it is possible that they are attacked by two separate parasites (K.S. Hagen, 1980; pers. comm.).

APPENDIX 1

Table of analysis of variance of fecundity of two species for data presented in Table 3.6.

Source of variation	df	SS	SS %	MS	VR	
Temperature	3	29.1	16.5	9.7	6.7	$P<0.01$
Species	1	2.6	1.4	2.6	1.8	
Temperature X Species	3	12.2	6.9	4.0	2.8	$P<0.05$
Residual	92	132.3	75.0	1.4		
Total	99	176.2	100.0	1.7		

Table of Means

Temperature	*O. schellenbergii*	*C. nasalis*
35°C	4.8	3.3
30°C	5.0	5.2
25°C	5.6	5.4
20°C	4.6	4.8

Approximate LDS = 0.94

APPENDIX 2

Table of analysis of variance for longevity of males of two species for data provided in Table 3.8.

Source of Variation	df	SS	SS %	MS	VR	
Temperature	4	42.9	28.2	10.7	17.0	$P<0.01$
Species	1	1.1	0.7	1.1	1.8	
Temperature X Species	4	0.8	0.5	0.2	0.3	N.S.
Residual	170	107.0	70.4	0.6		
Total	179	152.0	100.0	0.8		

Table of Means

Temperature	*O. schellenbergii*	*C. nasalis*
35°C	2.8	2.8
30°C	3.1	3.5
25°C	3.5	3.5
20°C	3.5	3.8
15°C	4.2	4.4

APPENDIX 3

Analysis of variance on longevity of females of two species for data presented in Table 3.8.

Source of Variation	df	SS	SS %	MS	VR	
Temperature	4	86.8	42.8	21.7	34.1	$P < 0.001$
Species	1	7.4	3.6	7.4	11.6	
Temperature X Species	4	0.5	0.2	0.1	0.2	N.S.
Residual	170	108.1	53.2	0.6		
Total	179	202.9	100.0	1.1		

Table of Means

Temperature	*O. schellenbergii*	*C. nasalis*
35°C	2.1	2.6
30°C	2.6	2.9
25°C	3.2	3.5
20°C	3.3	3.8
15°C	4.1	4.6

LSD = 0.49/0.5

APPENDIX 4

Table of Analysis of Variance for Data Presented in Table 4.2.

Source	df	SS	MS	VR	P
Species, ignoring sex	2	13.91	6.9543	3010.1472	P<.001
Sex, allowing for species	1	0.25	0.2502	108.298	P<.001
Residual*	35	0.081	0.0023		
Total	38	14.24			

Source	df	SS	MS	VR	
Sex, ignoring species	1	0.16	0.16143	69.874	P<.001
Species, allowing for sex	2	14.00	6.9987	3029.366	P<.001
Residual*	35	0.081	0.00231		
Total	38	14.24			

* Note: The interaction MS was non-significant at the 2.5 percent level - (F (2,33) = 3.4), so it was pooled with the residual SS and the main effects tested.

Table of Means

Sex	*T. nigrolincatus*	*O. schellenbergii*	*C. nasalis*
Female	5.7367 (8)	6.7401 (7)	7.1360 (6)
Male	5.5754 (7)	6.6611 (7)	6.9824 (4)
F - M	0.1613	0.079	0.1536
"LSD"	0.0498	0.0514	0.0620

APPENDIX 5

Analysis of variance for female *T. nigrolineatus* for data shown in Table 4.8.

Source	df (MV)	SS	MS	VR	
Temperature	4	28753.85	7188.46	74.754	P<.001
Residual	45 (5)	4327.29	96.16		
Total	49	33081.14	675.3		

Table of Means

15°C	20°C	25°C	30°C	35°C
311.6a	315.0a	313.0a	274.1b	260.7c

LSD = 8.36

APPENDIX 6

Analysis of variance for male *T. nigrolineatus* for data presented in Table 4.8.

Source	df (MV)	SS	MS	VR	P
Temperature	4	56655.7	14163.9	75.302	P<.001
Residual	41 (4)	7711.9	188.1		
Total	45	64367.7	1430.4		

Table of Means

15°C	20°C	25°C	30°C	35°C
254.6	253.8	256.1	189.3	183.2

LSD = 12.26

APPENDIX 7

Analysis of Variance of Data presented in Table 4.10 on Predation Against First Instar Caterpillars for II, III and IVth Stage Predators

Source of Variation	df	SS	MS	VR	P
Species	2	87.67	43.83	968.81	P < .001
Instars	2	126.36	63.18	1396.3	P < .001
Conditions	1	5.03	5.03	111.27	P < .001
Species x Instar	4	8.04	2.01	44.46	P < .001
Species x Condition	2	0.30	0.15	3.36	P < .05
Instar x Condition	2	1.27	0.63	14.11	P < .001
Species x Instar x Condition	4	0.93	0.23	5.17	P < .001
Residual	247(5)	11.17	0.04		
Total	264	240.81			

APPENDIX 8

Analysis of Variance of Data for 5th Stage Males and Females Presented in Table 4.10

The design was unbalanced so the following analysis of variance table is (at best) approximate.

