THE FEEDING BEHAVIOUR OF A SIT-AND-WAIT PREDATOR – ETHOLOGICAL STUDIES ON RANATRA DISPAR (HETEROPTERA : NEPIDAE), THE WATER STICK INSECT

By

Paul Charles Edward Bailey B.Sc. Hons. (A.N.U.)

A thesis submitted for the Degree of
Doctor of Philosophy in the Faculty of
Agricultural Science at the University
of Adelaide.

Department of Entomology,
Waite Agricultural Research Institute,
University of Adelaide.

April, 1984

Date of award [illegible]

How cheerfully he seems to grin,
How neatly spreads his claws,
And welcomes little fishes in
With gently smiling jaws!

Lewis Carroll
Alice in Wonderland

TO MY PARENTS

and

LOUISE

TABLE OF CONTENTS

SUMMARY

The aquatic bugs, Ranatra dispar and Anisops deanei, were used to study ethological and ecological interrelationships in the predatory behaviour of an extreme ambush predator (R.dispar) and its common, mobile prey (A.deanei).

The sequence of behavioural components in the predatory behaviour follows the basic ambush pattern, i.e. initial precapture posture, arousal, orientation, capture, consolidation of grip, exploration, injection of venom/enzymes, feeding, discard of prey, although much variation between components exists. Much of this variation is described, including the predator's defensive and evasive behaviour, along with their effect on the predatory behaviour. The predator's arousal and strike space are described. Both spaces increase with food deprivation.The capture space is dependent on the morphology and reach of the raptorial legs, there being no lunge or pursuit component in the predatory behaviour. Attempts to describe the shape of the arousal space and the effect of hunger using the model designed by Holling (1966) proved reasonably satisfactory, after slight modification, for the horizontal plane but totally unsatisfactory for the vertical plane. This is believed to be due to the unusual eye structure of Ranatra.

The additional effect on predatory behaviour of prey size was investigated. It was found that the hunger level determines whether R.dispar will initially be aroused or not but the distance at which the arousal takes place is influenced by the size of the prey. This is

believed to reflect the capacity and interrelation between visual and mechanoreceptor, sensory organs. The decision to strike at a prey is, although again influenced by hunger, significantly affected by prey size. The distance of the prey when the strike takes place is affected by hunger not the size of the prey. The outcome of the strike is determined by the size of the prey, not the hunger level of the predator. This is believed to reflect the relationship between strike trajectory, leg morphology and prey size. Food deprivation affects all components of predatory behaviour of R.dispar leading up to prey capture, by increasing not only distance of response but also the number of strikes, hits, and captures per unit presentation of prey. It does not affect capture efficiency which remains at about 70 to 80%. Food deprivation also increases the range of prey sizes that R.dispar responds to and attempts to capture. The effect of food deprivation is considered to reflect a motivational change in responsiveness to particular prey stimuli usually described as a sensitization of particular stimulus-response relations rather than the food deprivation affecting the sensory mechanisms. The predatory success in relation to size of model prey suggested an 'optimum' size that could be captured, irrespective of predator motivational level, which is based primarily on the relationship between the shape of the grasping leg and size of prey.

Functional response experiments were performed to examine the effect of prey density on feeding behaviour and to measure attack rates and handling times. In both the temperature and age structure of predator and prey effects, the most generally applicable response seemed to be the Type 2. Progressively more prey were eaten between 15.0°C and 29.0°C. Over the temperature range investigated the attack-rate

increases almost linearly while the handling-time increases dramatically between 15°C and 20°C after which it remains constant up to 30°C. Generally the handling-time increases as prey size increases and decreases as the predator size increases. The attack-rate surface is far more complex.The maximum attack rate for instars I and II occurred on the smallest prey size (1 and 2),while as the predator size continued to increase, so the attack-rate on each of the prey sizes increased. Unlike the previously published attack rate surface, with small predators attacking small prey and large predators attacking large prey, the maximum attack-rate stops at the intermediate prey size 3. Predator instar V has the largest attack rate values over all prey sizes. Adult R.dispar have noticeably lower attack-rates for various prey sizes than instars V, IV and to some degree III. The results suggest that small predator instars will usually compete with large instars for prey, unless there is spatial or temporal separation between them. Observations conducted in the field indicate that a distinct age-specific spatial distribution exists in R.dispar (and in the prey A.deanei) with the smallest individuals being found predominantly in the shallow (littoral zone) water while the larger individuals are found in the deeper water.

Related behaviours of the predator were investigated in order to identify factors that were believed to be involved in the observed increase in the numbers of prey eaten at different prey densities.

The feeding behaviour of R.dispar was examined with respect to the prey utilization, the time between successive captures (intercatch interval) and the feeding time. The feeding process consisted of three stages. (1) Injection of venom, (2) breakdown of tissue/digestive stage and (3) extraction of food. The rate of extraction from an individual prey decreases as the prey item is depleted. The extraction rate was shown to increase significantly during the first 15 minutes before decreasing. Even after 30 minutes the extraction rate was still marginally higher than the initial extraction rate. This phenomenon is quite different to what has previously been reported for sucking bugs. There was a negative relationship between increasing prey density and prey depletion, with the predators being significantly more 'wasteful',(i.e. prey were discarded before all extractable food was removed) at the two higher prey densities compared with those at the lower densities. As the prey density decreased from 60 to 1 prey per container, so the resultant intercatch interval and feeding time increased. In conjunction with this the average dry weight extracted per prey also increased. No correlation was found between individual intercatch interval and subsequent feeding time when examined through an 8 prey catch sequence. This is taken to support the Optimal feeding model in which the predator reacts to the average profitability of the environment (i.e. mean intercatch interval) rather than to the specific level of food in the gut which has resulted from the length of the intercatch interval. The overall effect of the extraction dynamics and duration of feeding on one prey item at different prey densities is that at higher densities, although spending less than half the time on a prey item compared with the low density, the predator still obtains almost 60% of the available prey contents before discarding.

By the use of fluorescent dyes it was shown that during feeding water from the external environment passes into the prey's body, through, it is believed, puncture holes from previous feeding sites. Such a phenomenon, resulting in the diluting of the prey body contents,

may be used as a physiological stimulus to detect the quality of the prey which may in turn be used in deciding whether to cease feeding at one site and move to another part of the prey's body or discard the prey.

R.dispar is shown to be able to capture and hold a number of prey simultaneously. Capture of prey characteristically occurs in three distinct patterns, each characterized by a different number of prey caught. The time since last feeding by the predator has a significant effect on whether the predator will capture more than one prey. Once feeding starts there is a critical period during which, if an encounter takes place, the predator will attempt to capture the prey. Once past that period prey are ignored. The critical period is longer the higher the motivational level of the predator. It is suggested that this multi-prey capture behaviour potentially increases the size of a meal as groups or schools of prey move pass the ambush predator.

Particular features of the prey's behaviour believed to be involved in determining its movement patterns, and thus encounter-rate with an ambush predator, were investigated.

Four basic swimming patterns of A.deanei are described. The effects of water temperature and density on movement patterns show that both have a significant effect, with animals moving more at higher temperatures but less as density increases. It is suggested that these intraspecific interactions in groups of A.deanei lead to the formation of groups or schools of individuals, and that this observed behaviour is an anti-predator defence. This aggregating behaviour is strongly supported by data obtained from the field. Additional results indicated

that the effect of this aggregating behaviour significantly reduces the encounter-rate with an ambush predator compared with a predicted rate based on the movement of one individual. This trend was repeated over the three experimental temperatures.

Prey density was also shown to influence the choice and duration of stay at an ambush site by R.dispar. It was shown that predators changed ambush sites significantly more frequently when prey density was low compared with when prey density was high. Initially, predators remain at an ambush site for significantly longer than later stays at different sites, irrespective of the presence or absence of prey. There was a tendency, over the three prey densities examined (0, 3, 15 prey per litre), for the duration of stay at a site to become shorter as the experiment progressed. Examination of the angular changes by the predator while at an ambush site showed that R.dispar remained stationary for significantly longer periods when no prey were present, while the incidence of moving through relatively small angular changes occur significantly more often when prey were present.

By using model prey that conferred no nutritional reward it was shown that encountering a prey caused R.dispar to remain significantly longer at a 'potentially' profitable ambush site compared with when no encounter was given. It is suggested that R.dispar uses not only a mean intercatch interval but a prey encounter rate mechanism in assessing the availability of prey. It is predicted that the assessment of prey availability by ambush predators may involved more than one factor and that, depending on the circumstances, predators may switch between different mechanisms or utilize information from several simultaneously.

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.

April, 1984 Paul C.E. Bailey

ACKNOWLEDGEMENTS

Many people have helped me in a great many ways throughout the duration of this study. To all of them I extend my thanks and appreciation for all they have done. There are some that I very much would like to single out however.

I wish to sincerely thank my two principal supervisors, Professor T.O. Browning and Dr. Roger Laughlin, for their advice, suggestions, profitable discussions, and critical reading of my thesis. 'Prof' continuously caused me to question and critically examine my work and pointed out my rapid jumping to conclusions. Roger was continuously available for discussion and advice on every aspect of this study, and provided additional help and suggestions in regards to the design (both theoretical and practical) of experiments and the analysis; all with incredible patience. I am very grateful.

Discussions with Dr. Derek Maelzer, Dr. Peter Miles, Mrs. Eve Lever, and other postgraduate students helped me in formulating and refining ideas and techniques that I used.

In particular I wish to thank the following very good friends for their help : Andy Austin and David Dall for their comments and advice, especially in regards to some of the results in Chapter 5 and the Brisbane Trip. George Hoffman, Duncan McKay and Peter Samson for the many hours spent in acting as 'sounding boards' for my ideas, discussing the results and helping to provide a stimulating atmosphere (not only on Friday evenings) for formulating ideas. Duncan provided much help in statistical advice and then shared long hours on the 'keyboard' with SPSS. I sincerely thank him. Special thanks to Jennifer Parke for her advice and supportive

comments concerning the layout and construction of Chapter 3, and along with George have been such good friends over the last 10 months.

I also wish to thank 'Uncle' Dr. Paul Madge for not only his friendship but his generous gift which enabled me to go to Brisbane in 1983. The discussions I had while attending the 18 I.E.C. were particularly helpful and came at a critical time. To other members of the Friday night Choir practice at the Edinburgh I extend my gratitude; the many hours spent in 'talking shop', the advice and discussions (and jugs of beer) were much appreciated. Marija Tadic kindly converted my rough sketches and drawings into the fine line illustrations in Chapter 2.

Drs. Stan Eckett and Debbie Street (Biometry Section, W.A.I.T.) provided much statistical advice in addition to which Stan kindly wrote the program for analysing the results in Chapter 4. Noel Stewart and Ken Wilkerson helped by obtaining many pieces of equipment and advising and helping to build much of the apparatus used; the Library staff at the Waite and S.A. Museum acquired innumerable (sometimes obscure) inter-library loans for me; Mr. Brien Palk photographed and printed the line illustrations and printed the half tones; Colour Quick Pty. Ltd. advised and printed the colour plates. I wish to thank all these people, and others that I may have forgotten.

The following people kindly gave me permission to either conduct field work in, or collect animals from, their properties :
Barry Riddle (former owner), Lee Majors (owner) Riddle's Dam, Hahndorf; Tim and Moira Atkinson (Crafers); Mr. Fred Donaldson (Hahndorf); Mr. Hilly (Lobethal); Mr. Munster (Lobethal); Mr. & Mrs. von Doosa (Crafers); Alice and Rod Wells (Uraidla).

I would like to especially thank Helen Miller for the hours spent in typing my thesis into the 'Apple' mini-computer and producing, as ever, an excellent typescript.

Finally, and most of all, I thank Louise for her untiring support and encouragement through this study, especially over the last 6 months during the gestation of this thesis. Without her advice and help in every phase of this work it would have been an unenviable task.

This project was supported by a Commonwealth Postgraduate Research Award and a Special Research Grant, Postgraduate Scholarship, University of Adelaide.

CHAPTER 1

INTRODUCTION

Early forms of life probably obtained their nutrients directly from the surrounding water, but the capacity to engulf other organisms developed very early in evolution. These were the first predators and predation has remained one of the important ways of obtaining energy along with photosynthesis, detritous feeding and herbivory (if one distinguishes herbivory and predation). Predation is therefore an ecological factor of almost universal importance for the biologist who aims at understanding the habits and structures of animals. Despite this, opinions differ as to what predation really is. The Oxford Dictionary defines predation as "the habit of hunting and killing other animals for food", whereas a cursory glance at current biological literature reveals that normally predation is defined (by biologists) in negative terms. Thus, it is thought not to be parasitism, the other common process by which an organism may gain benefit at the expense of another, nor filter-feeding, carrion eating, nor browsing.

Accordingly, one could define predation as a process by which an animal expends some effort to locate a live prey and, in addition, expends further effort to mutilate or kill it (Curio 1976, p.1). From the definition just proposed, consumption of the prey, following its capture, has been intentionally omitted. Hence, the biological significance of predation may be more than the maintance of nutritional homeostasis. In fact, predation may have something in common with the (?) more direct forms of competition (Curio 1976; see also Bergon and Mortimer 1981). Therefore predation may be best distinguished from other forms of foraging by only one of its consequences, in that it concludes with the mutilation or total destruction of an animal that generally offers some resistance against being discovered and/or being harmed. Obviously, one can cite various parasites that may harm and eventually kill their hosts, but whereas it is in the interest of the parasite to ensure that its host remains alive long enough for it to complete its life-cycle, such needs are not necessary in the case of the predator.

As in other disciplines, the significance of predation can be studied broadly from the point of view of the populations of predator and prey (see for example Bergon and Mortimer 1981; Bertram 1978; Hassell 1978; Kruuk 1972b; Schaller 1972), to its effect on the individual (for example Bauer 1982; Beard 1963; Evans 1976; Lubin 1980; M~~a~~oermond 1981; Rees and Offord 1969; Schlee 1983; Schmidt 1982). Irrespective of the point of view, whether from the population or individual level, the effect is the result of a predator-prey interaction.

Predation within an ecosystem can be considered to be the sum of all interactions between single predators and single potential prey animals. A single interaction can result in success or failure for the predator, corresponding to death or escape for the prey. If a successful interaction is defined as one that results in a meal for the predator, then the rate of successful interactions is the rate of predation. For a given predator or prey, within a certain time interval, there is an associated probability of a successful interaction (Gerritsen and Strickler 1977). To examine this, the predatory interaction needs to be dissected further.

A complete predatory interaction can be broken down into a series of chronological events, culminating in ingestion. The number of events is somewhat arbitrary; Edmunds (1974) considers two events, encounter and ingestion, while Gerritsen and Strickler (1977) list four, (1) the animals must first encounter each other, (2) the predator must recognise the other animal as a potential prey item and attack it, (3) it must capture the prey, and (4) it must successfully ingest the prey. It is to be expected that each of the animals in question (i.e. the predator and the prey) is likely to have a set of adaptations to change the probabilities in its favour at each of the four steps. As Dawkins and Krebs (1979) so elegantly suggest, the development of predator-prey interactions can be viewed as a co-evolutionary "arms race"; predator species evolve more efficient techniques for any of the above chronological steps and prey species counter with defensive adaptations.

Nevertheless, no matter how many arbitrary divisions that the predator-prey interaction is broken down into, the <u>encounter</u> of predator with prey is of paramount importance. Obviously, if there is no encounter between predator and prey, no predation can take place, irrespective of how efficient particular adaptations may be later in the series of events culminating in ingestion. However, prey species differ in their defence tactics (see Cloudsley-Thompson 1980; Edmunds 1974). Therefore, predators preying on more than one type of prey often employ a number of various hunting techniques to bring about the all-important encounter, while others employ one method throughout their lives. This, in addition to the fact that the diets of most predators are different from each other point to the existence of almost as many encountering techniques as there are types of prey (for example Chinery (1979) describes over 250 strategies and techniques). Yet, within the predators as a whole, two broad modes of predation can be identified: "those that go forth and hunt their prey and those that sit and wait" (Edwards 1963).

In the former category, Curio (1976) describes two techniques used by predators viz. sustained movement over, sometimes, considerable distances as shown, for example, from the seemingly random blundering into prey by predatory mites and insect larvae (Sandness and McMurtry 1972; Dixon 1959) to the relentless pursuit by African hunting dogs (*Lycaon pictus*) (Estes and Goddard 1967) and wolf (*Canis lupus*) (Burkholder 1959; Mech 1970). The second is the sudden rush onto a prey (normally over very short distances) which is often preceded by a period of stalking (Curio 1976, p.136), during which the predator manoeuvres itself into such a position that it is close enough for rapid assault. Examples of predators that often utilize such a technique are the lion (*Panthera leo*) (Schaller 1972), cheetah (*Acinonyx jubatus*) (Eaton 1970) and cuttlefish (*Sepia officinalis*) (Neill and Cullen 1974).

Stalkers are usually capable of at least a short run or a swift dash. Which mode of approach is used depends upon the speed or the manner of movement of the prey, with often some subtle properties of the situation as a whole having their influence (see Curio 1976). With a prey that moves slowly, praying mantises (Holling 1966), salticid spiders (Drees 1952), and cats (Colt 1957, p.143; Biben 1979) stalk as unobtrusively as possible, thus minimizing the risk of untimely discovery before the final rush or strike. Furthermore, dragonfly larvae, like lions (Schaller 1972), stalk prey that have ceased to move even more slowly than when stalking moving prey (Hoppenheit 1964b, quoted in Curio 1976), presumably because still prey are more likely to detect movement.

In contrast, prey with a rapid or jerky movement, that often precede sudden disappearance, is approached quickly until within striking distance by all of the above mentioned predators. Obviously, the predator is taking a chance, albeit a small one, instead of losing an opportunity. (In reference to the paper by Krebs and Dawkins (op.cit.) it is in all probability no chance coincidence that *escape* tactics may be similarly structured, see for example references in Cloudsley-Thompson 1980; Murie 1944; White and Weeden 1966).

The other principal mode of predation is often referred to as either, 'sit-and-wait' or 'ambush'. The difference is that, unlike pursuit predators, these predators rely on the movement of prey to bring about an encounter, while they remain motionless and often concealed in the surroundings. The term 'ambush' used in this context (as any persual of predation literature reveals, e.g. Curio 1976 pp. 138-140) is, I believe, unfortunate. Firstly, there is a teleological nuance in the word. Secondly, most references to an ambush situation involve~~s~~ the predator waiting until the predator comes to within a set distance and then rushing the prey in an attempt to capture it. Thus, the final component of the prey-capture sequence of a stalking predator is often via an ambush situation. Yet, in the 'sit-and-wait' technique no pursuit is observed in the capture sequence, i.e. the predator relies totally on the movement of the prey to bring about the encounter. Therefore, I believe that care should be taken in the use of the terms 'ambush' and 'sit-and-wait' and for those predators that do not utilize a rapid rush or pursuit, relying on the prey's movement, we should standardize and increase the use of the term, 'sit-and-wait'.

Sit-and-wait predators can be divided into two distinct groups, principally on whether or not the predator uses a trap (or snare), for example a spider's web or an ant-lion pitfall, which is normally constructed in the external environment. Examples of the trap constructing predators include all of the numerous web-building spiders (including the orb-web spiders, Argiopidae; the sheet web builders, Linyphiidae; the scaffold web builders, Theridiidae; and the web or net casting spiders, Dinopidae); the various trap-door and 'trip-wire' spiders that utilize silk; and ant-lion larvae (Myrmeleonidae). Common examples to be found in the non-trapbuilding group include, from the invertebrates, *Hydra*, tiger beetle larvae (Cicindelidae), scorpion fly (*Bittacus* sp.), certain praying mantises (for example, the flower mantis, *Hymenopus coronatus*), mantis flies (*Mantispa* spp.), crab spiders (*Thomisidae*), and water stick insects (*Ranatra*); while vertebrate examples include many of the vipers (for example the Gaboon viper, *Vipera xanthina*), the angler fish (Antennariidae, Lophiiformes) and the snapping turtle (*Chelydra serpentina*).

As found in the earlier group, much overlap of techniques exist within one species of predator where, depending on the prey sought, the predator adopts a different prey-capturing method. Furthermore, other predators, for example the mantid (*Paratenodera augustipennis*) (Inove and Matsura 1983) and the larvae of the water beetle, *Dytiscus verticalis*, as reported by Formanowicz (1982), switch between an ambush tactic (when prey density is high) to an active searching and pursuit of prey (when density is low). In addition, as Chinery (1979, p.28) correctly points out, there is often no clear-cut distinction in the technique adopted by a predator in capturing the prey, with many animals falling into the grey area between them.

To enable predators to be classified according to their predatory techniques, and thus prevent ambiguity and confusion creeping into the literature, thorough details of the predatory behaviour of the animal must be collected and classified.

The alleviation of such problems aside, the major significance of behavioural studies of predation is best seen in regard to two particular points: (1) Predators exert a significant selection pressure on their prey species because, in general, the action in terms of natural selection is unequivocal; the prey is either killed or escapes from the attack. Because of this, studies on the natural selection of prey species by predators provide opportunities to observe, both directly and numerically, the efficacy of the anti-predator mechanisms involved (see for example Glasser 1979; Schall and Pianka 1980; Vermeij 1982). (2) Predation has been widely studied in both ecology and ethology. Both of these fields have made significant advances in the recent past, most of which, unfortunately have been in isolation from each other (see for example Hinde 1982; Manning 1979; Thorpe 1979). Klopfer (1962) attempted to integrate ecological thinking into studies of behaviour but, as Curio (1976) points out, this pioneering work has been largely outdated by the conspicuous upsurge of model building by present ecologists. From these models Curio (1976) suggests that ethologists could profit through inspiration for a fresh and evolution-oriented approach. Ecologists, on the other hand, may profit by assimilating findings on behaviour into their models. These models (for reviews see MacArthur 1972; Emlen 1973) make assumptions on parameters of predatory behaviour, such as search-time, pursuit-time, selection of diets, etc., from which it is not clear, from an ethological point of view, how complete this list of behavioural parameters is, how they interrelate and interact in reality, and in which ways they are affected by the type and density of prey, and the presence of other predators. Holling (1965, 1966) attempted to study one aspect of predation, i.e. the factors influencing the number of prey captured, by 'experimental component analysis'. The rationale was that a complex behavioural phenomenon such as predation can be broken down into simple components. Each component could be analysed experimentally and the relationships within the component described mathematically. The mathematical relationships could then be synthesized into a model which would, it was hoped, describe what goes on in the real world.

The main criticisms levelled at the experimental component analysis is that this approach has been more concerned with determining the existence and effect of behavioural processes than with elucidating the mechanisms underlying each process. However, it is here that ethological studies of predatory behaviour can contribute greatly. Once the behavioural properties of a predator-prey system are more completely known, ecological models that make predictions about the system will almost certainly gain realism, precision, and perhaps, as Curio (1976) suggests, generality.

At present the extent of our knowledge on predatory behaviour is heavily biased towards those predators that actively search and/or pursue their prey. Little is known about either ambush or sit-and-wait predators. This is unfortunate, for, as listed above, the sit-and-wait predators constitute a significant proportion of predators in general. In addition, many of them (in particular the insects) are known to be beneficial in relation to biological control programs against various pest species (see examples in De Bach 1974).

With the above in mind, a study was initiated to examine the predatory behaviour of a sit-and-wait predator with one of its common prey.

The common aquatic bug, Ranatra dispar, that inhabits farm ponds or dams was selected for the study, as it was readily available, appeared to be abundant at most times of the year, nymphs and adults could be easily distinguished and they are large insects making them suitable for behavioural observations and manipulation. The prey animal, Anisops deanei, another water bug, was chosen because it was available in large numbers, relatively easy to identify and large enough for observation and experimentation.

Originally the program of study was designed to examine various behavioural components in the laboratory and then synthesize these with field observation and manipulations. However, due to the time involved in the laboratory experiments, coupled with the fact that R.dispar proved to be a difficult animal to work with in the field, due to the turbid nature of farm dams, the study developed into primarily a laboratory examination.

This thesis follows the following pattern. Initially, aspects of the natural history of R.dispar and to some extent A.deanei, are examined, in particular the temporal and spatial distribution of both species in the field. The behavioural components of prey-capture by R.dispar are then described and classified, following which the effect of food deprivation and prey-size are examined to observe their effect on arousal and prey-capture. Further, the effect of prey-density and associated encounter-rate are examined to determine the overall form of the functional response (i.e. the effect of prey-density on the observed number of prey eaten); the effect of water temperature and developmental stage of both predator and prey are also examined.

Next, the effect of prey density is examined in relation to (1) various feeding and prey-capturing techniques exhibited by R.dispar and (2) the swimming and aggregating behaviour of A.deanei; the subsequent effect on prey encounter-rate with a sit-and-wait predator was then examined. Finally, the effect of prey density and encounter-rate on the predator's duration at a foraging site and subsequent rate of movement between them was investigated in order to identify possible mechanisms involved in prey assessment.

CHAPTER 2

THE PREDATOR AND PREY

2:1 THE PREDATOR - Ranatra dispar

2:1.1 Introduction

Ranatra dispar Montandon (Nepidae : Heteroptera) belongs to a very cosmopolitan family of aquatic insects erroneously referred to in much of the literature as waterscorpions. The genus is found worldwide as Table 2:1 shows.

Table 2:1 Geographical distribution of the genus *Ranatra*

Location	Known No. Of Species.
Europe	1
Australia	3
America	12
Asia	16

Our scant knowledge of the biology of *Ranatra* is principally based on observations and studies carried out on either the European species, *R.linearis* or the North American species, *R.fusca*,the predominant species in each continent respectively. Additional studies have also been undertaken on a few oriental species. Table 2:2 summarizes an extensive literature search on *Ranatra*, and lists (1) the area of investigation or observation, (2) the species, and (3) the original source.

TABLE 2:2 Summary of published research material on Ranatra.

TOPIC OF STUDY	SPECIES	AUTHOR AND YEAR	
A. NATURAL HISTORY AND GENERAL BIOLOGY.			
1. Note on the habits of Ranatra linearis	Ranatra linearis	LAKER, A.G.	1879
2. The history of R.linearis.	" "	WILMOTT, C.	1889
3. General biology, note on habitat.	" "	LUCAS, N.J.	1900
4. Note on large numbers of R.linearis flying.	" "	KIRITSCHENKO, A.H.	1911
5. General biology.	" "	BUTLER, E.A.	1923
6. General biology.	" "	LARSDEN, O.	1936, 1949
7. General biology	" "	ARNOUD, Br.	1966
8. Aquatic heteroptera from the Cerutti Collection, Switzerland.	" "	DETHIER, M.	1973
9. New record from Leon, Spain.	" "	LUCAS, M.T. & SALGADO, J.M.	1977
10. New records from Norway with note on biology.	" "	HANSEN & JACOBSEN	1978
11. General biology.	Ranatra fusca	RADINOVSKY, S.	1964
12. New state records from Washington and faunistical notes.	" "	NIESER, N.	1972
13. As prey for the notonectid predator, Notonecta lobata.	" "	ZALOM, F.G.	1978
14. General biology and Anatomical notes.	Various Nth.Amer spp.	TORRE-BUENO, J.R.	1905b
15. General biology and Comparative anatomy.	" " "	HUNGERFORD, H.B.	1919
16. Notes on Geographical Distribution	" " "	GONSOULIN, G.T.	1974
17. General biology.	Ranatra elongata	RAGHUNATHA RAO, T.	1962
18. Description and habitats	" "	BAQAI, I.U. et al.	1977
19. General biology.	Ranatra vicina	TAWFIK & AWADALLAH	1975
20. General biology.	Ranatra	HAGUENDER, M.	1978
21. New records from Arkansas, USA.	Ranatra australis	HARP, G.L.& HARP, P.	1980
22. New state records from Virginia.	" "	CROSS, J.L.	1972
23. New record from Bhagalpur, India.	Ranatra filiformis	MANDAL, B.K. et al.	1974
24. New record from Hortobagy, Hungary, and contribution to knowledge.	Ranatra (?)	LASZLO, M.	1977
25. New records from Kansas, USA.	Ranatra	OLDHAM, T.W.	1978
26. New record of Ranatra in the Philippines.	Ranatra diminuta	POLHEMUS, J.T. & REISEN, W.K.	1976
27. New records from Arizona, Florida, USA. Africa	R.montezume, R.texana, R.spatulata	POLHEMUS, J.T.	1976
28. Notes and review of systematic position with American Ranatra	R.compressicollis	LANSBURY, I.	1974
29. Aquatic heteroptera of Ahmedabad	Ranatra spp.	VYAS, A.B. et al.	1972
30. A review of the Oriental species of Ranatra	Ranatra spp.	LANSBURY, I.	1972
B. BEHAVIOUR.			
1. Effect of water temperature on movement.	Ranatra linearis	KOSICKI, S.	1966
2. Respiratory behaviour and activity.	" "	CLOAREC, A.	1969a,b.
3. Rythms in respiratory behaviour.	" "	"	1972a
4. Postural variation in forelegs.	" "	"	1974a
5. Post-moult behaviour.	" "	"	1980b
6. The size of the binocular zone of the visual field in insects.	" "	FRANTSEVICH, L.I. & PICHKA, V.E.	1976
7. Notes on stridulation behaviour	Ranatra fusca	TORRE-BUENO, J.R.	1903
8. The reactions of Ranatra to light.	" "	HOLMES, S.J.	1905
9. Death feigning in Ranatra.	" "	HOLMES, S.J.	1906
10. Observations on young.	" "	HOLMES, S.J.	1907
11. Some reflex responses of R.fusca.	" "	ABBOTT, C.E.	1940
12. Salinity and temperature tolerance.	Ranatra elongata	SHIRGUR, G.A. & KEWALRAMANI, H.	1973

TOPIC OF STUDY	SPECIES	AUTHOR AND YEAR
C. ECOLOGY		
1. Association with aquatic vegetation.	*Ranatra linearis*	BUTLER, E.A. 1910
2. Reduced flight muscles and migration.	" "	BROWN, E.S. 1951
3. Abundance and energetics in field.	" "	WAITZBAUER, W. 1974.1976a&b
4. Use of in methods of bio-geographic research	" "	OKLAND, J. 1977
5. Seasonal fluctuations in population.	Various Asian spp.	JULKA, J.M. 1977
6. Bio-ecological studies.	*R.filiformis*, *R.elongata*	RAGHUNATHA RAO, T.K.1976
7. Preliminary observations on use of Malarial B oil to control aquatic insects in fish ponds.	*Ranatra* spp.	DESAI, V.R. & RAO, K.J. 1972
8. Distribution and abundance in desert stream.	*Ranatra*	BRUNS, D.A. & MINCKLEY, W.L. 1980
9. Association with annual temporary ponds in Canada.	"	WIGGINS, G.B. 1980
D. REPRODUCTION		
1. Note on oviposition.	*Ranatra linearis*	ENOCH, F. 1900
2. Structure and function of the egg shell.	" "	HINTON, H.E. 1961
3. Egg architecture, embryology and eclosion.	" "	COBDEN, R.H. 1968
4. Oogenesis,	" "	OGORZALEK, A. 1974
5. Growth on water lily leaves.	" "	SAUER, F. 1976
6. Note on egg.	*Ranatra fusca*	PETIT, R.H. 1902
7. Hatching.	" "	DAVIS, C.C. 1961
8. Life history.	*Ranatra quadridentata*	TORRE-BUENO, J.R. 1906
9. Notes on life history.	Ranatra chinensis	HOFFMANN, W.E. 1930
10. Some observations on the life history.	*Ranatra unicolor*	BAN, Y. 1981
E. ANATOMY		
1. Morphological and histological study of CNS	*Ranatra linearis*	CLOAREC, A. 1971a
2. Developmental changes of eye.	" "	" 1971b
3. The sensory nervous structure of the prothoracic leg.	" "	" 1973a
4. Variations in the structure of the prothoracic leg I.	" "	" 1973b
5. " " " " " " II, during nymphal development I Morphogenesis. II. Distribution of the sense organs.	" "	" 1974b
6. Anatomy and histology of Neuro hemal organ.	" "	BAUDRY-PARTHIAOGLOU, N.1978
7. Anatomy and physiology	*Ranatra fusca*	LOCY, W.A. 1884b
8. Anatomy	" "	MARSHALL & SEVERIN 1904
9. Anatomy of head and thorax	" "	NEISWANDER, C.R. 1926
10. The Pleuropodia	" "	HUSSEY, P.B. 1926
11. Structure and function of the thoracic/abdominal spiracles.	" "	PARSONS, L.1972a,b,1973,1974
12. Tonal apparatus	*Ranatra quadridentata*	TORRE-BUENO, J.R. 1905a
13. Anatomy of female genitalia.	*Ranatra*	CARLO, J.M.de 1968
14. Morphology and anatomy of alimentary canal	*Ranatra chinensis*	CHOWDHURY & BEGUM 1974
15. Morphology and secretions of the salivary glands.	*Ranatra filiformis*	QUAYUM, M.A. 1975
16. Comparative anatomy of the spiracles.	" "	BHATNAGAR, B.S. 1978
17. Structure of the compound eye.	*Ranatra segrega*	PELLERANO, G.N. & CARLO, J. 1977
18. Microscopic anatomy of maxillary glands.	" "	CARLO, J.M. & PELLERANO, G.N. 1980
19. Thoracic structural myology.	*Ranatra elongata*	DESHPANDE, S.B. 1980
20. Malpighian tabules.	" "	SHUKLA, G.S. & GOPAL, K. 1980
21. Adaptive feature of leg structure.	*Ranatra* (?)	PUCHKOVA, L.V. 1978

TOPIC OF STUDY	SPECIES	AUTHOR AND YEAR	
F. PHYSIOLOGY			
1. Ingestion rate.	*Ranatra linearis*	CLOAREC, A.	1975
2. Fine structure and function of the chloride cells.	" "	KOMNICK, H.	1976
3. Natural diet - Analysis by Electrophonesis	" "	GILLER, P.S.	1982
4. Pulsating organs	*Ranatra fusca*	LOCY, W.A.	1884a
5. Proline metablism.	*Ranatra filiformis*	SINGH, J.	1978
6. Histochemical observations on the Neuro endocrine complex.	" "	FARUQUI, S.A.	1977
7. Phospho-lipid content in Malpigian tubules and haemolymph.	" "	MAHOMED, U.V.	1977
G. PREDATORY BEHAVIOUR			
1. As voracious predator.	*Ranatra linearis*	SWAMMERDAM, J.	1937
2. Attacking small fish.	" "	OMEROD, E.A.	1878
3. Predator on mosquito larvae (precipitin test).	*Ranatra fusca*	BROOKE, M.M. & PROSKE, H.O.	1946
4. Descriptive study.	*Ranatra linearis*	CLOAREC, A.	1969b
5. Interactions between different receptors.	" "	"	1976
6. Estimation of hit distance.	" "	"	1979
7. Ontogeny of hit distance estimation.	" "	"	1980a
8. Effect on pred. performance of prey after moulting.	" "	"	1981
9. Effect on pred. performance of prey after deprivation.	" "	"	1982a
10. Role of visual and mechanical stimulation after moulting.	" "	"	1982b
11. Deprivation of prey during development.	" "	"	1983
12. Density dependent prey size selection	" "	BLOIS & CLOAREC, A.	1983
13. Predation on fish populations in S.W. Sweden.	" "	ERIKSSON, M. *et al.*	1977
14. Nocturnal rythm in predatory behaviour.	*Ranatra montezuma*	BLINN, D.W. *et al.*	1982

Studies on the Australian species, *Ranatra dispar*, are restricted to taxonomy :-

R.dispar Montandon, 1903; Lundblad, 1933; Hinton, 1961, 1962 (Structure of egg and key to eggs); Menke and Stange, 1964; Lansbury, 1972.

R.dispar var. *longicollis* Montandon, 1903; Lundblad, 1933; Menke and Stange, 1964.

R.australiensis Hale, 1924 syn.n.; Menke and Stange, 1964; Lansbury, 1967.

(after Lansbury, 1972)

The paper by Hale (1924) contained some brief notes on natural history, being primarily concerned with a taxonomic description. I have been unable to trace any additional published works on any aspects of the biology of *R.dispar*. Therefore, because of the depauperate state of our knowledge on even basic biological information concerning *R.dispar*, whenever possible observations and notes were collected on various aspects of the biology of this ambush predator. The following sections summarize these observations, obtained from both the laboratory and field. Aspects of the temporal and spatial distribution of all developmental stages of *R.dispar* in the field are given in Section 2:3.

2:1.2 Observations on General Biology

A. Reproductive behaviour.

(i) Mating: Copulation was observed on a number of occasions in the laboratory, but never in the field.It took place usually between 1700 and 1900 hours (i.e. towards dusk) during the Spring (September to November) and Summer (December to February), months.

Adult males have been observed to approach the female from below as well as from above, normally while the female is clinging to a submerged object (e.g. water plant stems or twigs). On several occasions, when the male approaches from above and in front of the female, the male was observed to move slowly, extending its prothoracic legs which in turn grasped the female's prothoracic legs, about the tibio-tarsi/femur, thus locking the 'claw' onto the femur. The male would then manoeuvre itself to the side of the female, adjusting its grip on the prothoracic legs, until it was positioned to the side of and slightly below the female. The male's meta- and meso-thoracic legs are such that they either grasped the female or remained in contact with the submerged object on which the female was clinging. Normally the former was observed however, with the male 'hooking' its meso-metathoracic legs over the body and legs of the female. Often, the female would swim away from the site with the male still clinging to her body. When positioned to the side (either right or left) of the female the male's prothoracic leg was inclined upwards and hooked over the thorax (pronotum) of the female. The dorsal aspect of the posterior portion of his abdomen faced the ventral part of the posterior region of the female. The ventrally situated aedeagus is then curved upwards (the two halves of the male's respiratory siphon (filaments) being separated near the base to permit this) to a dorsal position, where it is clasped by the female genital sclerites. The female genitalia were observed to move spasmodically before/until copula took place. Transfer of sperm persumably takes place at this time. Adults remained in copula for between 3 to 37 minutes ($\bar{x}$ = 17.1, SD = 11.7, Range 3 to 37 mins, n = 10), with up to three separate copulations being observed to occur within a one hour period. Following mating the animals separate with the female normally moving off, either swimming to the bottom of the tank or to other plant material.

(ii) Oviposition Behaviour. Eggs were laid between 24 and 48 hours after mating was seen to occur at a water temperature of 25.5 ± 1.5°C. The fertilized female 'selects' a suitable piece of submerged vegetation, for example the stem of water plants or submerged leaf, and grasps it with her second and third pair of legs, her head being lower than the abdomen. The head is raised about 2 cm vertically away from the stem with the tip of the ventral surface of the abdomen pressed against the plant. The prothoracic legs are held away from the head, normally at an angle of about 45° to the longitudinal body axis. As the ovipositor is extended the prothoracic legs are lowered to come to lie in the same line as the body being held flat together (similar to the 'leg extension' phase described in Chapter 3). The saw toothed ovipositor is then slowly driven into the plant by downward, backward and forward movements, while the respiratory filaments rest along the plant. After piercing the plant tissue the ovipositor is partially withdrawn, opened laterally and the egg is extruded and forced into the hole. The two long respiratory filaments of the egg spring apart in a 'V' shaped fashion as the ovipositor is withdrawn. The female then moves vertically down the plant, maintaining contact with the ventral tip of the abdomen, about 4 to 6 mm, and repeats the hole boring/egg laying process. Up to 20 eggs have been observed to be laid in one period, (see Plate 1c).

B. Life Cycle Stages

(i) The colour of the egg is pale yellow to white with the micropylar region being dark brown. The two respiratory filaments of the egg are pale yellow to amber becoming darker towards the base. Size of the egg is shown in Table 2:3.

TABLE 2:3 Size of egg of *R.dispar*.

	As Removed from Female	Following 24 hrs in water
Length (mm)	3.325 to 3.55	3.50 to 3.755
Greatest diameter (mm)	0.85 to 0.97	0.95 to 1.11
Respiratory filament (mm)	2.22 to 2.55	No observable change

During development the fertilized egg continues to increase in size before hatching while unfertilized eggs do not. About 5 days later (at 25 ± 1.0°C) two pinkish spots appear near the extremity of the anterior end (location of respiratory filament), these being the developing eyes, while one day later an area of a light orange tinge appears in this area. As development continues the area darkens until finally is distributed over the ventral surface of the ovum.

(ii) Eclosion : During the last days of incubation the egg becomes bulged at the cephalic end until finally rupture of the chorion takes place. The split always occurred in about the same place, occurring posterior to the end of the egg on the dorsal surface, spreading round to the side. A membrane (possibly two) was the first object to appear, pushing the partially detached 'operculum' or cap of the egg, with the attached respiratory filaments, towards the ventral surface of the egg. The membrane is attached to a protuberance on the vertex of the hatching nymph that apparently also presses against the operculum, affording additional 'lift' as the head emerges from the egg. After emergence of the anterior part of the head, emergence temporarily ceases while the head is observed to move rythmically back and forth with a pumping action. Following about 3 to 5 minutes of this movement the membrane(s) burst rapidly and the head pushes completely out of the egg, followed by active bending movements of the still- encased body segments. After about 2 to 5 minutes of this movement the appendages become freed by the continued effort of observed muscular movements within the head and the bending/pushing movements of the body (Davis 1961, attributes the muscular movements within the head to be associated with the 'drinking' of water by the nymph to increase the body volume. I am unable to substantiate his conclusions with my available observations). Complete eclosion is achieved with the aid of the liberated legs pulling the rest of the body free of the egg case. The complete eclosion process takes between 10 to 15 minutes.

The newly hatched nymph remains motionless for up to 1 minute after hatching, supported by any available plant or submerged material. Within a few minutes however, it takes up the characteristic head-down prey capturing position as described in detail for adults in Chapter 3. Ostrocod prey have been observed to be caught within 60 to 80 minutes following eclosion. The incubation period lasts between 7 days at 28.5 ± 2.5°C to 14 days at 20 ± 1.5°C (n = 10 in each case). No eggs hatched when maintained at 15 ± 1.0°C.

(iii) Duration of Instar Stages : Following egg hatch there are five nymphal stages. Hale (1924) has provided a detailed comparative account of the morphology of each of the instars and therefore following a routine comparison, the results of which were almost identical to Hale's, no additional descriptions seemed necessary. However, where additional work did seem warranted was in ascertaining the duration of each stadium at both constant (laboratory) and fluctuating (field) temperatures. For laboratory observations, animals were housed individually in either small (250 ml) or large (1 litre) plastic beakers containing water to a depth of 3.0 cm and 10.0 cm respectively. Each beaker was provided with aquatic plant material and an appropriate piece of cocktail stick for support. Each day animals were fed either a mixture of ostrocods and small (instar 1 and 2) notonectids for predator instars I and II, or a mixture of larger notonectids for instars III to V, in sufficient numbers to maintain ad libum conditions, in addition to checking for moulting activity. For field observations animals were maintained in 2 large children's plastic paddling pools (2.0 x 2.0 x 0.30 metres) the bottom of each being covered in a sloping 'bed' of pond mud (with associated pelophile organisms) to produce a graded water depth profile of 5 to 20 cm. The pools had been set up 12 months previously and supported moderate breeding populations of various notonectid species and ostrocods in addition to various transient visitors (for example Zygoptera, Coleoptera, Diptera). Various aquatic plants had also been established along with their various phytorheophile populations. During observation periods the populations of ostrocods and small notonectid instars were supplemented handsomely 2 to 3 times per week.

Both pools were covered by a tent of shade cloth (Sarlon,80%) two metres above, but were opened on two sides (North and South) which prevented localized heating but permitted normal air circulation and rain fall. The temperature regime of both pools was very similar to that of a monitored farm pond for comparable water depth, although the rate of both increase and decrease of temperature in the morning and evening was moderately faster in the pools.

R.dispar individuals were individually housed in either small (7 x 5 x 5 cm deep) or large (10 x 10 x 15 cm deep) cages for instars I and II, and III to V respectively. The cages were constructed from a wire frame and covered with either a coarse nylon netting (small cages) or a wire gauze (large cages). This permitted the passage of water and prey animals into the cages but prevented the escape of the predators. In addition, when possible, cages were supplemented with freshly caught prey of the appropriate type. Water and air temperatures were recorded each hour by way of a thermistor wired to a calibrated Rustrak recorder. Each predator was checked twice daily; early each morning and late afternoon for signs of moulting or an obvious absence of prey. Table 2:4 shows the observed durations for each instar, (see Plate 1a).

(iv) Moulting. Animals were observed not to feed at least 24 hours before moulting, and in most cases there was a significant reduction in the number of prey eaten up to 48 hours before moulting. Prior to moulting the individual becomes completely inactive, unresponsive to prey (natural or model) and somewhat enlarged. As moulting begins, the skin splits first just posterior to the head on the dorsal surface. The split increases in length along the pronotum and remainder of the thorax as shown in Fig. 2:1. As the new individual moves forward out of the exuvia the legs remain pressed against the body. The body moves in a rhythmic, pulsating fashion with 'peristaltic' waves of musculature (?) movement passing down the body as the animal slowly extricates itself. When the thorax and the majority of the abdomen are out of the exuvia the legs are freed and are used in the final part of the extraction process. When completely free of the exuvia the nymph, which is pale cream with a tinge of yellow in colour, remains stationary for about 3 minutes, before swimming and coming to rest on a suitable piece of submerged vegetation on which it remains stationary while the sclerotization and melanization of the cuticle takes place. Although the predator performed various movements with the

Fig. 2:1 The stages of the moulting process of *R.dispar* as depicted in plan and lateral views.

(1) 1058 h

(2) 1102 h

√

√ (2a) ?

(3) 1104 h

(3a) 1107 h

(4) 1109 h

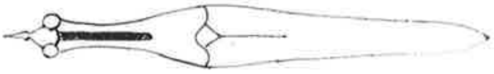
(4a) 1111 h

(5) 1115 h

(6) 1122 h

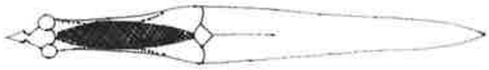
See text for details.