Source of Variation	df	SS	MS	VR	P
Sex	1	2.50	2.50	121.05	P .001
Species	2	61.74	30.87	1494.24	P .001
Condition	1	1.88	1.88	91.38	P .001
Sex x Species	2	0.18	0.09	4.42	P .001
Sex x Condition	1	0.03	0.03	1.87	N.S.
Species x Condition	2	0.14	0.07	3.46	P .05
Sex x Species x Condition	2	0.10	0.05	2.58	P N.S.
Residual	53	1.09	0.02		
Total	64	67.69			

APPENDIX 9

Table of analysis of variance for data presented in Table 6.5.

Source of Variation	DF	SS	MS	F	P
Between classes	2	253.40	126.70	8.83	< 0.05
Within class	27	387.30	14.3		
Total	29	640.70			

APPENDIX II

NATURAL MORTALITY AGENTS OF *OECHALIA SCHELLENBERGII* AND *CERMATULUS NASALIS*

INTRODUCTION

O. schellenbergii and *C. nasalis* showed high reproductive potential in laboratory (Chapter 3) but their numbers in the field remained relatively low. *C. nasalis* had the lowest numbers of the two species. Cordingly (1977) described that eggs of *O. schellenbergii* were parasitized by an anonymous scelionid parasite in vineyards.

Several wasp species belonging to Scelionidae, Encyrtidae and Eupelmidae are known to parasitise pentatomid eggs, but scelionid genera *Telenomous* and *Trissolcus* contain by far the majority of the parasite species that attack pentatomid eggs. (Esselbaugh, 1948). Furthermore, *Trissolcus basalis* has been introduced to several countries as a biological control agent of *Nezara viridula*, and appears to have been studied more intensively than any other egg parasite of stink bugs (Bartlett *et al.*, 1978).

MATERIALS AND METHODS

Field studies were conducted in lucerne plot near Waite Institute during 1980-81 season. Naturally deposited eggs of *O. schellenbergii* and *C. nasalis* were collected from the study plot at weekly intervals, brought to the laboratory and held at 25°C and their development and 'hatchability' was monitored. The eggs that failed to hatch were dissected to ascertain the prescence of parasites.

RESULTS AND DISCUSSION

Results indicated a differential parasitism pattern for two species (Table 2A). Egg batches of *O. schellenbergii* were relatively more common and less parasitized than egg batches of *C. nasalis*. Parasitized eggs of two species were much darker in colour. Moreover, batches of *C. nasalis* that were discovered by the parasite were heavily parasitized and in some batches degree of parasitism reached nearly 100 percent. However, eggs of *O. schellenbergii* were not parasitized so heavily, and some eggs at the centre of the batch escaped parasite attacks. This probably may be due to the morphological differences in the eggs of two species or probably due to differences in the numbers of eggs per batch or possibly due to two separate parasite species being involved. But whatever the reason may be, eggs of *C. nasalis* always suffered higher mortalities.

Table 2(A). Parasitism of naturally-oviposited eggs of *O. schellenbergii* and *C. nasalis* egg masses collected from lucerne plot.

Host species	Total eggs collected	No. of egg batches collected	No. of egg batches parasitized	Not parasitized	Percentage parasitism	No. [illegible]
O. schellenbergii	1050	45	25	20	64.2*	55.6
C. nasalis	975	19	13	6	89.0	68.4

* Percentage based on the number of eggs parasitized.

Furthermore, it appeared that degree of egg parasitism of both species increased in the months of January and February. This would have important implications for the overall numbers of predators that may appear in the following season. Since eggs laid in January-February give rise to the adults of last generation that overwinter and appear in the next spring to start the first generation in a new season. Although this hypothesis seems logical and explains the reasons for low numbers of *O. schellenbergii* and *C. nasalis* in lucerne fields, nevertheless direct or indirect impact of egg parasites on populations of predacious pentatomids in lucerne crops or elsewhere, is a challenging problem, and a project in itself that needs further investigation. There is distinct possibility that parasite in question is a single species and is attacking eggs of phytophygous as well as predacious pentatomids. If so, then the species is a 'generalist' with a dual status, 'beneficial' as well as 'pest' (Yeargan, 1979).

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