(1)

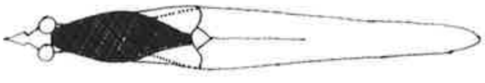


(2)

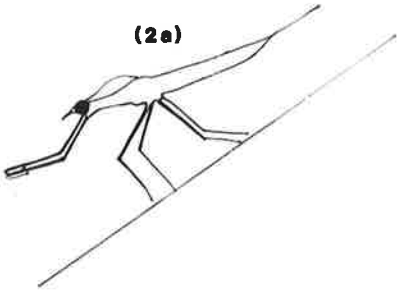
(3)



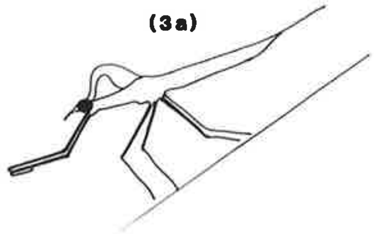
(4)



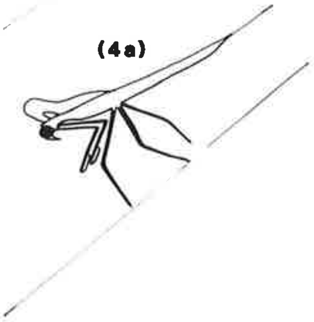
(2a)



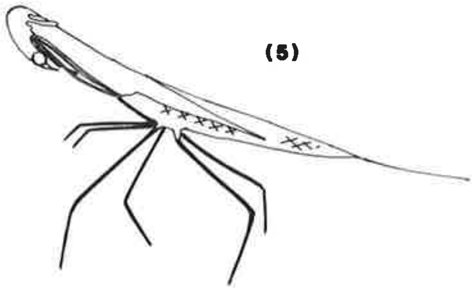
(3a)



(4a)



(5)



(6)

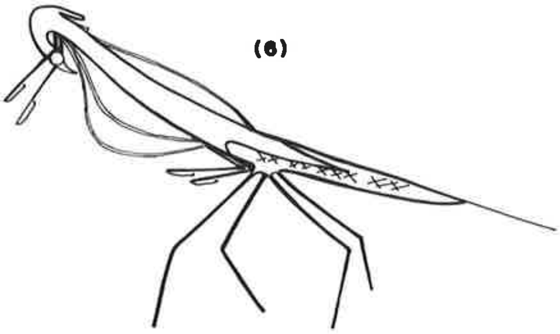


TABLE 2:4 The mean (± Std.Dev.) duration (days) of each instar of R.dispar when maintained at either (A) Constant laboratory or (B) fluctuating semi-natural water temperatures (see text for details).

IMMATURE STAGE (A)	WATER TEMPERATURE (°C)			
	15 ± 1.5	20 ± 1.0	25 ± 1.0	30 ± 1.5
I*	12.8 ± 6.8	6.0 ± 4.0	3.0 ± 0	2.7 ± 1.1
(BL = 8.3 mm)	(3 to 22)[a] 5	(2 to 14) 5	(0) 5	(2 to 5) 5
II	15.0 ± 10	7.6 ± 3.1	7.5 ± 1.3	6.6 ± 1.3
(BL = 13 to 13.2 mm)	(3 to 33) 40[b],18[c]	(4 to 14) 40, 38	(6 to 9) 40, 36	(6 to 9) 40, 27
III	ALL DIED	10.6 ± 3.7	9.2 ± 1.6	12.3 ± 2.5
(BL = 17.2 to 20 mm)		(3 to 14) 38, 31	(8 to 12) 36, 34	(10 to 15) 27, 8
IV		16.2 ± 5.9	19.7 ± 1.5	20.4 ± 3.2
(BL = 24.5 to 30 mm)		(9 to 22) 31, 25	(19 to 22) 34, 24	(18 to 24) 8, 4
V		18.0 ± 4.7	18.0 ± 1.0	ALL DIED
(BL = 39.5 to 41.5 mm)		(14 to 23) 25, 17	(16 to 20) 24, 17	

	TEMPERATURE (°C)			DURATION (days)			
(B)	RANGE	$\bar{x}$	SD	RANGE	$\bar{x}$	SD	N
I	17.0 to 2.5	20.3	2.4	3 to 8	5.2	1.7	9
II	17.5 to 25.5	22.1	3.6	9 to 12	10.5	1.1	13
III	17.0 to 21.2	21.2	4.4	5 to 15	10.2	3.1	9
IV	17.0 to 30	22.7	5.9	12 to 16	13.6	1.5	21
V	18.0 to 30	24	6.3	17 to 20	18	1.3	19

a. Number in parenthesis is the range

b. Number of animals tested

c. Number of animals that successfully moulted and used in calculating the mean.

BL. Body length of instar excluding rostrum and respiratory siphon.

* The small sample size (5) used is due to lack of fertilized eggs.

prothoracic legs for a number of hours following moulting no prey were observed to be caught until 6 hours had elapsed since the moult. Cloarec (1981, 1982a, 1982b) has shown that the first 4 hours following a moult are crucial in the subsequent predatory performance of R.linearis, the European species. Predators that moulted in the presence of prey performed more prothoracic leg movements and showed a higher subsequent strike efficiency than those individuals that moulted in the absence of prey. Time did not permit the required observations and experiments to see if R.dispar exhibited the same dependence of presence of prey at moulting. Following moulting, R.dispar were observed to perform numerous prothoracic leg movements however.

C. Feeding Behaviour

(i) Range of Prey Types taken by R.dispar. Ranatra has developed a reputation from the earliest literature for being amazingly voracious. A good example is that of Swammerdam (1737):- "There is not perhaps in all the animal creation so outrageous or fierce a creature against those weaker than itself than the water scorpion. It destroys like a wolf among sheep, twenty times as many as its hunger requires. I have often seen one of these when put into a basin of water in which were 30 or 40 of the worms of the middle Libella, which are at least as large as itself, destroy them all in a few minutes." Such dramatic descriptions aside, Ranatra does capture (often in a 'spectacular' fashion) and consume a large array of both invertebrate and vertebrate prey.

Chapter 3 presents a detailed account of the significant effect that both the internal motivational state (i.e. hunger) of the predator and the size of the prey have in the prey capturing behaviour of R.dispar. What I propose to do in this section however is to present additional records of observations on the range of prey types taken (in both the field and laboratory) and predatory behaviour.

The range of prey taken by all instars of R.dispar is wide in regards to both prey size and type. First instars capture prey ranging in size from less than 1 mm (small ostrocods) to 1.5 cm (small tadpoles) in length, with a body mass of some 3 to 4 times (small tadpoles) that of the predator. Adult R.dispar will capture and consume ostracods, Daphnia spp. (some 50 times smaller in body length) up to small fish and tadpoles, three quarters of their body length and probably significantly more in body mass.

When capturing larger prey it is not uncommon for the smallest instars to be pulled from their ambush support and pulled round by the swimming prey, often for a considerable period, before being able to locate a suitable intersegmental membrane and inject the venom/enzymes into the prey. All instars are capable of capturing prey that are on the water surface, either terrestial in origin or semi-aquatic, surface film dwellers. To do this the predator positions itself in such a way that on striking it can break through the water surface and thus capture the prey. This is in turn pulled beneath the water surface where feeding takes place. Table 2:5 presents a list of various prey types that were either observed in the field as they were being fed on, or presented to the predator in the laboratory. Only those prey that were subsequently fed on are listed.

(ii) Cannibalism : All stages of R.dispar have been observed to cannibalise in both the laboratory and field. Table 2:6 summarizes the stages that either feed on or are fed on as observed in the laboratory. All stages are susceptible to cannibalism following moulting. This is especially noticeable for the larger instars that, following a moult, require up to 4 hours before sclerotization and melanization of the cuticle render it hard enough to apparently prevent cannibalism by smaller instars. It was not uncommon to observe, in the laboratory, up to 3 smaller instars (e.g. II) all feeding on a newly moulted individual (e.g. V or adult), although I have not observed this phenomenum in the field.

Radinovsky (1964) suggests that the observed tendency in R.fusca for the eggs to hatch in darkness, during the evening or early morning, is adaptive in that it offers some protection to the newly emerged first instars from older siblings during those first critical hours.

TABLE 2:5 Summary of the various prey types (both aquatic and terrestial) that were seen to be fed on by *R.dispar* in either the laboratory or the field.

	LABORATORY						FIELD					
	I	II	III	IV	V	A	I	II	III	IV	V	A
AQUATIC PREY												
A. INVERTEBRATES												
ANNELIDA												
Branchiura sp.	+	+	+	+	+	+						
Lumbriculus sp.	+	+	+	+	+	+						
ARANEAE												
Dolomedes sp.	-	*	*	+	+	+						
ACARINA												
Hydracarina	-	-	-	-	-	-						
CRUSTACEA												
Ostracoda	+	+	+	+	+	+	+	+	*	*	*	*
Daphnia spp.	+	+	+	+	+	+	+	+	+	*	*	*
Austrochiltonia	-	-	+	+	+	+	*	*	*	*	+	*
Artemia salina	+	+	+	+	+	+						
Cyclopoida	+	-	-	-	-	-	*	*	*	*	*	*
Paratya spp.	-	-	-	+	+	+						
Macrobrachium	-	-	-	-	-	+						
INSECTA												
EPHEMEROPTERA												
Cloeon sp.	+	+	+	+	+	+	*	*	+	*	+	*
ODONATA												
Zygoptera	+	+	+	+	+	+		*	+	+	+	+
Anisoptera	-	-	-	+	+	+		*	*	*	+	+
HEMIPTERA												
Anisops deanei	+	+	+	+	+	+	+	+	+	+	+	+
Anisops doris	+	+	+	+	+	+	*	*	*	*	*	*
Enithares bergrothi	-	-	+	+	+	+	*	*	*	*	*	+
Hydrometra sp.	+	*	*	+	*	+	+	*	+	*	*	+
Mesovelia sp.	+	*	*	*	*	+	*	*	*	*	+	*
Gerridae	+	+	+	+	+	+	*	*	*	+	*	+
Laccotrephes tristis	-	-	-	+	+	+		*	*	*	*	*
Ranatra dispar	+	+	+	+	+	+	+	+	+	+	+	+
Sigara sp.	+	+	+	+	+	+	*	+	*	+	+	+
Micronecta sp.	+	+	+	+	+	+	+	*	*	*	*	*
DIPTERA												
Chaoborus	*	*	*	+	+	+	*	*	*	*	*	*
Anopheles sp.	+	+	+	+	+	+	*	*	*	*	*	*
Culex sp.	+	+	+	+	+	+	*	*	*	*	*	*
Aedes sp.	+	+	+	+	+	+	*	*	*	*	*	*
Chironomidae	+	+	+	+	+	+	*	*	*	*	+	*
TRICHOPTERA												
Leptoceridae (+ case)	-	-	-	-	-	-						
Leptoceridae (- case)	-	-	-	-	-	-						
COLEOPTERA												
Cybister tripunctatus (A)	-	-	-	-	+	+						
Cybister sp (L)	+	+	+	+	+	+	*	*	*	*	*	*
Sandracottus sp.	-	+	*	+	+	+	*	*	*	*	*	*
Hydrophilidae	-	-	-	-	-	+	*	*	*	*	*	*
Gyrinidae (A)	-	-	-	-	-	+					*	*

	LABORATORY						FIELD					
	I	II	III	IV	V	A	I	II	III	IV	V	A
B. VERTEBRATES												
ANURA (Larvae)												
Limnodynastes tasmaniensis	+	+	+	+	+	+			*	*	*	+
Litoria (?)	+	+	+	+	+	+			*	*	*	*
PISCES												
(Mosquito fish)												
Gambusia affinis	+	+	+	+	+	+				*	*	*
(Guppy)												
Poecilia reticulata	+	+	+	+	+	+						
TERRESTIAL INSECTS												
BLATTODEA												
Peripleneta americana	+	+	+	+	+	+						
Blattella germania	+	+	+	+	+	+						
Calolampra irrorata	+	+	+	+	+	+						
Mantidae nymph												+
ORTHOPTERA												
Teleogryllus (N)	+	+	+	+	+	+			*	*	*	*
Teleogryllus (A)	-	-	-	-	+	+			*	*	+	*
Macrotona sp. (A)	*	*	*	*	*	*			+	*	+	+
Atractomorpha sp. (A)	*	*	*	*	*	*			*	*	*	+
HETEROPTERA												
Lygaeidae (N)							*	+	+	*	+	*
Lygaeidae (A)							*	*	*	*	+	+
Nabidae (A)							*	*	*	+	+	+
Miridae (N)							*	+	*	+	*	*
Miridae (A)							*	*	*	+	+	+
COLEOPTERA												
Lycidae												
Metriorrhynchus rhipidius (A)												+
Elateridae (A)												+
Tenebrio molitor (L)	+	+	+	+	+	+						
DIPTERA												
Tipulidae									+			+
Syrphus sp.								+			+	+
Tabanidae												+
Asilidae										+		+
Drosophila	+	+	+	+	+	+	*	*	*	*	*	*
Lucilia cuprina (L)	+	+	+	+	+	+	*	*	*	*	*	*
Lucilia cuprina (A)	+	+	+	+	+	+	*	*	+	*	+	+
Calliphora (A)	+	+	+	+	+	+	*	*	*	+	+	+
Musca spp. (A)	+	+	+	+	+	+	*	*	*	*	+	+
Others									+	+		
HYMENOPTERA												
Formicidae												
Myrmecia										+		+
Ichneumonidae											+	+
Pompilidae												+
Sphecidae										+	+	+
Thynnidae										+	+	+
Vespidae											+	+
Apis mellifera										+	+	+
Others								+	+	+	+	+

(+) Observed being fed on (*) Lab: not offered

(-) Offered but NOT fed on (*) Field: likely as prey

TABLE 2:6 The incidence of cannibalism by *R.Dispar* on various developmental stages observed in the laboratory or field.

	R.dispar stage acting as Prey					
Acting as Predator	I	II	III	IV	V	A
I	+	+	+	+[2]	+[2]	+[2]
II	+	+	+	−	−	
III	+	+	+	+	+	+
IV	+	+	+[1]	+	+	+
V	+	+[1]	+	+[1]	+	+
A	+	+	+[1]	+	+[1]	+

[1] Observed in field.

[2] More than 1 predator has been observed feeding on the same individual at same time .

D. Natural Enemies

(i) Predators : Apart from conspecifics the principal invertebrate predators appear to be Odonata and Coleoptera. Observations in the field revealed on two occasions Anisoptera nymphs feeding on a II and III instar, while a Zygoptera nymph was seen to capture and consume a I instar. In the laboratory both Anisoptera and Zygoptera nymphs have been observed feeding on instars I to IV. In addition adults of the dytiscid beetle, *Cybister tripunctatus*, capture and feed on instars I to V, and probably adults although

I have not observed this. I conducted no feeding trials using vertebrate predators. I did observe, however, a white-faced Heron, Ardea novaehollandiae, take either a V instar or adult R.dispar on one occasion during field observations.

(ii) Parasites : R.dispar, like a number of other aquatic Heteroptera, have been observed to often carry considerable numbers of epizoic Hydrachnid water mites. I have observed all stages of R.dispar to have these external parasites, carrying populations of 2 to 40 individuals.

Following moulting, R.dispar is susceptible to invasion by various hydromycete fungi. In the laboratory this can prove to be fatal. However, whether this is a natural occurrence I am unsure, although dead R.dispar collected in the field inevitably show the presence of fungal hyphae.

Following overwintering in particular, adult R.dispar often have a rich growth of algae over their body. This may be particularly thick along the respiratory filaments and legs. Hale (1924) reported that one adult R.dispar he collected had "a mass of Spirogyra attached to and growing from the base of the (respiratory) filaments" ... and that it "rendered these organs wholly non-functional by forcing them apart at the base; notwithstanding this disability, the bugs appeared quite healthy." I have also observed R.dispar to have, in some cases, masses of Spirogyra attached to various regions of the body. For small instars encountering and becoming entangled in this filamentous algae can prove fatal.

2:1.3 Maintenance of R.dispar in the laboratory

Attempts to maintain an adequate breeding culture of R.dispar did not prove possible, therefore in the vast majority of cases animals were collected from field locations and maintained in the laboratory as outlined below.

Following the final moult, adults were separated by sex and placed into 4 large plastic tubes (60 x 36 x 52 cm deep) filled to a depth of 50 cm with aged, dechlorinated tap water. Each tank had an abundance of stems of Phragmites sp suspended from the side walls and across the top onto which the Ranatra settled. Between 30 and 50 adults were housed in each tank and they were fed 4 times weekly a collection of notonectids, corixids and mosquito larvae, tadpoles, and young guppies. Usually several hundred prey were added to each tank per feeding (except tadpoles and fish). In addition, two tanks were set up and maintained containing both males and females. From these the few fertilized eggs used in described studies were obtained over a 3 . 5 year period. The instars of R.dispar are easy to identify because of the non-overlapping size range. Individual instars collected from the field were identified and, depending on the instar, transferred to a suitable container (see Table 2:7 for list).

PLATE 1

(A) From left to right : Instars I to V and adult female of *R.dispar*. (Scale bar 1 cm).

(B) Adult *A.deanei*.
Scale bar 5 mm.

(C) Eggs (one arrowed) of *R.dispar* in aquatic vegetation.

(D) Leg extension behaviour of *R.dispar*
(See Chapter 3:3 for description).


a
Ranatra dispar


b


c


d

TABLE 2:7 Size of container used to hold various instars of *R.dispar* in the laboratory.

INSTAR	CONTAINER DESCRIPTION
I	Plastic trays (34 x 22 x 6 cm), Water depth 2 cm.
II	Plastic trays (34 x 22 x 6 cm), Water depth 4 cm.
III	Plastic trays (30 x 20 x 10cm), Water depth 8 cm.
IV	As III above
V	Plastic tubs (53 x 35 x 20cm), Water depth 18cm.
Ad	Plastic tubs (60 x 36 x 50cm), Water depth 48cm.

Each container had adequate plant or cocktail stick supports for the *Ranatra*, and animals were fed mixtures of suitably sized prey as shown in Table 2:8 every second day.

TABLE 2:8 Types of prey given to each *R.dispar* during maintenance.

INSTAR	PREY MIXTURE
I	Ostrocads, small notonectid and corixid nymphs, small mosquito larvae.
II	As I above.
III	Notonectids, corixids, mosquito larvae.
IV	Notonectids, corixids, mosquito larvae, various aquatic insects as available.
V	As IV above plus tadpoles and young guppies.
Adults	As V above.

All containers were housed in a cubicle within a solar central heated insectary building. Tanks were arranged out of direct sunlight but the adequate glass area of the room meant no additional lighting was required. The air temperature ranged from 17 to 30°C in Winter and 23 to 35°C in Summer. This produced a range of water temperatures from 17 to 24°C and 20 to 30°C in Winter and Summer respectively.

2:2 THE PREY - *Anisops deanei*

2:2.1 Introduction

Anisops deanei Brooks (Notonectidae : Heteroptera), as do the nepids, belongs to a world wide family of aquatic bugs (Brooks 1951). Members of this family are easily recognizable because of the active swimming movements whilst they are upside-down (hence their common name 'backswimmers'). They have a pronounced convexly keeled dorsal surface, a feature related to their method of swimming while the abdomen has a mid-ventral keel, with a hydrofuge hair- covered grove on each side, for trapping air. Prey consists of small submerged animals, including mosquito larvae and *Daphnia* spp., while the larger individuals take tadpoles and small fish (Ellis and Borden 1970; Giller 1980; see references in McCormick and Polis 1982). Cannibalism has also been reported to occur (for example Fox 1975a).

The cosmopolitan genus *Anisops* is represented in Australia by 23 species (Lansbury 1969). They are very commonly found in ponds, farm dams, small freshwater lakes, creeks and slow lowland rivers the water bodies not needing to persist for all the year. Sweeney (1965) has published an account of the geographical distribution in S.E. Australia, to which Lansbury (1969) has added additional reports.

At present, as far as I can ascertain from the literature, our knowledge of A.deanei is restricted to taxonomic studies (Brooks 1951; Hale 1923; Lansbury1964, 1969)and two unpublished honours thesis concerning studies on a polymorphic backswimmer,Anisops thieremanni Lundbland , later found to have been misnamed ,(Lapworth 1978) and prey size selection on various morphs of Daphnia (Reynolds 1980).

Lansbury (1964) pointed out that A. deanei is very similar to A.hyperion,and only males can be separated with certainty. Care was taken during behavioural observations for any signs of swimming or other abnormality of prey animals. Apart from the natural variation no marked behavioural differences were seen. Therefore, for this thesis the Anisops species used has been regarded as A.deanei, (see Plate 1b).

Because of the time constraints, no additional laboratory observations on general biology were carried out on A.deanei. Hale (1924) briefly reported some general natural history observations he made on the closely related species A.hyperion. The results of a field censuring program to identify the temporal and spatial distribution of A.deanei in the field are presented in Section 2:3.

2:2.2 Maintenance of A.deanei in the Laboratory

Because the nature of the experiments often required large numbers of various size classes of A.deanei to be available at any one time, attempts were made to develop and maintain a culturing program. Unfortunately, apart from some minor success, the program proved unsatisfactory and therefore animals were collected at regular intervals from local field populations and maintained through the different instars in the laboratory. Different A.deanei instars (hereafter referred to as Size Classes) were kept in 8 large plastic tubs (53 x 35 x 20 cm deep) that were arranged on a large stand by a window but out of direct sunlight. The top of the stand supported a large (150 litre) water reservoir tank which in turn 'trickle' fed each of the holding tanks through a system of pipes at a rate of 100 to 120 ml per hour. Two overflow pipes per tank, connected to the 'waste plumbing' of the stand, maintained a constant level of 18 cm in the tanks. As animals moulted they were netted and transferred to the next appropriate tank (there were 2 tanks per size class 1 to 4). As animals of a particular size class were required they were removed, acclimatized to the experimental conditions and used. Adult A.deanei were maintained in separate 4 large plastic tubs (60 x35 x 52 cm deep) in the same room as the stand but not connected to it. All water used was filtered, dechlorinated tap water either directly from the mains (for reservoir tank) or from 200 litre plastic drums left to stand for 48 hours.

Animals were fed every second day a variety of different aquatic organisms as they were available, as shown in Table 2:9.

TABLE 2:9 Types of prey given to different Size Classes of *A.deanii* during maintenance.

SIZE CLASS	PREY MIXTURE
1	Ostracods, small mosquito larvae, *Daphnia*
2	As above plus small corixid nymphs.
3	As above, larger mosquito larvae.
4	As above, small notonectids.
5	As above, other notonectid spp.

All tanks were housed in the same room as *R.dispar* described in Section 2:1.3. Because of the rapid growth and thus short duration of the juvenile *A.deanei*, especially the smallest size classes, in Summer, the running water tanks provided cooler conditions that resulted in extending the duration of each size class by up to 8 to 10 days. This provided extra time for experiments during the summer when juveniles were available from the field. In Summer the running water temperature rarely got above 20 to 22°C compared with the still water tanks that would reach 30°C.

2:2.3 Collecting Techniques and Initial Identification and Size Grading

Animals were hand-netted from field locations previously selected because of their large and dominant populations of *A.deanei*, and returned to the laboratory for identification. Animals were poured through two nets, a coarse and fine, to separate the larger from the smaller individuals. Subsamples were transferred, in water, to a white plastic tray that in turn was resting on a bed of ice. The cooling process slowed the movement of the animals sufficiently for sorting, without causing significant mortality.

The other species of notonectid that were collected at the field sites were A.hyperion, A.thieremanni Lundblad, A.gratus Hale and Enithares bergrothi Montandon. For adults and larger size classes A.deanei/A.hyperion could be separated quite easily from A.thieremanni as the latter has a significantly larger pronotum; A.gratus has a longer pronotum and long shaggly hairs on the vertex, and Enithares is a much larger (> 10 mm) very robust and generally much darker in colour (Lansbury 1964, 1969). The smaller size classes proved extremely difficult to separate as no adequate keys are available for the juvenile notonectids in Australia. Therefore, in all likelihood the size classes 1 to 3 contain a number of different species, this was however unavoidable. To compensate to a certain degree, the size grading procedure (described below) ensured that individuals were of very similar sizes when used and pilot experiments, using the smaller size classes, showed no significant differences in the behaviour or swimming pattern of the animals used.

Following the initial sorting and approximate size grading described above animals were washed through a set of Edicott Sieves and then, following a visual inspection, emptied into the appropriate holding tank. Table 2:10 lists the 5 size classes of Anisops used along with various physical measurements, and the corresponding instar stages.

TABLE 2:10 Summary of certain physical characteristics of *A.deanei* used in categorizing Prey Size Class.

SIZE CLASS	INSTAR STAGE	BODY LENGTH (mm)			WET WEIGHT (mg)			DRY WEIGHT (mg)		
		$\bar{x}$	SD	RANGE	$\bar{x}$	SD	RANGE	$\bar{x}$	SD	RANGE
1(50)*	I and II	2.39	0.09	2.2 to 2.5	0.439	0.130	0.20 to 0.7	0.195	0.047	0.105 to 0.256
2(50)	III	3.32	0.163	3.1 to 3.7	1.203	0.310	0.75 to 2.0	0.476	0.129	0.257 to 0.73
3(50)	IV	4.36	0.243	3.6 to 4.7	3.292	0.636	2.30 to 4.75	0.959	0.364	0.51 to 1.75
4(50)	V	5.74	0.247	5.3 to 6.3	8.028	1.693	5.70 to 12.55	2.150	0.600	1.16 to 3.40
5(120)	Adult	6.81	0.433	5.7 to 7.9	12.674	2.702	8.10 to 20.00	3.626	0.770	2.39 to 5.99

* Number in parenthesis equals number of animals measured.

2:2.4 Techniques used in measurement of lengths and wet and dry weights of *Anisops*

2:2.4.1 Body Length

Animals were placed on their lateral surface under a Zeiss binocular microscope fitted with a calibrated ocular eye piece. The measurement was taken from the anterior outer curvature of the eye to either the posterior tip of the wing (adults) or the posterior tip of the abdomen (juveniles). This latter method introduced some variation due to the telescopic nature of the abdomen. However, because of the numbers of animals and speed that was required in the measurement, it was decided to adopt this quicker method rather than take other measurements (for example tibia or femur) to classify the size classes and later correlate with weight.

2:2.4.2 Wet Weighing Technique

To allow for the variation in wet weights caused by water clinging to the external surface of the animal after blotting, a standard drying curve was constructed using a range of different size classes of *A.deanei*.

Animals were removed from the water, carefully blotted on absorptive tissue and placed onto the weighing tray of an electric microbalance (Beckman Ltd. Model LM600) which is accurate to 10^{-3} mg. The weight of the animal was read directly from the dial every 30 seconds over a ten minute period. This was repeated for 35 animals. Following the construction of a drying curve the rate of water loss was found to be constant at 0.05 mg min^{-1} after 5 minutes drying. This was taken to demonstrate that the variable amounts of external water which was still adhering to the insect had evaporated and that the water loss from the insect was constant.

From this pilot experiment a standardized wet weighing method was used throughout this thesis as follows :
Animals were carefully removed from the water, blotted on absorptive tissue (in the same way each time), placed into a small petri dish, covered with a gauze lid and left for 5 mins. It was then placed onto the balance and the weight read immediately.

Dry Weighing Method

Individual animals were placed into numbered glass durham tubes (15 x 5 mm) and dried at 105°C for 48 hours, transferred in dessicator jars over silica gel and weighed within 15 to 30 minutes.

2:2.4.3 Prey Length/Weight Regressions

In order to predict the initial weight of a prey animal (± error) prior to experiments, separate regression equations of dry weight (mg) on body length (mm) were constructed for each of the size classes of *A.deanei*. 50 control animals from each size class 1 to 4 and 120 animals from size class 5 were measured and weighed as outlined above. Table 2:11 shows the resultant regression equations for each of the size classes. By substitution of the appropriate terms into a polynomical equation the initial weight (± S.E.) of the animal from its body length could be calculated. These weights were then used in turn to predict the body weight loss, due to feeding by the predator, by simple subtraction.

TABLE 2:11 Summary of the regression equations of dry weight (mg) on body length (mm) for five size classes of *A.deanei* used to predict initial dry weights of individual prey.

SIZE CLASS		INTERCEPT	SLOPE	R	t-statistic	Sig.
1	WET	-1.887	0.973	.69	4.518	$p < 0.001$
	DRY	-0.654	0.355	.70	4.652	$p < 0.001$
2	WET	-4.292	1.656	.87	9.126	$p < 0.001$
	DRY	-1.528	0.604	.76	6.01	$p < 0.001$
3	WET	-6.424	2.228	.85	8.58	$p < 0.001$
	DRY	-3.450	1.011	.67	4.84	$p < 0.001$
4	WET	-26.922	6.080	.88	10.04	$p < 0.001$
	DRY	-9.052	1.949	.80	6.98	$p < 0.001$
5	WET	-28.151	5.997	.96	25.31	$p < 0.001$
	DRY	-7.893	1.692	.95	22.46	$p < 0.001$

2:3 THE TEMPORAL AND SPATIAL DISTRIBUTION OF R.dispar AND A.deanei IN THE FIELD

2:3.1 Introduction

Field studies on any species of Ranatra are conspicuous in the literature because of their absence. Reference has already been made to a number of short papers (see for example Blinn 1982; Hale 1924; Hungerford 1919; Raghunatha Rao 1962; Radinovsky 1964; Tawfik and Awadallah 1975) that are primarily concerned with reporting some aspects of the natural history. Two exceptions however are those by Waitzbauer (1976a,b) who provides a detailed account of the energy turnover of a number of water bugs (including Ranatra) and the problems encountered in sampling and determining the abundance of water bugs in lakes.

Field studies on various notonectid species are far more numerous with aspects of their field biology, for example comparative life histories and general ecology (Bane 1926; Essenberg 1915; Gittleman 1973), predatory behaviour (Ellis and Borden 1970; Fox and Murdoch 1976; Toth and Chew 1972), cannibalism (Fox 1975a,b,c; Zalom 1978), age-dependent intraspecific interference (Murdoch and Sih 1978; Sih 1979, 1981; Streams and Newfield 1972; Streams and Shubeck 1982; Taylor 1968), foraging strategies (Giller and McNeill 1981; Sih 1982a,b) and development and energetics (Toth and Chew 1972; Waitzbauer 1976b) being well documented. This is by no means an exhaustive list, but a selection of what I considered to be extensive studies rather than short reports or natural history observations.

In reference to the two species concerned in this study, R.dispar and *A.deanei*, the aim of this section was to investigate the spatial and temporal structure of a field population of both species to determine intraspecific and interspecific similarities and differences. Rather than being an extensive field study, this work is intended to provide basic information supported by the more detailed laboratory studies of principally, Chapter 4.

2:3.2 Materials and Methods

2:3.2.1 Study Sites

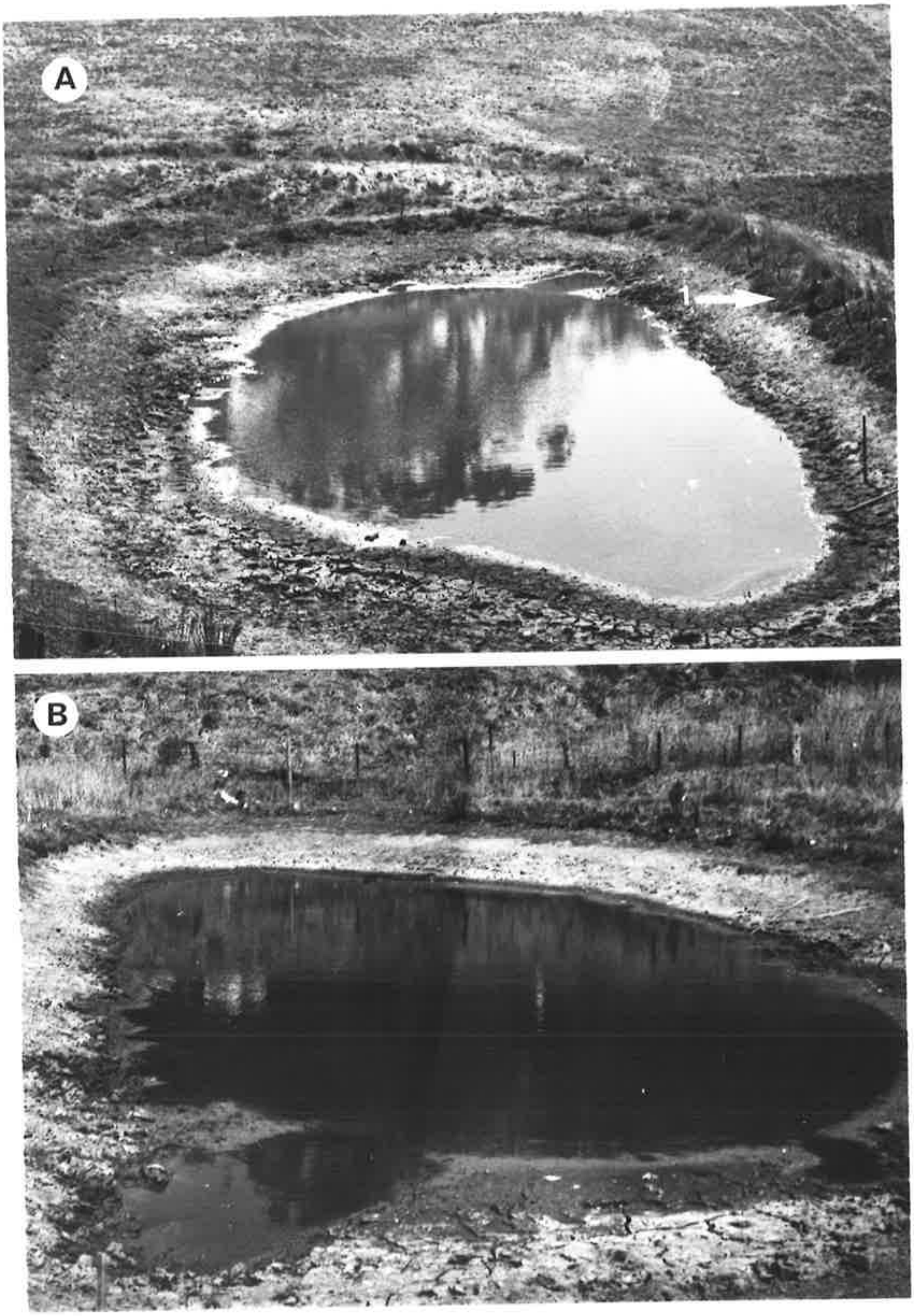
Two dams (ponds) (Riddle's Dam and Golf Course) were regularly censused during 1981/82 for both *R.dispar* and *A.deanei*, while a third dam (Waite Dam) was censused at the same time, but for *A.deanei* only. One dam (Riddle's) was selected for a more detailed study of the spatial distribution of *R.dispar* and *A.deanei* in relation to the changing topography of the dam as a consequence of drying up and vegetation distribution. These results however, are not presented in this thesis as they were not considered to be directly related to the main theme of the study.

Riddle's Dam (Grid Ref. UG025194, Map Number 6627-1, Echunga) is situated about 3.5 km South- east of the township of Hahndorf (56 km South- east of Adelaide), South Australia. It is a small dam (< 0.25 ha) constructed in the 1920's by horse-drawn scoop. As a consequence of this mode of construction and its age, the dam is shallow (< 1.0 m deep) with three gently sloping sides (north, south and west), the eastern side acting as the 'dam' face with the water depth being about 75 to 100 cm. It is fed by run-off from the surrounding south and west hills which are made up of open grazing land with a few intermittent

PLATE 2

(A) View of Riddle's Dam, Hahndorf, in late January 1982, looking North. (Arrowed section shows the stake boundary of the dam perimeter when full).

(B) View of Riddle's Dam, Hahndorf, looking South (same date as (A)).


A
B

crops of native eucalyptus forest. It reaches its maximum size rapidly in June and due to a natural 'spill-over' course on the eastern bank, remains at this size throughout July to September (Winter/early Spring). During Summer (December to February) the dam has been known to dry up as a result of evaporation and stock. Although this did not happen during the duration of this study (1979 to 1983) the dam was reduced in size by about 50% each Summer through evaporation (no stock being present).

The dam has a rich layer (up to 50 cm in depth in some areas) of "ooze" or Schlamm (Ruttner 1974) sediments that are mainly allochthonus in nature, resulting from the run-off. The main constituent of the sediments are clays along with organic matter washed from the surrounding grazing land. As a consequence the water is extremely turbid, with much suspended particulate and flocculate material present.

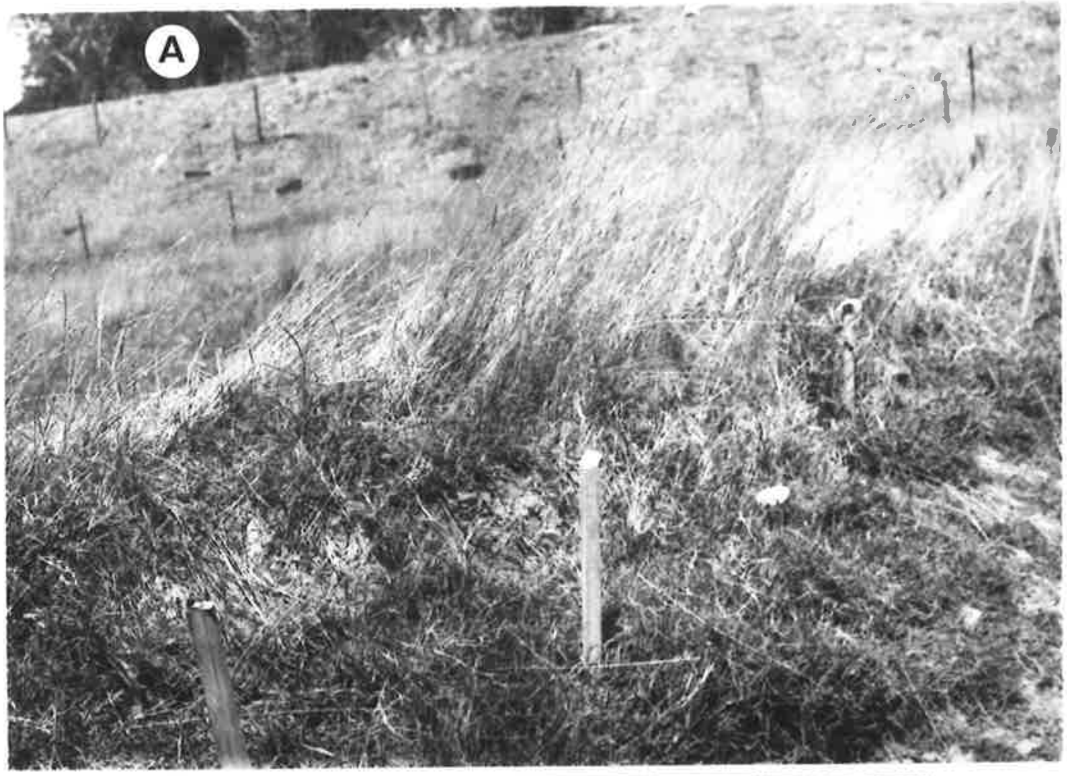
The dam supports no emergent aquatic vegetation, the only vegetation being the littoral zone submerged marsh grasses along with intermittent clumps of sedges and reeds. During the Spring and early Summer (September to November) the littoral zones of all four banks consist of submerged grasses. In particular the eastern bank has a thick mat of swamp grasses that overhang the water and extend down to depth of about 20 to 40 cm into the water. During the Summer (December to February/March) the dam dries up to become almost devoid of littoral vegetation being surrounded by a zone of dry, cracked sediments,(Plates 1&2).

The 'Golf Course' dam (Grid Ref. TG984138, Map Number 6627-1, Echunga) is situated about 1.0 km North- west of the township of Echunga

PLATE 3

(A) Close view of arrowed section 1 (Plate 2A) to show wooden stake and littoral zone vegetation. When the dam was full (i.e. late Autumn/Winter/Spring/early Summer) the area of swamp grasses shown would be completely submerged.

(B) The eastern wall of Riddle's Dam, photographed in January 1982.


A


B

(64 km South- east of Adelaide), South Australia. It is a very small dam (< 0.1 ha) being principally an overflow depression from a much larger dam ($\simeq$ 1.0 ha) situated on the Echunga golf course. The dam is shallow (< 50 cm), very gently sloping sides, with a sandy/clay littoral zone with clumps of swamp grass that tend to become submerged in Winter. As in Riddle's Dam, during Summer the dam dries up to some extent, but it is reduced in size by only about 15 to 20%. This is due to run off from the golf course during Summer following extended periods of watering.

The third dam (Grid Ref. TG835275, Map Number 6628-111 and PT.6528-11, Adelaide) is situated on the campus of the Waite Institute 5 km South- east of Adelaide, South Australia. It is a large dam (> 0.5 ha) with steep sides ($\simeq 45^{\circ}$) on the east and north banks and rather less (15° to 20°) on the south and west. Its depth ranges from a few centimeters at the dam's edge to more than 12 metres in the middle. It has a large population of A.deanei and a number of other notonectid species but as far as I could ascertain no R.dispar. It also supports a large number of Rainbow Trout (Salmo trutta) that were introduced in 1978/79 under the University of Adelaide Sports Association restocking program.

2:3.2.2 Collecting Technique

During June 1981, when Riddle's dam was full, the perimeter was ringed with wooden stakes (2.5 x 2.5 x 100 cm) situated 1 meter apart along the water's edge. Each stake bore an inverted white plastic beaker stapled to the top bearing a sequential grid number from 1 to 77 (the perimeter distance of the dam).

Ten grid locations were selected at random and two samples (Shallow and Deep) were taken from each location,on each sample date .

The shallow sample was taken along the water's edge by holding the net vertical to a depth of 5 cm and towing through a 1 meter distance (i.e. between 2 consecutive stakes). The deep sample was taken 1 meter from the water's edge at a water depth of 35 to 40 cm towing the net through 1 meter.The same collecting technique was used at the Echunga Golf Course and Waite dams, except for the deep sample, the water depths ranging from 25 to 30 cm in the Golf Course dam and 100 to 125 cm in the Waite dam. Furthermore the grid location was estimated by 'stepping out' from a set position and putting down two markers 1 meter apart, the dam not being marked out with stakes.

The contents of each net tow were emptied into a large white tray for sorting. The R.dispar were picked out by hand, aged by instar class and returned to the sample site. The remainder of the sample was placed into 80% V/V ethanol, in large, screw top containers. In the laboratory samples were hand sorted, the A.deanei being removed and size classed as outlined in Section 2:2, and counted. Because of the large numbers of ostracods (Ostracoda : Crustacea) and the time required in counting (even using a sub-sampling technique) it was decided to estimate the relative abundance by a 'gross' method. For very few animals this was done by visual inspection and counting under a binocular microscope, for large numbers of individuals, the animals were decanted into a pre-calibrated, drawn-out tip of a pasteur pipette, suitably sealed, and the number directly read off from the calibration. This method had an error of between 25 and 30%. The seven categories of ostrocod density used are shown in Table 2:12.

TABLE 2:12

CATEGORY	NUMBER OF OSTROCODS COLLECTED PER SAMPLE
1	< 10
2	11 to 50
3	51 to 100
4	101 to 500
5	501 to 1000
6	1001 to 5000
7	> 5000

All collecting was done with a square bottom aquatic net (F.B.A. mesh aperture 0.5 mm 20 meshes/cm, net month dimensions 20 cm wide x 25 cm deep) throughout November 1981 to July 1982.

The dispersion index (ID) for the various size classes of A.deanei were calculated from Southwood (1978) as the ratio of the sample variance to sample mean. The index is then used to test the null hypothesis that the observed pattern is random :

$$ID = \frac{S^2(n-1)}{\bar{x}}$$

where n = the number of samples. ID is approximately distributed as χ^2 with n-1 degrees of freedom, so that if the distribution is in fact Poisson the value of ID will not lie outside the limits (taken as 0.95 and 0.05) of χ^2 for n-1 as given in any standard table. Thus for organisms that are regularly distributed the mean/variance ratio will approach zero, while a large value implies aggregation.

2:3.3 Results

Table 2:13 shows the mean number of A.deanei caught per sample and the related dispersion index, over the eight collecting periods at the three sites. Much higher densities were found in the shallow compared with the deep samples in all three locations. Two sample dams (Riddle's and Golf Course) showed very few significant disperison indexes in the shallow samples suggesting that the animals were regularly spaced in the shallow water. Visual observation made at the time of collecting supports this with the shallow water zone supporting a large population of smaller size class of A.deanei round the dam's edge. Where aggregations did occur they were present at the earlier periods of the season. Whether this represents aggregations caused by oviposition or hatching areas or preferred microhabitats around the dam's edge I am unsure. A. deanei, in the ~~the~~ larger Waite dam, apart from having apparently a smaller density of A.deanei, exhibited a constant aggregating behaviour in the shallow water as shown by the significant dispersion indexes. Whether this was due to the size or depth profile characteristic of the dam or as a consequence of the numbers of fish present, I cannot say.

When comparing the deep water samples the incidence of significant dispersion indexes increases significantly. A.deanei, in all 3 dams, showed a consistent trend to form aggregations of individuals in the deeper water.

TABLE 2:13 The mean density (N/sample) and related dispersion index (DI) of *A.deanei* in either shallow or deep water at three field locations collected through November 1981 to February 1982. (See text for additional details)

SAMPLE DATE	SHALLOW						DEEP					
	RIDDLE'S		ECHUNGA		WAITE		RIDDLE'S		ECHUNGA		WAITE	
	$\bar{x}$	DI	$\bar{x}$	DI	$\bar{x}$	DI	$\bar{x}$	DI	$\bar{x}$	DI	$\bar{x}$	DI
6.11.81	107.7	181*	243.6	110*	76.4	25.0*	23.5	26*	61.8	32.5*	8.4	25*
3.12.81	30.4	112*	70.7	139*	21.4	30.8*	6.2	20*	48.5	20.8*	4.2	26*
18.12.81	2.4	11					59.7	88.6*				
23.12.81	2.0	9.2					56.3	50.4*				
5.1.82	10	12	19.6	10.2	7.6	55*	16.5	8.31	31.9	21.9*	1.2	71*
15.1.82	1	2.2					29.9	18.8*				
24.1.82	4	8.0					4.9	6.0				
1.2.82	1.4	3.2	13.5	5.7	2.1	48*	8.3	5.1	24.1	8.3	0.8	51*

* $p < 0.001$ (see text for details)

When the composition of the individuals in both shallow and deep water samples was examined (Fig. 2:2) there was a consistent trend exhibited over the three monthly sample periods (November, December, January) with the smallest individuals making up a significant percent of the samples taken in the shallow water. The number of larger A.deanei collected in the shallow water was significantly fewer. In the deep water the reverse was true, with very few small individuals being collected while the majority of the sample was made up of larger individuals.

A similar, if not more obvious, trend was observed when examining the spatial distribution of R.dispar in both dams (Fig. 2:3). In the shallow samples the significant percent of the sample consisted of smaller individuals (Instars I and II) with very few III and IV instars (< 10% combined). No larger instars or adults were collected in any shallow water sample. As in the A.deanei results, the reverse was found when the composition of the deep water sample was examined. The significant component was made up of the larger individuals (Instar IV to Adult) with the smaller instars making up less than 5% of the sample.

Table. 2:14 shows the relative densities of ostracods in both the shallow and deep water on the various collection dates. The highest density of ostracods is found in the shallow water.

Fig. 2:2 The composition of the *A.deanei* population in either shallow or deep water on three dates during Summer 1981/82.
(Numbers in parenthesis indicate total number of individuals sampled).
See text for collecting technique and details.

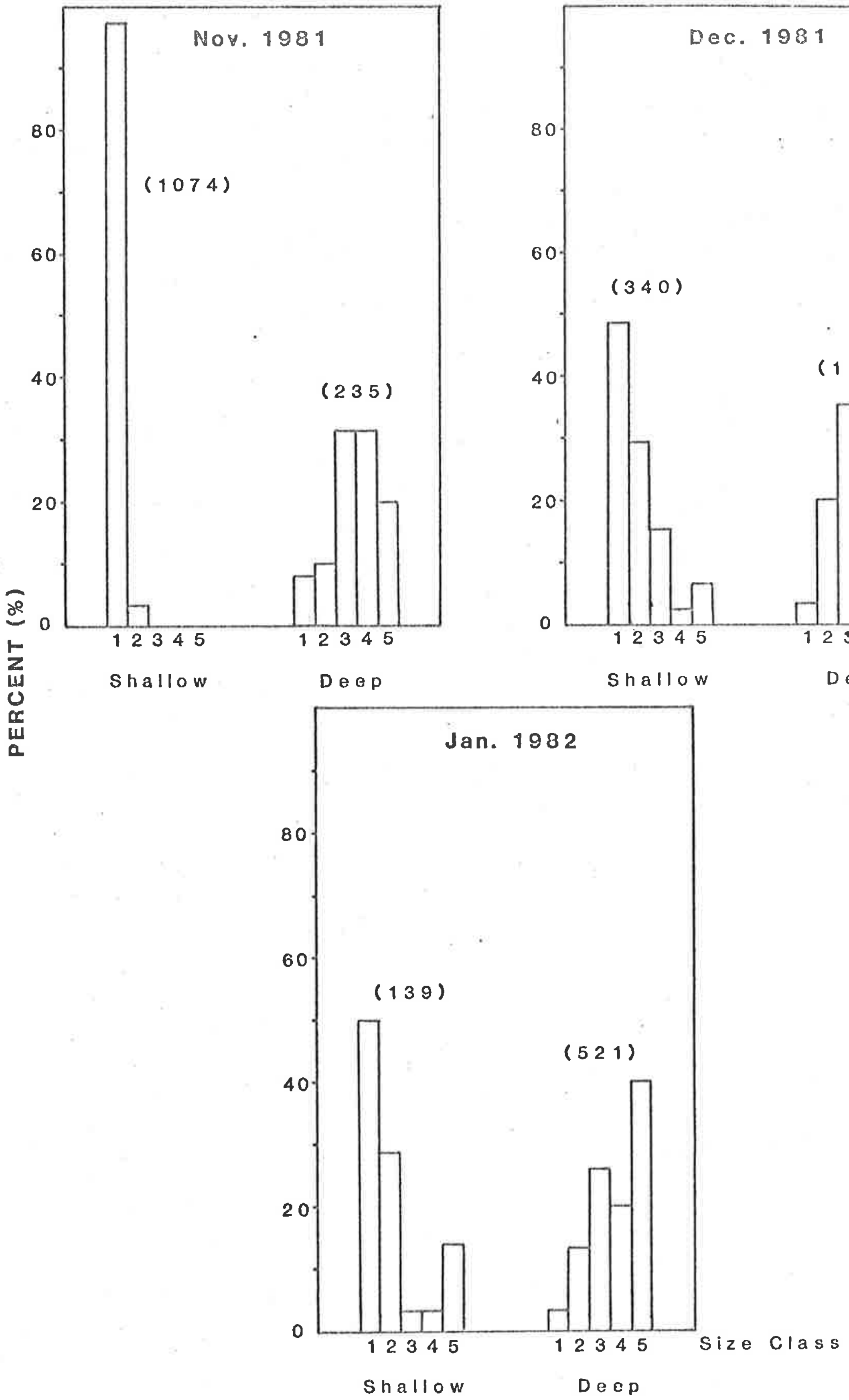
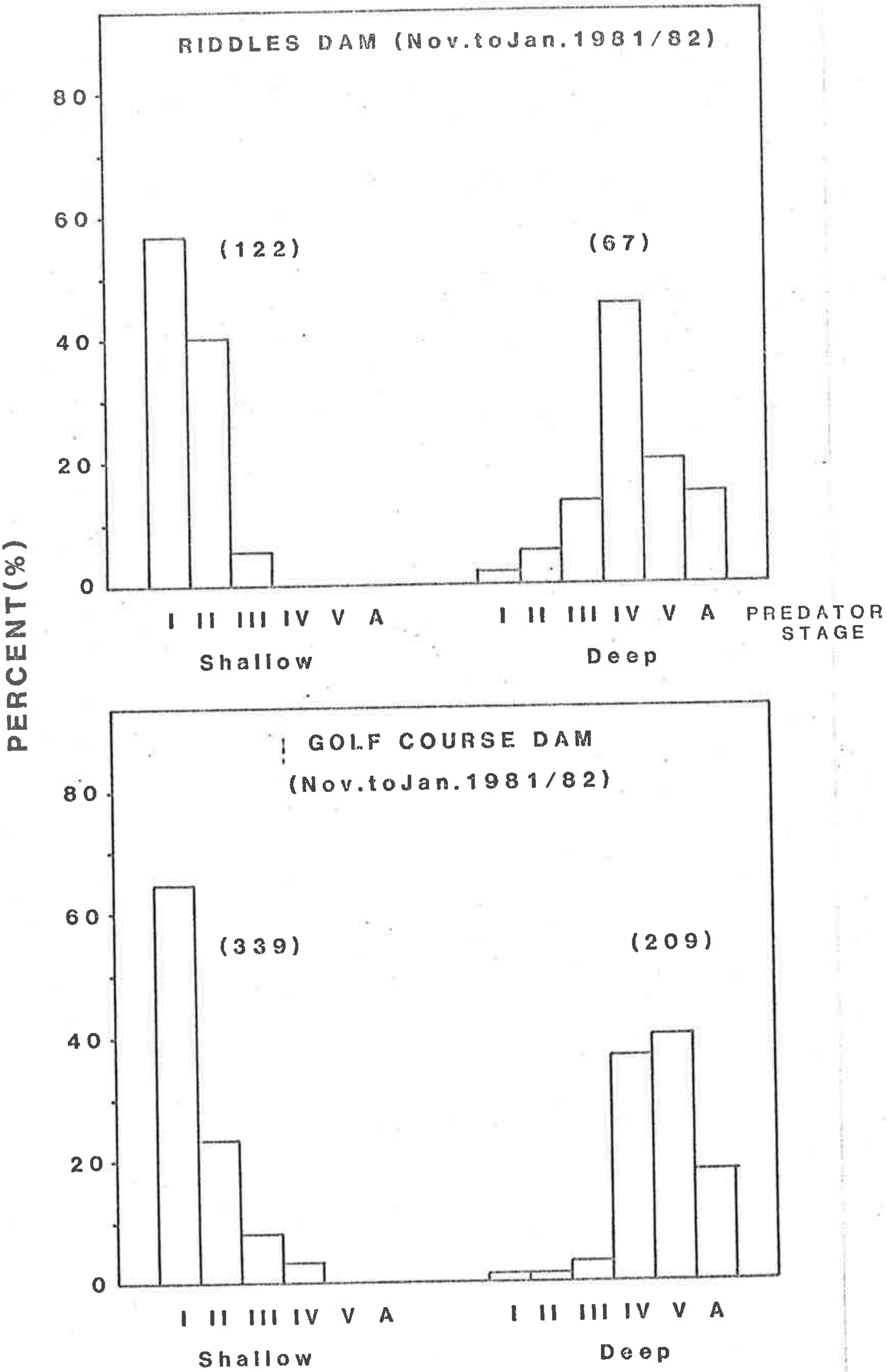

Nov. 1981
(1074)
(235)
Dec. 1981
(340)
(1106)
Jan. 1982
(139)
(521)
PERCENT (%)
0
20
40
60
80
1 2 3 4 5
Shallow
Deep
Size Class

TABLE 2:14 The relative densities of Ostrocods in the shallow (S) or deep (D) water of Hahndorf dam on various dates from November 1981 to February 1982. (See Table 2:12 for category definitions).

DATE	OSTRACOD DENSITY CATEGORY															
	0		1		2		3		4		5		6		7	
	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D
6.11.81	1	8	1	2	2	0	4	0	1	0	1	0	0	0	0	0
3.12.81	7	7	1	2	2	1	0	0	0	0	0	0	0	0	0	0
18.12.81	2	9	0	1	2	0	2	0	2	0	1	0	1	0	0	0
23.12.81	2	8	3	2	2	0	1	0	1	0	1	0	0	0	0	0
5.1.82	0	3	0	5	2	2	5	0	2	0	1	0	0	0	0	0
15.1.82	0	6	1	0	4	1	1	1	1	2	1	0	1	0	1	0
24.1.82	0	3	0	0	2	3	3	3	2	1	2	0	1	0	0	0
1.2.82	0	0	1	2	1	4	1	4	4	0	2	0	0	0	1	0

Fig. 2:3 The composition of the R.dispar population in either the shallow or deep water in two dams sampled on three occasions from November 1981 to January 1982. Numbers in parenthesis indicate total number sampled. See text for further details.


RIDDLES DAM (Nov.toJan.1981/82)
(122)
(67)
80
60
40
20
0
I II III IV V A
Shallow
I II III IV V A
Deep
PREDATOR STAGE
PERCENT(%)
GOLF COURSE DAM
(Nov.toJan.1981/82)
(339)
(209)
80
60
40
20
0
I II III IV V A
Shallow
I II III IV V A
Deep

2:3.4 Discussion

The results show that in the smaller dams (Riddle's and Golf Course) whereas aggregations of A.deanei are present in both the shallow and deep water during November but disappear in December and January, in the large dam (Waite) the aggregations in both shallow and deep water remained throughout the study period (November to January). In addition the composition of the aggregations shows a significant difference in the distribution of the smaller and larger size classes; the smaller individuals being found predominantly in the shallow (littoral zone) water while the larger individuals were found in the deeper water. This age-specific distribution was also observed in instars of R.dispar. In this case no large instars were found in the shallow water, being restricted to their deeper water. Few small instars were collected in the deep water, being found predominantly in the shallows. In addition to finding the smallest instars of both A.deanei and R.dispar, the shallow water was also found to contain the highest densities of ostracods.

The effect of water depth and an age-specific spatial distribution has been reported for other notonectid species. Murdoch and Sih (1978) showed that the presence of adult or older Notonectid instars depressed the feeding rate of younger stages, and that the small juveniles moved less and spent most of their time close to the edges of both laboratory containers and large field stock tanks. They proposed that the apparent 'avoidance' behaviour of juveniles in the presence of adults is an adaptation to avoid being eaten by adults. Additional work (Sih 1981) demonstrated that the addition of prey to the adults decreased the level of inference by the adults. This led to the suggestion that since the magnitude of interference decreases with increasing the number of prey, interference may play a critical mediating role in determining the magnitude of the predator population's functional and developmental responses. More recently Streams and Shubeck (1982) showed that populations of Notonecta lunata and N.undulata decreased with increase in water depth. However the age-specific distribution was only shown in N.undulata, where again the younger individuals were found in the shallow water whereas older nymphs and adults were more numerous in the deeper water. They attributed this restricted spatial distribution of the young to cannibalism by the larger individuals, discounting the importance of predation (by larger invertebrates and fish) as a factor affecting the distribution of the older age classes of notonectids.

My results from A.deanei support the above works in relation to the effect of water depth and the associated decrease in density. The continued nonrandom distribution of A.deanei in the Waite dam may be due to the presence of the fish predators. The aggregating behaviour being an anti-predation adaptation in the same sense as a fish school (see also Chapter 6). Why A.deanei should aggregate in the shallow water during November and early December and yet not do so for the remainder of the collecting period (mid-December to early February) I am unsure. It may be due to the much larger densities found at the beginning of the period. Implied aggregations are very evident however, in the deeper water, in both the smaller dams. The fact that no fish are present does not necessarily negate the anti-predation hypothesis. Both dams support populations of R.dispar, the larger individuals of which, as Fig. 2: shows, are restricted to the deeper water. (Chapter 5 of this thesis discusses the effect of prey aggregation and the resultant decrease in encounter rate with an ambush predator). The non-random distribution of *A.deanei* may reflect however, their reaction to other conditions in the dam. For example, areas of shadow cast across the water surface by a tree or bush seem to attract higher numbers of *A.deanei*. Furthermore it was noticed in all three dams, particularly the Waite dam, that particular regions consistently had many more *A.deanei* swimming in them, and that individuals would remain in that zone for many hours. I could not see any obvious feature (prey density, substrate type, etc.) that apparently made these areas more attractive. Obviously additional work is required to identify possible explanations.

In relation to the observed age-specific distribution of *A.deanei* and *R.dispar*, it is believed that both avoidance of cannibalism and the presence of prey, as suggested by Streams and Shubeck (1982) are the main causative factors. Observations in both the field and laboratory have shown that both *A.deanei* and *R.dispar* are cannibalistic. Unlike *Notonecta* spp., that generally hangs from the water surface and forages from that site (Fox 1975; Streams and Shubeck 1982), *A.deanei* forages in the mid-water column. This would make foraging in the shallow water difficult for the larger individuals and may lead to a tendency for them to avoid it. Thus the shallow waters offer, at least, a partial refuge from the adults and larger instars for the smaller individuals. Furthermore, the presence of an abundance of littoral zone vegetation (particularly when the density of adults is high) may offer additional refuge areas. It has been shown that the presence of vegetation very often significantly reduces the efficiency of foraging predators, both intra- and interspecific (see for example Bowen and Allanson 1982;

Fraser and Cerri 1982; Heck and Thoman 1981; Savino and Stein 1982; Stoner 1982). In addition to providing a potential refuge from intraspecific predation the shallow water also contains high densities of ostracods, a common prey of small A.deanei instars.

Either hypotheses could be used in explaining the observed distribution of R.dispar nymphs. In all likelihood both the avoidance of cannibalism and the availability of prey are involved in the spatial separation, although I believe the presence of potential prey to be more significant. Although the intermediate size nymphs (II and III) are found in the shallow water alongside the I instars, probably the potential threat of cannibalism is more than offset by (1) the larger instar's relative low density, in particular the III instar, and (2) the availability of high densities of potential prey; small notonectid nymphs and ostracods.

A a third hypothesis can be suggested, especially in the light of the results from Chapter 4, that being that the size-dependent distribution reduces the intraspecific competition for similar size prey (somewhat similar to the interference competitive interaction between a large, dominant species and small, subordinate one (Morse 1974)). Full particulars of this hypothesis, with supportive results, are presented in detail in the discussion of Chapter 4. Nevertheless,sufficient to say that the same reasoning can be applied to explain the distribution found in A.deanei (see also McArdle and Lawton 1979; Murdoch and Sih 1978). By maintaining the observed distribution, the small instars have access to prey that otherwise could be captured by the older, competing conspecifics; the larger individuals being able to capture and handle both large and small prey, the small predators being able to generally only handle the smaller prey.

Of course this field study has not taken into account the resultant consequences of oviposition sites and possible preferred substrate types on the observed distribution. Unfortunately time did not permit these areas of importance to be examined. Perhaps R.dispar affords contemplation as a suitable contender for a field and laboratory study of this nature, and the interrelation with foraging behaviour.

CHAPTER 3

THE PREY CAPTURING BEHAVIOUR OF R.dispar

3:1 INTRODUCTION

To be successful an organism must procure nutrients. In order to do this animals have evolved a vast array of methods enabling them to exploit every available source of food. Predation is just one such method or strategy of obtaining the required materials, enabling the animal to maintain a steady body state, grow and reproduce. Predator species evolve more efficient modes of prey capture, and prey species counter with defensive adaptations; the so called co-evolutionary 'arms race' of Dawkins and Krebs (1979). Therefore, the examination and identification of the mechanisms of prey capture are fundamental to our understanding of predator-prey complexes. Answers to such questions as "Why can this predator successfully capture organism A and yet not capture organism B (often with A and B being closely related)", can often be sought in examining the prey capturing process.

As a consequence of this obvious importance there have been numerous studies on the prey capturing behaviour of predators (for reviews see Curio 1976; Whitfield 1978; Owen 1980; Peckarsky 1982).

The study of prey-capturing mechanisms can be approached from a number of different directions. For example, a Morphological approach was taken by Holling (1964), Holling et al. (1976), Loxton and Nicholls (1979) and Kramer (1960), working with Mantids, and Dussault and Kramer (1981), Rand and Lander (1981), Bauer (1982) and Spence and Sutcliffe (1982) working with the guppy (Poecilia reticulata), pike (Esox niger), and two ground beetle larvae (Notiophilus biguttatus) and (Nebria spp.)

respectively. While a morpho-hydraulic description was given by Tanaka and Hisada (1980). Other studies have been primarily concerned with the physiological interaction involved in prey capture (for example : Mittelstaedt 1957; Roeder 1958; Rilling, Mittelstaedt and Roeder 1959; Maldonado, Levin and Barros-Pita 1967; Maldonado *et al.* 1974; Copeland and Carlson 1979; Garton and Strickle 1980; Shelly 1982). Schaller (1972), Kruuk (1972a, b), Wilson (1972) and Krebs (1979) were primarily interested in the social intraspecific relationships involved in prey capture, while Ford (1977a, b), Goss-Custard (1977), Wise (1979), Garton and Stickle (1980), Paul and Paul (1980) and Nakamura (1982) for example, approached the prey capturing mechanism by examining the metabolic or energetic costs involved.

Some studies of the behavioural mechanisms involved in prey capture are listed below:-

Richard (1970) and Etienne (1972) used dragonfly larvae to study the various behavioural components and the initiating stimuli involved in prey capture, while Wankowski (1981), working with salmon (*Salmo salar* L.), Jubb, Hughes and Rheinallt (1983) working with the marine crab (*Carcinus maenas* L.) and Winfield, Peirson, Cryer and Townsend (1983) working with two species of fresh water fish, Bream (*Abranus brama* (L.)) and Roach (*Rutilus rutilus*(L.)), studied the behavioural basis of prey size selection and associated prey capture. Crowley (1979), also working with damselfly nymphs, investigated the behavioural basis of prey switching in addition to a detailed analysis of some of the behavioural components of nymph predation on cladocerean prey. Additional important works on the behavioural basis of prey capture may be found in Arnold (1978) (Common Garter Snake, *Thamnophis sirtalis*);

Lindquist and Bachman (1980) (Tiger Salamander, *Ambystoma tigrinum*); Pastorok (1980) (*Chaoborus* larvae); Gardner (1964); Jackson (1977); Lubin (1980) and Rovner (1980) (Salticid Spider, *Phidippus clarus*; Cribellate Spiders, *Mallos* spp. and *Dictyna* spp.; Orb web Spider, *Cyrtophora* spp.; Wolf Spiders, *Lycosa* spp., respectively); Beissinger (1983) (Snail Kite, *Rostrhamus sociabilis sociabilis*); Ruggiero, Cheney and Knowlton (1979) (American Kestrel, *Falco sparverius*); Peckarsky (1980) (Various species of Stoneflies and Mayflies); and finally Molles and Pietruszka (1983) (Stoneflies, *Hesperoperla pacifica* and *Megareys signata*). Surprisingly few workers have examined the various components of prey capture by sit and wait predators. This is unfortunate for, as mentioned in the first chapter, these predators constitute an extremely important component in virtually all ecosystems, and it is only as we begin to unravel the prey capturing mechanism that we start to understand the complex predator-prey interactions that exist. In addition, because the predators are predominantly reliant on the movement of the prey to ensure encounter, the sit and wait predators constitute a particular group where intense selective pressure has focussed, to some extent, on the act of prey capture *per se* rather than on the pursuit or searching component of prey capture. They, therefore, form a unique group for studies on many aspects of prey capture, from neurophysiological to morphological.

Holling (1964, 1966) and Holling, Dunbrack and Dill (1976) studied behavioural and ecological aspects of the prey capturing behaviour of the mantis, *H.crassa*, while the actual physiological and morphological aspects of prey capture were studied in detail by Mittelstaedt (1957), Roeder (1959), Maldonado and Levin (1967), Maldonado, Levin and Barros-Pita (1967), Maldonado, Rodriguez and Balderrama (1974), and Copeland and Carlson (1979). However, the fact that the majority of mantids use a stalking or pursuit stage in the predatory repertoire disqualifies them from being considered as true sit-and-wait predators contrary to what is commonly thought. Griffiths (1980a) and Wilson (1974) documented prey capture in ant-lion larvae, relating changes in pit morphology and prey capturing techniques to prey type and habitat differences, while Łomnicki and Slobodkin (1966) and Murdock and Murdock (1972) studied the increase in tentacle length and nematocyst content of <u>Hydra littoralis</u> relating it to food deprivation and prey capture. Sit and wait predators may be aided by various auxiliary devices such as webs (see for example Savory 1952; Robinson and Robinson 1971; Kullman 1972; Lubin 1980; Olive 1980), sticky threads (see for example Gilmer 1972; Alcock 1978 p. 343-344), traps or pits (see for example Wheeler 1930; Bristowe 1958; Buchli 1969). Actively closing snares seem to be employed only by certain predatory nematodes (Pramer 1964) with fast death being achieved by the excretion of ammonia (Balan and Gerber 1972). Additional important studies of prey capturing behaviour in web-building spiders may be found in, for example, Austin and Blest (1979); Eberhard (1967); Lubin (1973, 1980); Robinson (1975); Robinson and Mirick (1971); Tolbert 1975).

Predator 'hunger', prey size and movement have all been shown to be intimately involved in the prey capturing process (see reviews in Curio 1976; Edwards 1963; Marler and Hamilton 1966 pp. 236-237; Cloarec 1972c) although detailed studies of the stimuli eliciting various components of the prey capture are scarce (Curio 1976).

Some aspects of the prey capturing behaviour of Ranatra linearis have been studied by Cloarec (1971a). Additional work (Cloarec 1974a) showed that there was a correlation between the foreleg posture, position and amount of food in the alimentary canal and the predator's responsiveness to an 'alimentary' stimulus. The emptier the midgut, the more the legs are bent backwards towards the head. A study of the extinction of prey capture behaviour showed that the more the forelegs are bent backwards towards the head the more numerous will be the responses to repeated presentations of an alimentary stimulus.

Later work (Cloarec 1976) showed that an interaction between visual and mechanoreceptors was involved in prey capture and that the high hit efficiency rate (i.e. correct distance estimation of prey) could be characterized by two behavioural aspects, reactivity and strike efficiency (Cloarec 1979, 1980a). Earlier work showed that R.linearis responded to a model prey moving in an irregular fashion vertically downwards; this evoked the highest response. She also showed that the space for successful capture lies above and in front of R.linearis (Cloarec 1969b).

The aim of this chapter is initially to describe and classify the behavioural components involved in prey capture by R.dispar (Sections 3:2 and 3:3). Having identified these it then expands them by examining the effects that food deprivation ('hunger') has on both the predator arousal and prey capturing components (Section 3:4). Finally the combined effects of food deprivation and prey size are investigated in order to compare their effect on each of the various behavioural components involved in prey capture (Section 3:5).

3:2 DESCRIPTION OF BASIC PREY CAPTURE AND FEEDING BEHAVIOUR

3:2.1 Materials and Methods

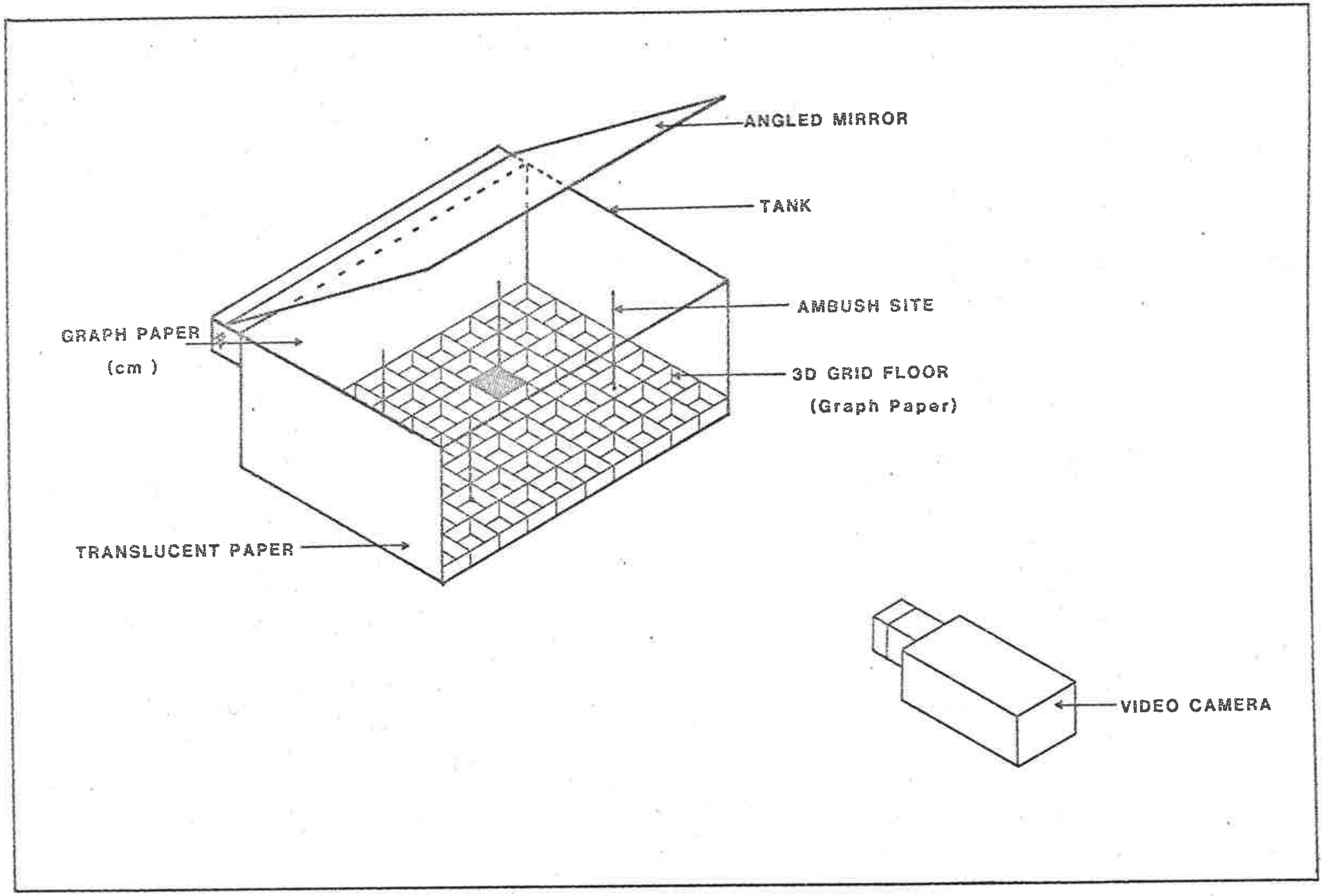
Animals were maintained as outlined in Chapter 2. For the experiments individual animals were chosen at random and placed in a plastic tank (25 cm Dia. x 20 cm Deep) or a large glass aquarium (50 x 35 x 20 cm) for observation. Prey animals (either singly for plastic tanks or in groups of up to 10 for the glass aquarium) were added and observed:

(i) directly whilst a continuous narrative of behavioural events was recorded on a tape recorder; or

(ii) by closed circuit video recording using a National T.V. camera (Model WV-1050 AE/A) fitted with a low light intensity NEWVICON picture tube and either a Canon zoom lens (12.5 to 77 mm) or an automatic iris lens (Model KF-54) with a focal length of 5.4 mm. Recordings were made on 1/2" tape on a National NV-7000 video recorder fitted with a pause/still/single frame advance control. Videos were played back through a normal 35 cm black and white T.V.monitor, as shown in Fig. 3:1. Where necessary two fibre optic lamps were used to supply additional lighting. No detectable change in water temperature was observed when the lights were on. During playback analysis of video tapes, comparable measurements in both the lateral and plan elevations could be taken with the aid of waterproof 1 mm graph paper secured to the bottom/side wall of the tank together with a previously calibrated transparent acetate

Fig. 3:1 Diagram of apparatus used in video observation. The grid floor was either mm graph paper or a plastic 3-D grid.

See text for additional details.


ANGLED MIRROR
TANK
AMBUSH SITE
GRAPH PAPER
(cm)
3D GRID FLOOR
(Graph Paper)
TRANSLUCENT PAPER
VIDEO CAMERA

overlay sheet fitted to the T.V.Monitor. The calibrated sheet was necessary to take into account the distortion caused by the mirror parallax observed in the plan elevation on the monitor. It was made beforehand using objects of known length being moved across the tank at various water depths. The sheet permitted therefore accurate measurements to be taken directly from the image on the screen. Cloarec's terminology (Cloarec 1969b) have been used in classifying the various components of the predatory process.

3:2.2 Results

1. Prey Capture Posture.

(i) In Relation to Support :- Normally R.dispar adults and larger instars (Instars 3, 4 and 5) position themselves on some submerged solid object, for example stem of water plant or twig, before taking up their characteristic capture posture. R.dispar normally holds its body parallel to the object irrespective of the angular position of the support with its head positioned lower than the abdomen and thorax (see Fig. 3:2B). R.dispar is very similar to R.linearis in this respect (Cloarec 1969b).

(ii) Body Posture :- Fig. 3:2 shows the position of the legs of R.dispar in relation to the body and to each other while in the pre-capture position. The meso- and meta-thoracic legs are supportive leaving the prothoracic legs free. R.dispar has also been observed, in both the field and laboratory, floating just below the water surface (Fig. 3:3) and remaining there for an indefinite period. In such a position the respiratory siphon is

Fig. 3:2 (a) The position of the legs of *R.dispar* in relation to the body and to each other in the pre-capture position.

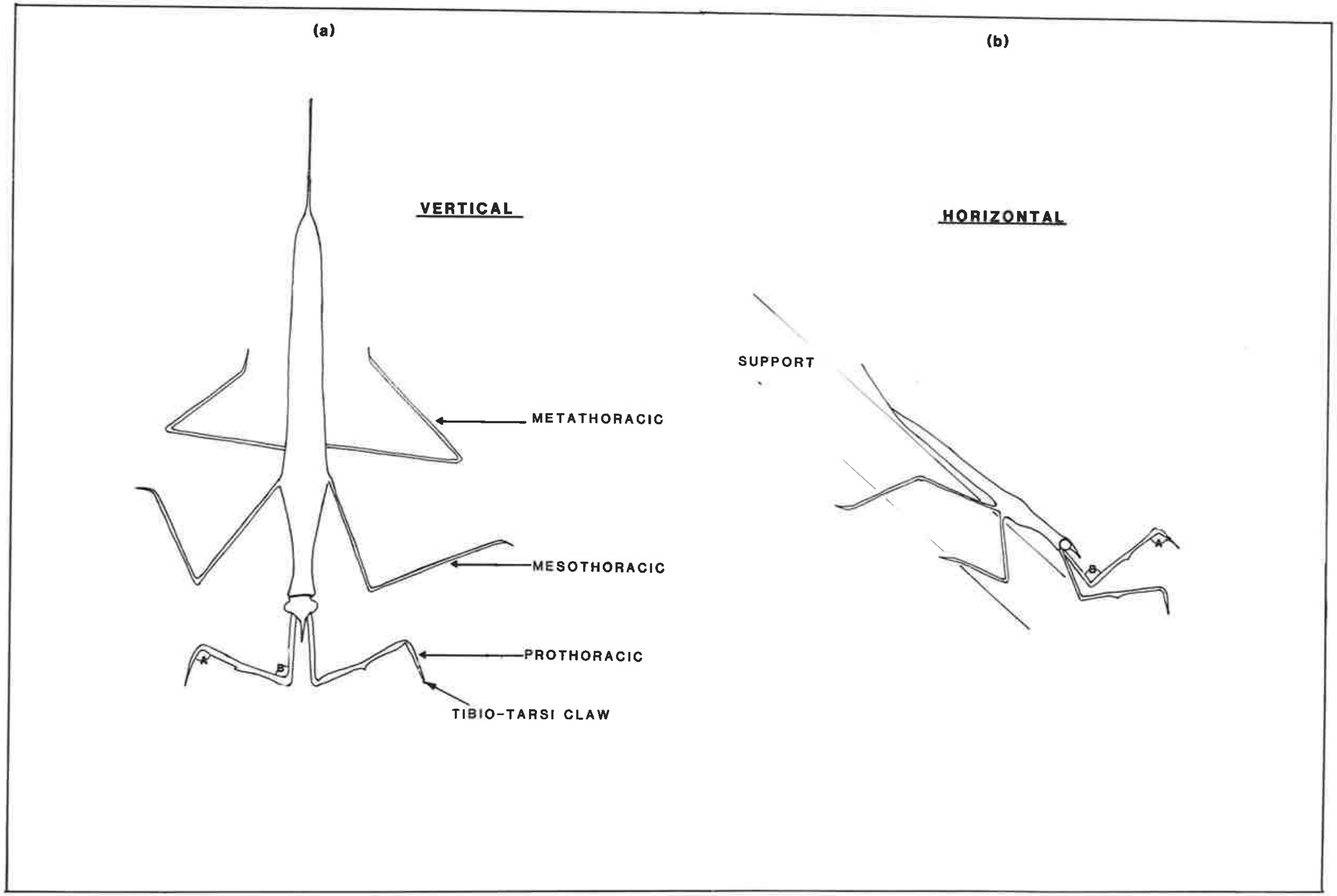
A = Angle of Tibio-tarsus/femur = 90° ($85-100^{\circ}$)

B = Angle of femur/coxa = 80° ($70-90^{\circ}$)

Fig. 3:2 (b) The position of the legs and body of *R.dispar* in relation to the support.

A = Angle of tibio-tarsus/femur = 90° ($85-100^{\circ}$)

B = Angle of femur/coxa = 90° ($80-100^{\circ}$)


(a)
VERTICAL
METATHORACIC
MESOTHORACIC
PROTHORACIC
TIBIO-TARSI CLAW
A
B
(b)
HORIZONTAL
SUPPORT
A
B

normally protruded through the water surface all the time. (Whilst floating R.dispar is quite capable of capturing small prey that either collide with the raptorial legs (see also Cloarec 1969b) or come very close. This was not reported for R.linearis, although Cloarec (1971) did report that R.linearis is unable to capture prey during any stages of the respiratory behaviour).

2. Predator 'Arousal'

When a potential prey comes close the posture of R.dispar changes by

(i) the body, while remaining parallel to the support moves vertically away from it, i.e. the coxa/femur angle of the meso- and meta-thoracic legs increase; and

(ii) the prothoracic femora are brought closer to the head, i.e. there is a reduction in the coxa/femur angle. Depending on the relative position of predator and prey, R.dispar can remain in the aroused position for an indefinite period or return to the earlier described posture. If the prey moves closer to the predator, orientation towards the prey occurs.

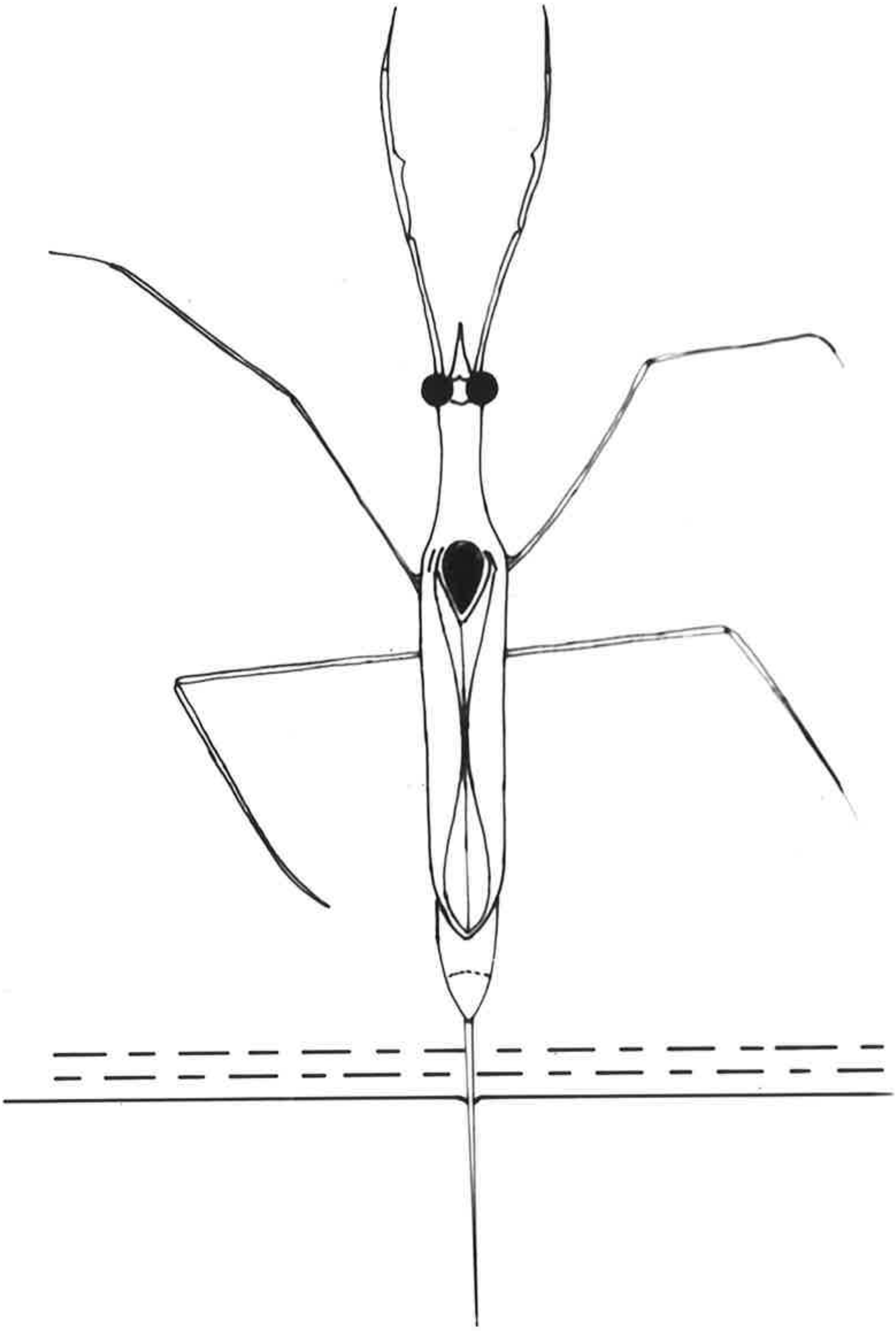
3. Predator Orientation

Orientation towards the prey can involve large changes in position, in relation to the support (Predator Orientation I) - (see Chapter 7) in addition to the normal posture changes (Predator Orientation II) given below :-

(i) The position of the body of R.dispar changes by a continuation of the rising of the whole body as outlined in 'arousal'. The head is lifted up between 3 and 5 mm which brings the sagittal axis in line

Fig. 3:3 The position of R.dispar when floating just below the water surface. The metathoracic legs have just been moved from the water surface.

Drawing taken from a slide.



with the prey. This is brought about by an extension of both the meso- and meta- thoracic legs - i.e. the coxa/femur angle increases and there is some degree of change in the point of articulation between the tarsal segments and the support (see also Cloarec 1969b).

(ii) the prothoracic femora continue to move towards the head (i.e. a reduction in the coxa/femur angle) in addition to the fused tibio/tarsi opening away from the femora (i.e. there is an increase in the tibio-tarsus/femur angle). When open the fused tibio/tarsi are directed towards the prey.

4. Prey Capture

The prey is captured by the rapid lowering of the femora on which the tibio/tarsi are closing. The angle of the femur/tibio-tarsi articulation changes rapidly from about 150° to 0°. The resolving speed of the video analysis did not permit timing of the strike to be made more accurately than 0.04 sec. (4/100 sec.). This compares with 0.03 sec. (3/100 sec.) for R.linearis as measured by Cloarec (1969b). The prey is held between the tibio/tarsus and femur very close to their point of articulation.

5. Post Capture Movements including Consolidation of Grip.

Following capture the femurs continue in the downward movement. This is accompanied by the body moving closer to the support. The femora then move back towards the head (coxa/femur angle reduced) whilst the tibio-tarsi remains closed, holding the prey. If the prey has been caught with one prothoracic leg the second leg then grasps the prey and consolidates the hold.

6. Exploration.

The prey is brought to the head until it reaches the extremity of the rostrum. The rostrum is flexible, especially the third (final) segment. The prey is held between the two prothoracic legs while the rostrum first makes contact and then proceeds to move over the surface of the prey. Normally the prey is manipulated by changing the position of the grip of the holding legs. This allows further exploration to take place. Exploratory movements continue until a suitable feeding site is located, normally an intersegmental membrane.

7. Injection of Venom.

It appears that the mandibular stylets penetrate the prey cuticle first and secure the predator's hold on the prey. The maxillary stylets are then pushed in perpendicular to the prey. [In 85% of observations (n = 169) with *A.deanei* as prey, this initial penetration site is located in one of the rear metathoracic legs, normally in the femur/coxa intersegmental membrane]. That venom/toxins are injected at this time is concluded from observing the behaviour of the prey (but see also Chapter 5 for supportive details).

The immediate effect of injection of venom of *R.dispar* into the prey is convulsive struggling leading rapidly to tremors, and to flaccid paralysis. The time interval between initial injection (as measured from the first convulsion) to paralysis is very much dependent on prey size. For A.deanei, prey size 1 (Instars 1 and 2), paralysis occurs between 1 and 3 minutes ($\bar{x}$ = 108.5 secs, SD = 37 secs, Range = 52 to 190 secs, N = 66) while for adult A.deanei paralysis takes about 4 minutes ($\bar{x}$ = 272.6 secs, SD = 57.8 secs, Range = 161 to 420 secs, N = 196).

The rapid paralysis, which is also a striking feature of so many arthropod predator/prey encounters (see Edwards 1963), may be due as much to the vulnerability of the organs within the haemocoel as to any special potency of the secretions used, for once it is within the body the injected toxins have access to the membranes surrounding nerve and muscle tissue, and the brief but convulsive struggling of the prey doubtless serves to speed its distribution through the haemocoel. In addition, the location of a pulsating organ in the metathoracic leg of heteroptera (Chapman 1971, p.667; Locy 1884a) where the initial injection of toxins occur, may aid in rapidly moving the venom into the haemocoel in addition to almost instantaneously rendering the 'kicking/swimming' leg inoperative.

8. Feeding.

Once paralysed the predator inevitably changes the location of the penetration site, normally moving to an intersegmental membrane on the abdomen or abdomen/thorax junction. During feeding the maxillary stylets move deep within the prey body cavity, and the prey is seen to start rythmic oscillations whilst 'speared' on the stylets. This is believed to be due to the regular alternating forward and backward shearing movement of the maxillae (see also Cobben 1978).

The penetration and grip of the stylets is such that after a short while of feeding either one or both prothoracic legs can be removed from the prey. This enables, if required, the capture of additional prey as described in Chapter 5:3.

9. Finish of Meal.

When finished the prey's remains are discarded usually by grasping the cadav~~a~~er with either one or both prothoracic legs, retracting the stylets and moving the prey away from the rostrum and allowing it to drop by opening the tibio/tarsi. When both legs are holding new prey the stylets are simply withdrawn and the cadav~~a~~er falls to the bottom. Unlike *R.linearis*, as reported by Cloarec (1969b), I have observed *R.dispar* to clean both its mouthparts and eyes with its prothoracic legs after some meals.

The above description outlines the sequence of events that normally occur in one feeding cycle. As expected however, much variability can and does exist with either parts or entire sections of the cycle being modified in some way or completely absent. Far from being a linear sequential pattern of behaviours, each being dependent on the preceding one, a far more complex pattern exists. The predator exhibits a versatile repertoire of behaviour which permits a great degree of efficiency in prey capture dependent on the prevailing circumstances. Fig. 3:4 shows diagrams of prey captures taken from video recordings, while Fig. 3:5 summarizes in a flow diagram the sequence of behavioural components and the interrelationships between them. Two principal groups of components are obvious in Fig. 3:5; those associated with the predator's initial interest or 'arousal' towards the prey and those associated with the capture. Most of the

Fig. 3:4 Summary of the sequence of behaviours of *R.dispar* leading to prey capture.

(1) Pre-capture position.

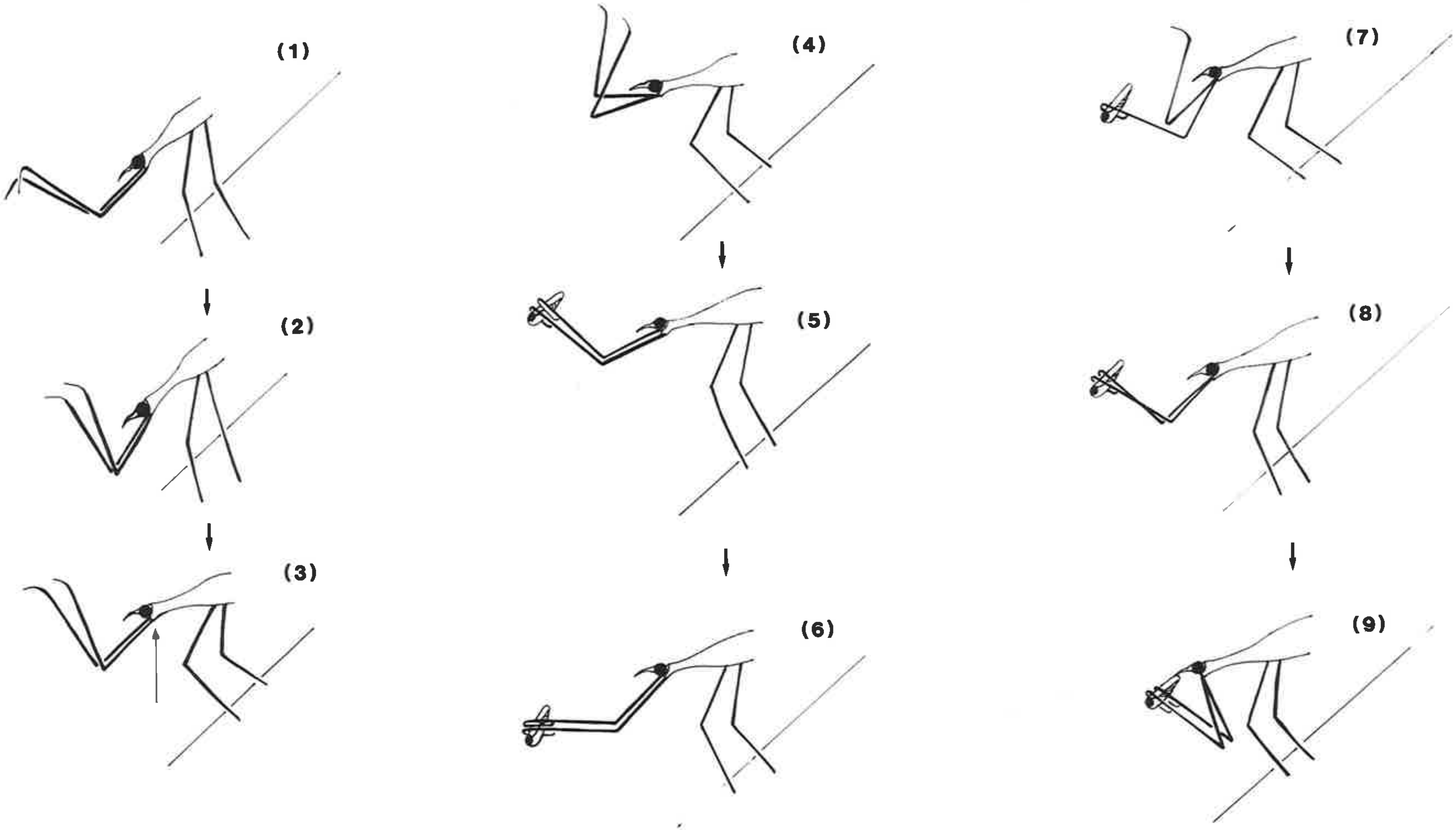
(2) Beginning of Arousal)
) Arousal
(3) Arousal)

(4) Orientation.

(5))
) Capture.
(6))

(7))
) Consolidation of Grip.
(8))

(9) Exploration commences.


(1)
(2)
(3)
(4)
(5)
(6)
(7)
(8)
(9)

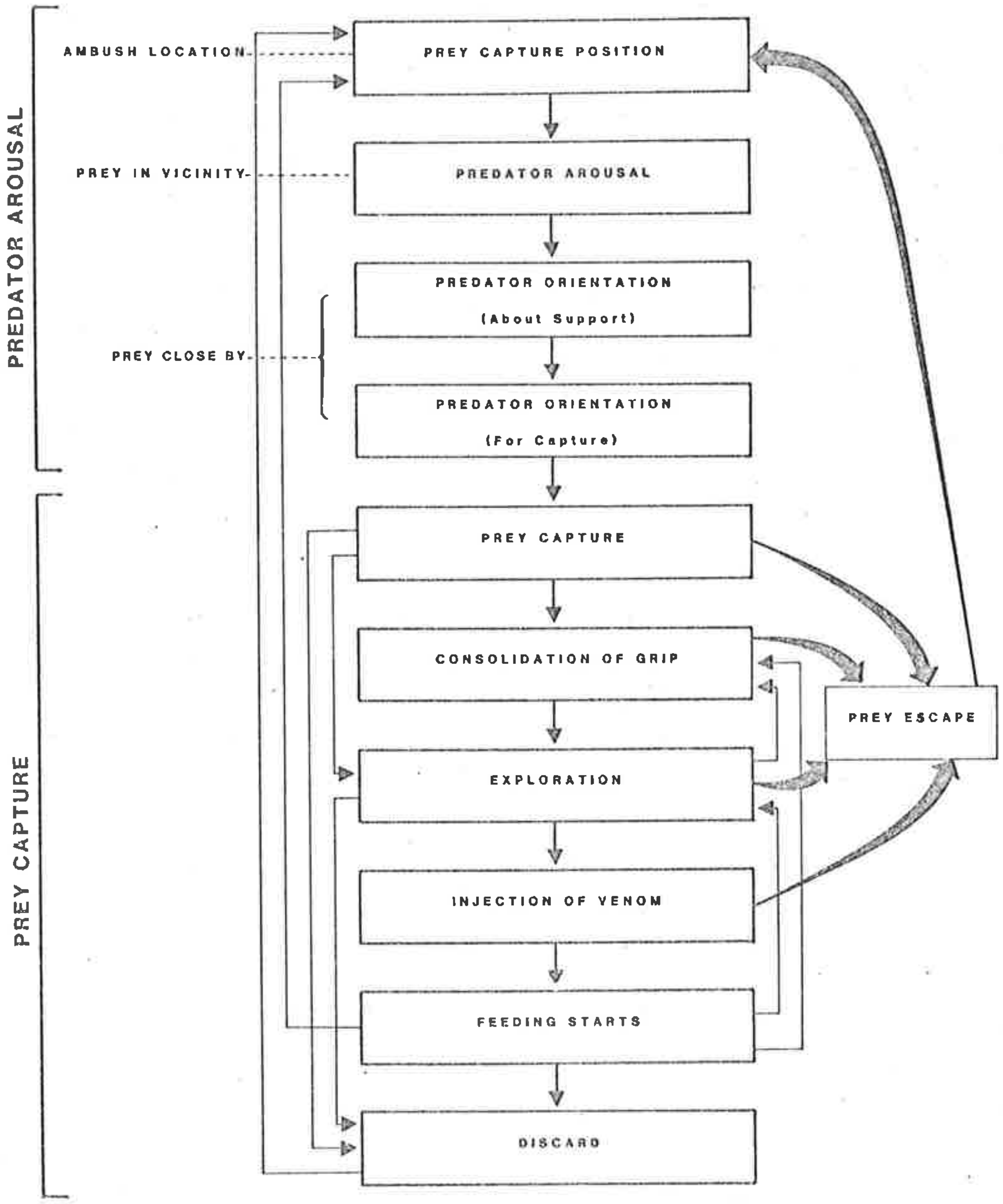
rest of this chapter will focus on these sections - Predator Arousal and Prey Capture - in order to examine them more closely and, perhaps more importantly, to study the effect of two previously identified prey capturing stimuli, those of 'hunger' and prey size (see references in for example Curio 1976; Edwards 1963; Peckarsky 1982). First however, Section 3:3 outlines some of these variations found in prey capture behaviour in more detail, along with some additional observations.

3:3 VARIATION IN PREY CAPTURING BEHAVIOUR AND OTHER OBSERVATIONS

The previous section, 3:2.2, describes the sequence of events that normally occur in one feeding cycle. However, as expected, much variability and plasticity or behaviour does exist, with either entire sections or parts of the cycle being modified or completely absent. The variability falls into two distinct categories. That of changes in predator posture during prey capture and feeding periods, and secondly that of changes resulting from the actual interactive process between the predator and the prey, for example a prey animal attempting to escape. Much of this mutability of posture, especially prothroacic leg positioning, has been reported in detail for the related species R.linearis by Cloarec (1969b, 1974a) who correlated it with the amount and position of food in the gut.

To a significant extent the same degree of variability in leg position and overall body posturing has been observed in R.dispar. As a result of this obvious interspecific similarity no descriptive studies are reported here apart from where R.dispar showed marked departure from that reported for R.linearis. Where behavioural disparity existed or

Fig. 3:5 Flow diagram summary of behavioural components, and interrelationships between them, in the predatory behaviour of R.dispar.
See text for detailed description.


PREDATOR AROUSAL
PREY CAPTURE
AMBUSH LOCATION
PREY CAPTURE POSITION
PREY IN VICINITY
PREDATOR AROUSAL
PREDATOR ORIENTATION
(About Support)
PREY CLOSE BY
PREDATOR ORIENTATION
(For Capture)
PREY CAPTURE
CONSOLIDATION OF GRIP
PREY ESCAPE
EXPLORATION
INJECTION OF VENOM
FEEDING STARTS
DISCARD

when R.dispar displayed a behavioural repertoire not previously reported, additional observations, and in some cases simple experimental manipulations, were carried out, the details of which are presented under the appropriate sub-heading below.

3:3.1 Observations on the Arousal Component of Predatory Behaviour

Examination of Fig. 3:5 shows that the sequence of events in the predatory behaviour of R.dispar fall into two distinct stages : (1) AROUSAL/ORIENTATION and (2) PREY CAPTURE/FEEDING. As mentioned previously, Cloarec (1969b, 1974a) has shown that there exists a strong correlation between the angular posture of the capturing prothoracic legs and the position of food in the gut. Therefore, the intervals between and duration of each meal will be reflected in associated changes in leg position and capturing ability (NB Ranatra is only capable of capturing prey when the prothoracic legs are in a few particular positions - see Cloarec 1969b, 1974a for full details). Thus it appears that the initial first stage of the predatory cycle is very much influenced by the amount and position of food in the gut, which is also used by Holling (1966) in defining the 'hunger' level of the predator.

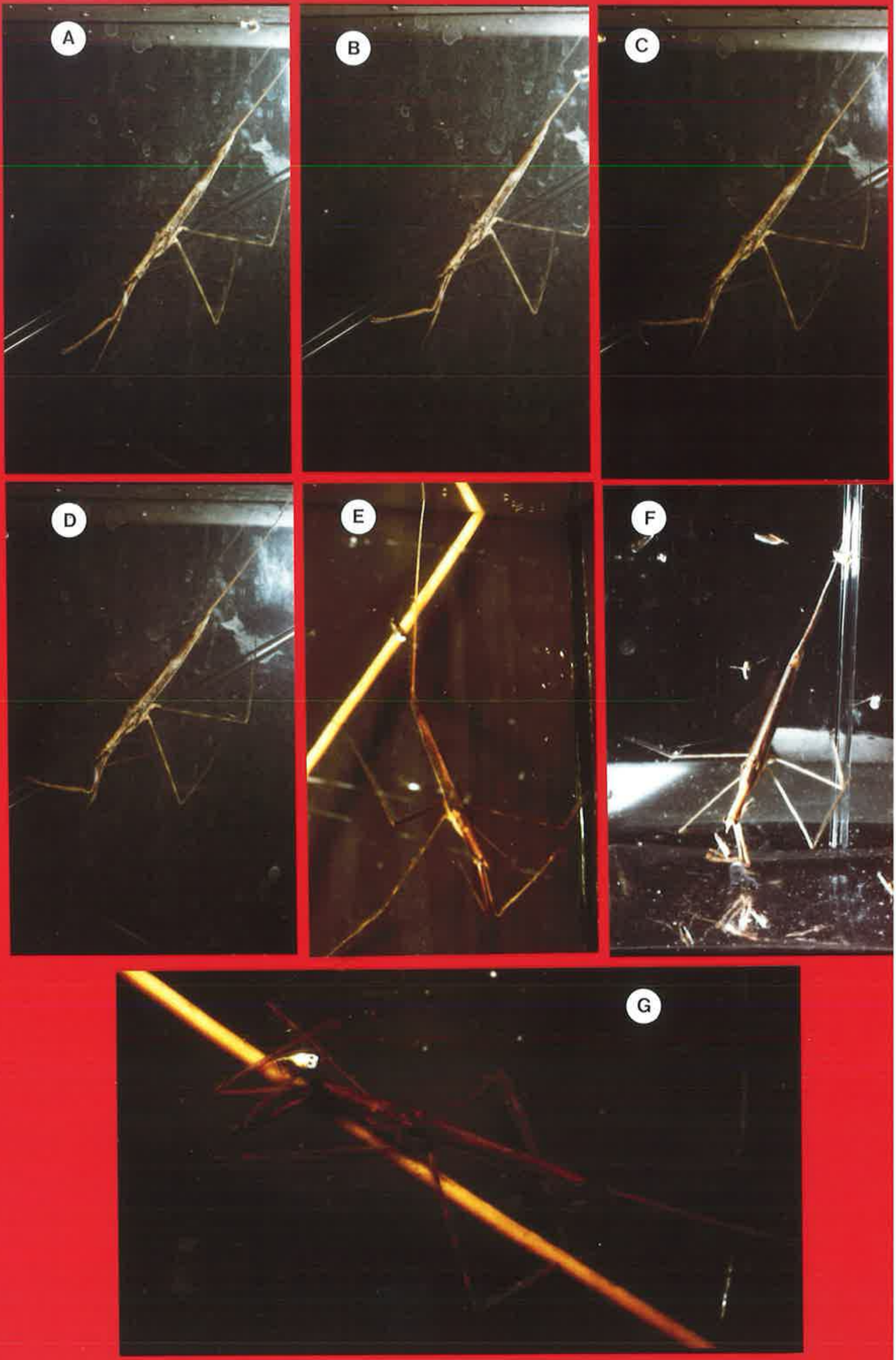
The 'arousal' stage of the predator is always present and provides a useful 'handle' in identifying particular stages of the capture cycle. Occasionally prey items will collide with the predators raptorial leg(s) and the tibio/tarsal claw will close on them. Feeding has not been observed to follow such events, however.

Movements about the vertical support, whilst still maintaining

PLATE 4

Various behavioural components of predatory behaviour of *R.dispar.*

(A) and (B)	Pre-capture position
(C) and (D)	Arousal
(E)	Orientation (to capture)
(F)	Capture
(G)	Exploration


A
B
C
D
E
F
G

contact with the meso- and metathoracic legs, during the 'orientation' stage may be absent and/or combined with the additional 'orientation' movements outlined in Section 3:2.2. (Further details of movements/orientations about the foraging site are presented in Chapter 7).

3:3.2 Observations on the Prey Capture component of Predatory Behaviour

The capture success or efficiency of R.dispar is very much associated with the 'hunger' level of the predator and the size of the prey. (See Section 3:6 this chapter for detailed observations and analysis). However from an additional study of 220 capture attempts by adult R.dispar on adult A.deanei I observed about a 76% capture success for the prey captured in a feeding period. This result is complicated by R.dispar's ability to capture and hold more than one prey at a time. This unusual phenomenon is discussed more fully in Chapter 5 where additional experimental details are given.

If the capture is unsuccessful, but the prey remains within strike distance, the predator will attempt repeated captures. Up to three or four strikes have been observed in a time interval of 1.5 to 2.0 seconds. Following unsuccessful capture attempts, R.dispar resumes one of the earlier 'postures' of the capture cycle, depending on whether prey are nearby or not.

After the successful capture of a prey, the exploratory stage always follows. (This may be delayed for a considerable time if the Ranatra is already feeding on a previously caught prey).

During prey exploration the rostrum is normally moved over the entire body surface as the prey is manoeuvred by either one or both raptorial legs. If being manoeuvred by one leg (i.e. the other leg is holding a second prey) the incidence of successful escape by the prey is greater than if it is held and manoeuvred by both legs. Table 3:1 summarizes these observations.

<u>TABLE 3:1</u> The incidence of successful escape by adult prey during the exploratory stage of the feeding cycle when held and manoeuvred by either one or both of the predator's prothoracic legs.

	No. of animals	No. of escape attempts	No. of successful escapes
Prey held by both legs	41	32	2
Prey held by one leg	29	21	11

Exploration always occurs and precedes any feeding activity, whether it is the initial puncture and subsequent feeding location or later feeding sites on the same animals.

When tested with model prey that conferred no nutritional reward and following various periods of food deprivation, <u>R.dispar</u> responded by increasing the initial exploratory time and number of exploratory bouts before rejection of the prey (Table 3:2).

TABLE 3:2 The effect of food deprivation on the average time of the initial exploratory bout, the average number of subsequent exploratory bouts per prey, and the average exploratory time per bout, before rejection of a model prey.

	FAST PERIOD			
	0-6 hrs	24-30 hrs	48-54 hrs	>240 hrs
1. Aver.Time (mins) of initial expl.bout	0.84	1.24	1.45	2.42
N	40	120	112	86
Range	.26-1.8	0.4-2.06	.57-1.90	0.94-4.33
2. Aver. # subsequent expl. bouts	0	1.5	1.7	7
N	-	11	14	36
Range	-	1-3	1-4	1-20
3. Aver. time/bout of subsequent expl. bouts.	-	.21	.34	.71

The style and techniques of collecting data did not permit a statistical analysis to be undertaken. Nevertheless the influence of food deprivation on the time budget and number of exploratory attempts is obvious. The longer the deprivation time the longer the initial exploratory bout, the greater the number of subsequent exploratory attempts, and the longer the average time spent in exploring during each bout before the model is discarded. Following the exploratory movements by the predator the initial feeding site is selected, which in 85% (n = 169) of the observed cases is one of the prey's rear (metathoracic) legs. The duration of the initial feeding stage was 4 minutes ($\bar{x}$ = 4.0 mins, SD = 0.86, n = 68) and it is during this stage that a mixture of toxins and digestive enzymes are injected into the prey (see Chapter 5 for a detailed study of feeding behaviour and dynamics). Subsequent manipulation of the prey enables further exploratory and feeding sites to be located on the prey. Table 3:3 gives a brief summary on exploratory and feeding data collected from over 100 different adult Ranatra individuals taken at various times throughout the study.

TABLE 3:3 Summary of number and duration of exploration or feeding by adult R.dispar on adult A.deanei.

(Time in minutes)	$\bar{x}$	SD	N	Range
1. Aver.Exploration Time/Site	1.3	0.6	560	1 to 3
2. Aver.Total Expl.Time/Prey	6.8	7.7	112	1 to 26
3. Aver.# of Expl.Sites/Prey	5.0	4.1	112	1 to 27
4. Aver.Feeding Time/Site	14.9	9.3	545	4 to 36.5
5. Aver.Total Feed.Time/Prey	58.2	31.9	109	5 to 141
6. Aver.# of Feed.Sites/Prey	4.9	3.9	109	1 to 27

These tables emphasize the extent of manipulation of prey by the predator during exploration and feeding. Although it is to be expected that this confers an advantage to the predator (for example further nutritional sites in different parts of the body may be found) it also involves a 'risk' factor, in the possibility of losing the prey. This can happen by the prey actually escaping (as mentioned previously) or by being dropped (apparently unintentionally, as subsequent behaviour patterns indicated) both of which can influence the subsequent predatory pattern.

3:3.3 Observations on the Defensive and Evasive Behaviour of R.dispar and their influence on Predatory Behaviour.

3:3.3.1 Introduction

Although not directly linked with predatory behaviour, two additional patterns of behaviour of R.dispar are given below, as they have the potential to affect all of the various stages in the predatory cycle.

The first concerns the predator's reaction to objects that are moved in reasonably close proximity to it. When an object, for example a 5 cm plastic disc, is moved near R.dispar that is, for example, in the pre-capture posture or feeding, it may respond by extending its prothoracic legs away from the head so that they lie in the same horizontal plane as the body and in elongation to the anterior end (Plate 1 d). The body may also be brought closer to the support, whilst remaining parallel to it, by reducing the coxa/femur angles of articulation of the meso- amd metathoracic legs. Also the predator may respond (either immediately, or following the leg extension response) by swimming to the bottom of the tank (in this case 50 cm depth) and remaining motionless for a variable time.

3:3.3.2 Material and Methods

SUBJECTS:- Subjects were either classified as FASTED (F), having gone at least 5 days (120 hrs) without feeding (Range 5 - 7.5 days), or NONFASTED (NF), animals which had fed within previous 36 hours.

STIMULI:- Plastic disc stimuli were either 5 or 10 cm in diameter, suspended on fine nylon fishing line and weighted with plasticine.

PRESENTATION:- All stimuli were presented when the predator was situated at about 10-15 cm depth.

(A) Submerged Presentation. The disc was brought from as far away as possible from the predator (>50 cm) and moved directly towards it at a depth of about 10 cm (a small marker on the line acted as a depth guide) and speed of about 6 cm sec.$^{-1}$.

(B) Surface Presentation. As above but with model held about 10 cm above water surface.

(C) Hand Movement. As in surface presentation but with either a slow speed (<2 cm sec.$^{-1}$) or fast speed (>10 cm sec.$^{-1}$).

Subjects were scored if they responded either with leg extension or by swimming to the bottom of the tank. The duration of the response was also recorded

3:3.3.3 Results and Discussion

Table 3:4 summarizes the results of observations on 296 adult

TABLE 3:4 The Response of Fasted or Non Fasted adult *R.dispar* to various model stimuli. (see text for presentation details).

			RESPONSE											
			EXTENSION PROTHORACIC LEGS						SWIM TO BOTTOM					
			FASTED			NON FASTED			FASTED			NON FASTED		
	TOTAL N TESTED	TOTAL N RESPONSE	DURATION (m) n	$\bar{x}$	Range	DURATION (m) n	$\bar{x}$	Range	DURATION (m) n	$\bar{x}$	Range	DURATION (m) n	$\bar{x}$	Range
1. 5 cm DISC SUBM.	46	24	8*(26)	2.6	.5 - 4	11*(20)	4.6	2 - 11	1*(26)	4	2 9	4*(20)	5	4 - 6
2. 10 cm DISC SUBM.	65	53	15*(37)	2.7	.3 - 5	19*(28)	6.9	2 - 15	8*(37)	14	8 20	11*(28)	19	5 - 49
3. 5 cm DISC SURF.	40	27	7*(20)	3	.3 -3.8	12*(20)	2.4	2 - 7	2*(20)	3	.4 8	6*(20)	8	3 - 28
4. 10 cm DISC SURF.	67	67	21*(36)	3.5	1 - 6	26*(31)	5.4	1.5- 9	14*(36)	13	3 30	17*(31)	17.6	9 - 69
5. SLOW HAND	38	11	3*(21)	.8	.5 -1.3	8*(17)	2.2	1 - 8	0*(21)	-	- -	0*(17)	-	- -
6. FAST HAND	40	37	3*(20)	3.9	.8 -8.4	13*(20)	8.8	5 - 13	6*(20)	11	2 26	15*(20)	24	15 - 59

* Number of animals that responded.

() Number of animals observed.

(m) Equals minutes

R.dispar (both female and male) subjected to the various stimuli either below or above the water surface. The data was collected intermittently over three and a half years and in many cases the reproductive state and past history of the individuals was unknown. No statistical analysis was performed on these data due to this mode of collection and unequal sample sizes. Nevertheless the main trends are obvious, with the fasted predators responding proportionally less and for shorter duration than the non-fasted subjects. Animals responded more towards the large model in both submerged and surface trials, while no appreciable difference was observed between the two smaller discs.

Clearly the 'hunger' level and size of stimulus have a marked effect on the responses observed. Time did not permit further experimentation to be undertaken to elucidate these interesting results and therefore I can only speculate as to why these trends are found. However, it would appear that for any given threat stimulus (no capture attempts were observed throughout the observations), the predator's probability of an evasive or defensive response is very much dependant on its current 'hunger level'. The longer the food deprivation the more likely it is that the predator will risk remaining at a potential prey capturing position irrespective of the threat. Furthermore, if the predator does respond to a threat, the duration of the response is much shorter, and they reposition themselves into a potential prey-capturing position sooner than non-fasted individuals. A somewhat similar result was reported by J.H. Lawton (cited as a personal communication in Hassell and Southwood 1978), for the damselfly, Ischnura elegans, that are at significant risk from predators when swimming and will therefore remain at their ambush site even when threatened by starvation.

The leg extension response described above is also observed if the prey struggles violently. Following a capture, prey are often observed to struggle. These struggles include leg kicking, leg levering against the raptorial legs, body rotation and 'swimming action', especially if they are held by only one leg. If these struggling movements are intense, especially if the prey is one of the larger instars or adult A.deanei, the prey is moved away from the rostrum. This is made possible by the predator's prothoracic legs extending, thus moving the prey away from the head region.

Prey have been observed to struggle immediately after capture, during the exploratory stage and particularly when the stylets are being inserted. The length of time that the prey is held away from the head is very variable, but again the period of food deprivation appears to be related to the observed results.

Table 3:5 summarizes a total of 67 such observations, made on both non-fasted (0 to 24 hour fast) and fasted (5 - 8 days) individuals. During the observations the time the prey was held away from the rostrum was recorded.

TABLE 3:5 The mean period for which a struggling prey was held away from the head region of the predator following either a short fasting (0-24h) or a long fast (5-8 days) (For the t-test 30 individuals were randomly chosen from each treatment).

TIME HELD AWAY FROM ROSTRUM (secs.) BEFORE MOVING IT BACK			
	$\bar{x} \pm$SD Duration (secs)	Range	N
Short fast predators (0-24 h)	19.6 ± 4.2	11.2 to 57	31
Long fast predators (5-8 days)	8.3 ± 2.1	4.2 to 24	36

$t = 4.4$, $p<0.01$, df 30.

As in the previous observations, the effect of food deprivation is very marked, with the 'hungrier' predators moving the prey back to the rostrum significantly faster. Whether this increases the 'risk' element taken by the predator (damage by the kicking metathoracic legs to the head and eye region could be possible) is unclear. Obviously further work is needed to shed light on this aspect of predatory behaviour.

3:4 DESCRIPTION OF THE PREDATOR'S 'AROUSAL' SPACE AND THE EFFECT OF FOOD DEPRIVATION

3:4.1 Introduction

A sit-and-wait predator lying in wait for food must be able to detect the approach of potential prey, and it must also be equipped to capture it efficiently when it comes within range. Cloarec (1976) has determined that both visual and to some extent mechanoreception are utilized by *Ranatra* in detecting prey.

As mentioned in Section 3:2, if an object is moved into the vicinity of *R.dispar* it can respond in either of two ways : a characteristic 'arousal' movement, which may lead to prey capture, or an evasive or defensive movement. The following series of experiments were conducted to map the size and shape of the 'arousal' space of *R.dispar*, i.e. that volume of space surrounding the predator within which the movement of an object stimulates arousal behaviour.

3:4.2 Material and Methods

Pre-experimental Procedure

Adult female *R.dispar* were removed from the holding tanks and fed abundant prey (Notonectids, mosquito larvae) for 2 days preceding the experimental period. On Day 1 of the experiment they were removed from the feeding tanks and assigned at random to two groups, A and B. Animals in Group A were individually housed and tested in large plastic cylindrical containers (25 cm Diameter x 20 cm) each, filled to a depth of 15 cm with filtered dechlorinated tap water, and fitted with a calibrated (mm) glass rod which acted as a support. The animals remained in these containers for the duration of the experiment.

Animals in Group B were individually placed into 1 litre plastic beakers which acted as holding containers between experiments which were performed in large glass tanks (50 x 35 x 20 cm deep) arranged for video observations.

Model Prey Stimulus

The model prey used throughout the experiments was made from a piece of fine wire 1.0 mm in cross section. It was fashioned to resemble (as far as possible) an adult notonectid. The top half was painted a dull orange/brown with a non-toxic matt paint, while the lower section of the model was left bare to resemble the sheen created by the wings with the associated air bubble. (Notonectids swim upside down - hence their common name 'backswimmer').

A piece of fine gauge nylon fishing line was used to suspend and move the model during experiments.

Notonectids swim in what is best termed a 'jerky' motion, short bouts (<0.5 sec) of propulsion can be separated by periods of motionlessness ranging in duration from 1-10 seconds (see also Chapter 6). To represent this type of movement in the model, the thread suspending it was slowly rolled between thumb and forefinger to produce a 'jerky' rotational action as the prey was presented to the predator. With sufficient practice and a long enough piece of thread (about 50 cm) repeatable movements could be produced.

Test Procedure

Animals were observed both laterally and from above by either video camera or direct observation. For video recording the apparatus was arranged as shown in Fig. 3:1. The use of the angled mirror permitted both lateral and vertical fields to be observed simultaneously on the T.V. Monitor. Both the floor and back wall of the tank were covered with mm graph paper (the cm lines outlined in black ink) to permit relative measurements to be made. For more accurate measurements a calibrated transparent acetate sheet was attached to the T.V. Monitor screen to produce an overlay from which distances could be read and measured.

Presentation of Model Prey:-

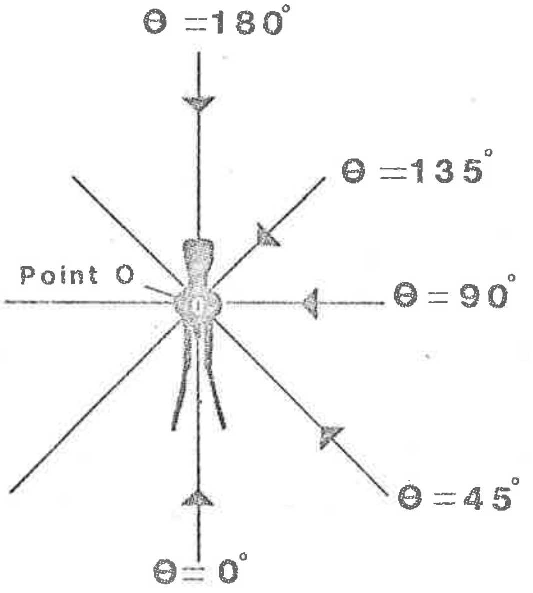
The direction of approach of the model prey could be along any one of eight predetermined directional paths in either the horizontal or vertical plane, as shown in Fig. 3:6. For Group A predators (held in plastic containers) the animal and direction of approach were chosen at random without replacement for each presentation until all animals and directions had been tested. For Group B predators, (video observation) one animal was chosen at random and put into the glass tank and allowed 15 minutes to acclimatize. Normally on reaching the support the predator took up the characteristic 'prey capture' posture within a few minutes. Presentations were never conducted unless the predator was in this position. Following this 'settling in' period the order of the direction of approach of the model prey was chosen at random without replacement until all the directions had been tested. The predator was returned to the holding tank and another animal chosen at random. This procedure was repeated until all Group B individuals had been tested.

Fig. 3:6 The direction paths used for presenting model prey to R.dispar to determine the arousal distance of the predator.

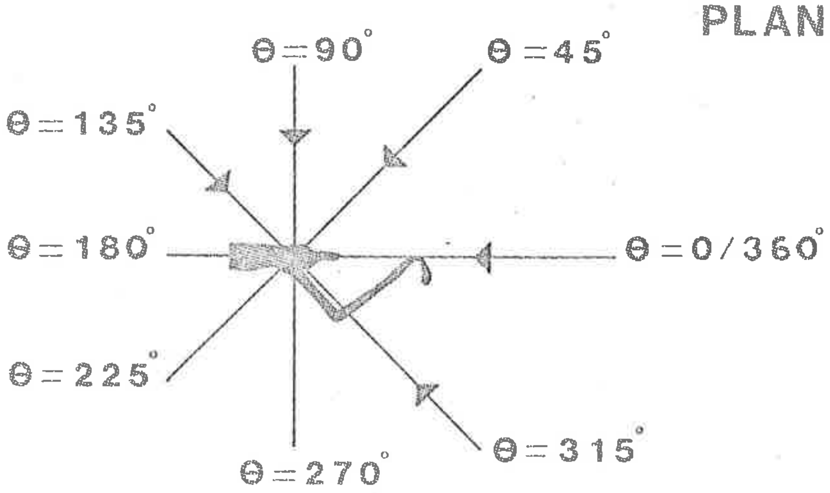
Point O, between predator's eyes, was used as the reference position for distance measurements.

See text for additional details.

HORIZONTAL PLANE



VERTICAL PLANE



In both Groups A and B each animal was tested 4 times. The entire procedure of 10 (animals) x 16 (directions) x 4 (repeats/animal) normally took between 5 and 6 hours.

Animals were tested on Day 2 (following 24-30 hour fast (hf)), Day 3 (48-54 hf), Day 4 (72-78 hf), Day 5 (96-102 hf) and Day 6 (120-126 hf).

The 'arousal distance' (as defined below) was measured between a point 0 (Fig. 3:6) mid-way between the predator's eyes and the anterior tip of the model prey.

Arousal Distance - (as outlined in Section 3:2), when a potential prey moves in the vicinity of R.dispar the predator's posture changes in 3 distinct, measurable ways. All 3 changes were used as indicators of predator's 'arousal' although changes in coxa/femur angle were used primarily.

Definition:- The arousal distance was defined as that distance of the model prey from the predator that was associated with a reduction from 90^{o} in the coxa/femur articulation angle of the predator's prothoracic legs.

NB. It has been shown with a related species, Ranatra linearis, (Cloarec 1976), that during normal predatory behaviour mechanical stimuli from prey, in addition to visual stimulation, play a part in the perception of prey. Receptors involved, situated on the prothoracic legs, and their area of stimulation, below the foreleg femurs, have been well documented (op. cit.). In the experiments reported in this thesis no additional mechano-stimulation was provided apart from that associated with the rotational movement of the model, as outlined above. Therefore it seems appropriate to point out that the results obtained in this section (and that of 3:5 & 3:6) could be due to a combination of both visual and some unquantifiable mechanical component. Every effort was made to standardize the movement of the model during experimentation to reduce any variation caused by it.

3:4.3 Results

As the variance within and between groups A and B was found not to differ significantly ($F < 1.5$, $p > 0.05$ in all cases) they were pooled for analysis.

HORIZONTAL PLANE: Figure 3:7A shows the symetrical shape of the 'arousal' field, in the horizontal plane, of R.dispar at 5 different food deprivation levels. The overall shape is elliptical, with each ellipse being essentially the same shape for each fasting period.

Two tendencies were noted in the results (1) the arousal distance between Ranatra and the prey increased as the period of food deprivation increased; (2) the distance was greatest for prey in front of the predator and decreased as the model was moved to the sides and rear.

To test the validity of these apparent tendencies, the mean

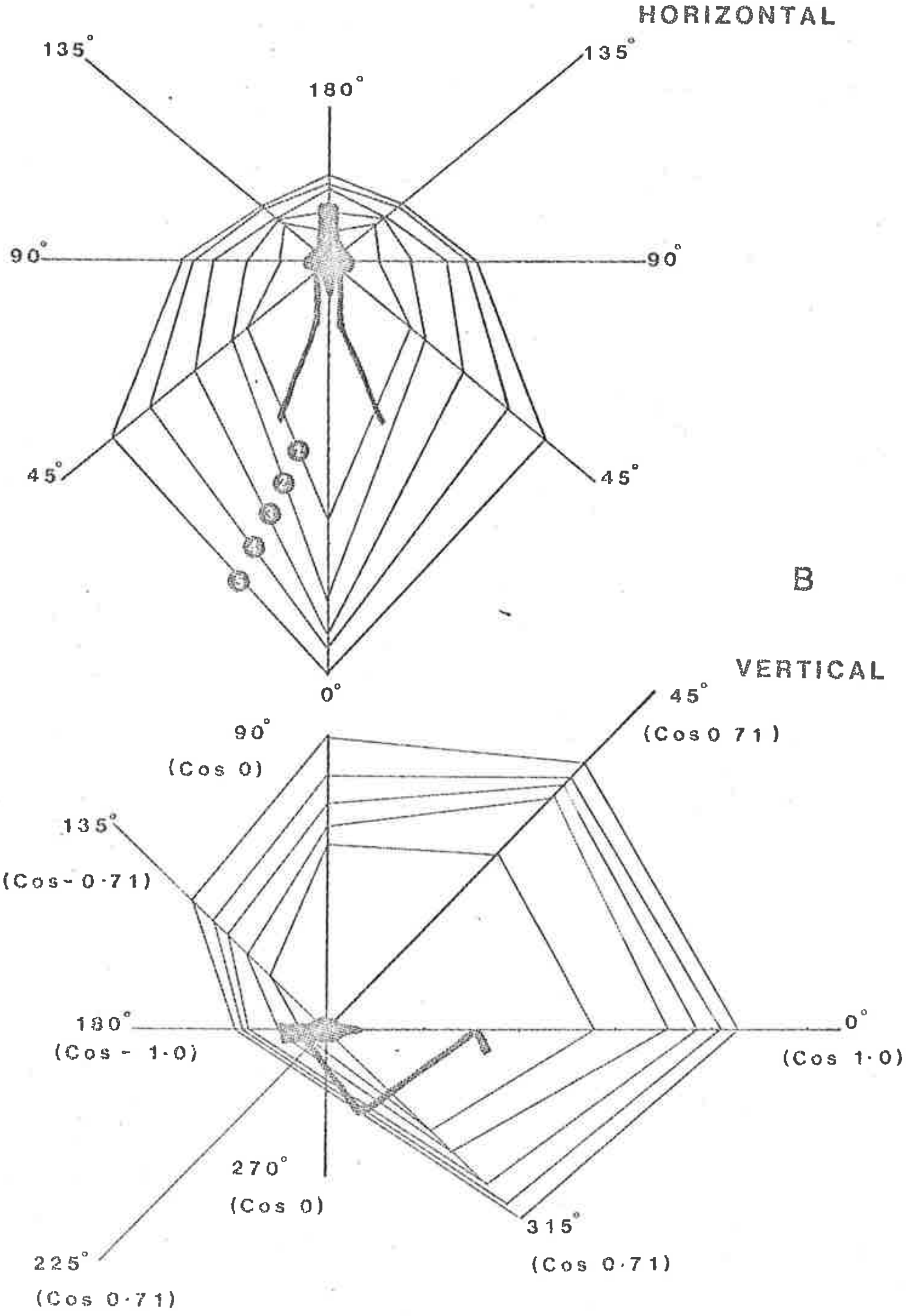
Fig. 3:7 The arousal fields of *R.dispar* as seen in the horizontal and vertical planes following 5 periods of food deprivation.

(①) = 24 h fast
(②) = 48 h fast
(③) = 72 h fast
(④) = 96 h fast
(⑤) - 120 h fast.

Intervals between dashes on 0° axis = 1 cm.

AROUSAL

FIELDS



arousal distances (AD) between the Ranatra and the model prey were plotted against fasting time for each of the angles of presentation.

In all cases the slopes were significantly positive (Fig. 3:8 A to E). The t values, degrees of freedom and associated level of probability for the angles of presentation in Table 3:6.

TABLE 3:6 Table of t-statistics, degrees of freedom, and level of significance for regression of mean arousal distance on fast time. (t-statistic tests null hypothesis that the slope is not different from zero).

ANGLE OF PRESENTATION	t-value	df	Significance
0^o	5.89	3	$p < 0.002$
45	11.31	3	$p < 0.001$
90	7.62	3	$p < 0.001$
135	4.69	3	$p < 0.005$
180	6.87	3	$p < 0.001$

These results show that the distance at which a Ranatra is aroused to a model prey increases as food deprivation time increases and that this is irrespective of the angular position (in the horizontal plane) of the model prey.

Analysis of covariance, to test the null hypothesis that the five slopes are equal, showed that significant differences in the slopes did exist : $F = 16.36$; df 3, 15; $p<0.001$.

Fig. 3:8 Regressions of Arousal Distance (AD) against fast time (FT) for R.dispar when model prey are presented along 5 different directional paths to the body axis in the horizontal plane.

(A) Presentation path $\theta = 0^{o}$

(B) Presentation path $\theta = 45^{o}$

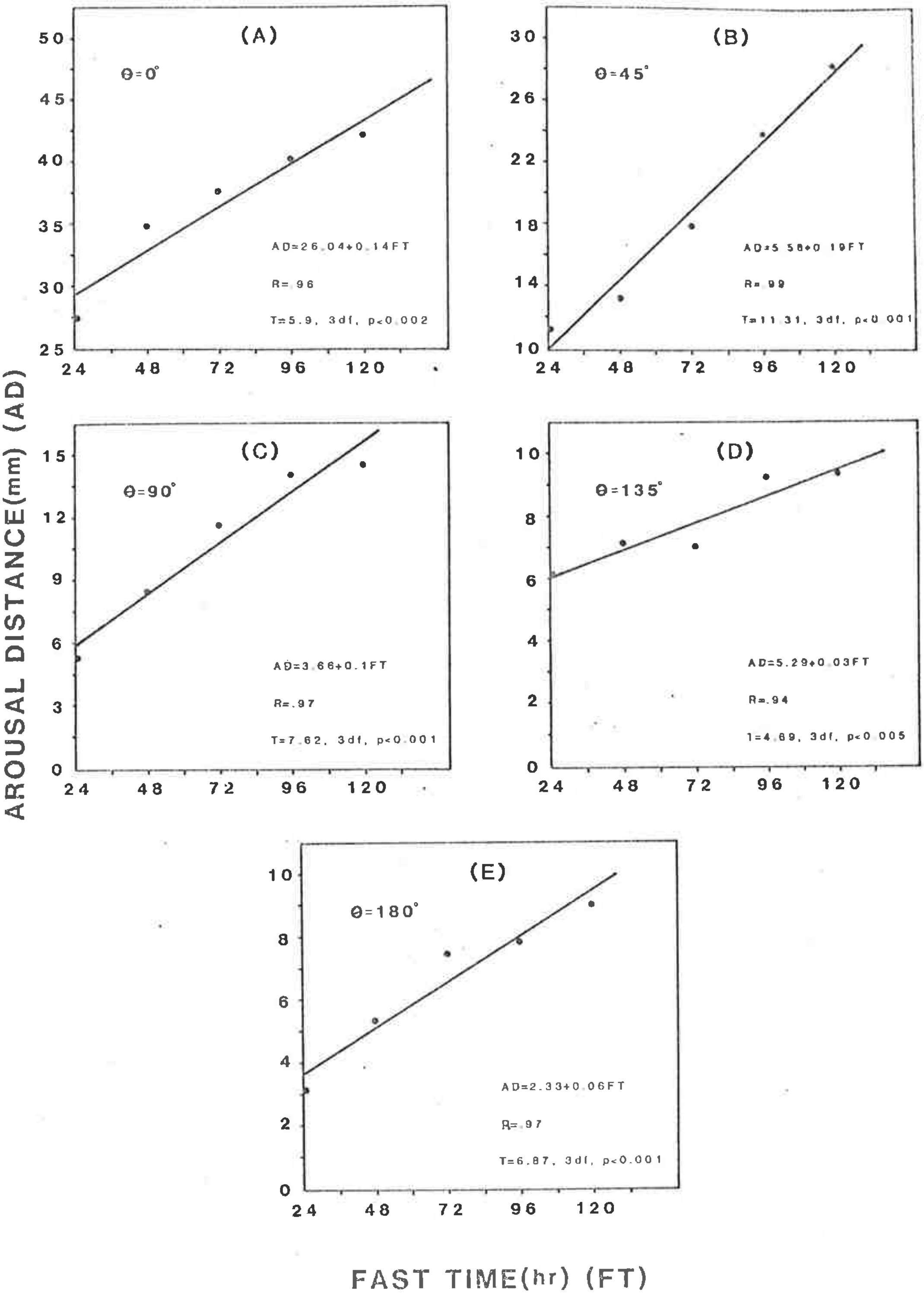
(C) Presentation path $\theta = 90^{o}$

(D) Presentation path $\theta = 135^{o}$

(E) Presentation path $\theta = 180^{o}$

Angle 0^{o} is directly in front of predator.

Angle 180^{o} is directly behind the predator.


(A)
θ=0°
AD=26.04+0.14FT
R=.96
T=5.9, 3df, p<0.002
50
45
40
35
30
25
24
48
72
96
120
(B)
θ=45°
AD=5.58+0.19FT
R=.99
T=11.31, 3df, p<0.001
30
26
22
18
14
10
24
48
72
96
120
(C)
θ=90°
AD=3.66+0.1FT
R=.97
T=7.62, 3df, p<0.001
15
12
9
6
3
0
24
48
72
96
120
(D)
θ=135°
AD=5.29+0.03FT
R=.94
T=4.69, 3df, p<0.005
10
8
6
4
2
0
24
48
72
96
120
(E)
θ=180°
AD=2.33+0.06FT
R=.97
T=6.87, 3df, p<0.001
10
8
6
4
2
0
24
48
72
96
120
AROUSAL DISTANCE(mm) (AD)
FAST TIME(hr) (FT)

As the slopes were not equal, a multiple comparison procedure was used to determine which of the slopes were different from which others. The Student Newman Kuels multiple range test (MRT) was used to test differences between each pair of β values, by H_o: $\beta_1 = \beta_2$ and H_A: $\beta_1 = \beta_2$ where 1 and 2 represent any two of the regression lines (Zar 1974). The test statistic is given by

$$q = \frac{b_1 - b_2}{SE}$$

As Σx^2 are the same for lines 1 and 2 the

$$SE = \frac{(S^2 Y.X) \text{ pooled}}{\Sigma \quad x^2}$$

Table 3:7 shows the comparison of each pair of β values with the calculated q statistic and probability level, and suggests the proposition that although a 'hunger' effect does exist in arousal distance around the Ranatra (Fig. 3:7A) this effect is not the same in front as behind the Ranatra.

TABLE 3:7 Table to show the comparison of regression slopes using the Student Newman Kuels MRT (q statistic). Regression 1, $\theta = 0^\circ$; Regression 2, $\theta = 45^\circ$; Regression 3, $\theta = 90^\circ$; Regression 4, $\theta = 135^\circ$; Regression 5, $\theta = 180^\circ$.

Regressions to be compared	b values	q Statistic	p.
1 & 2	0.1458, 0.1875	-2.085	Not Significant (NS)
1 & 3	0.1458, 0.1000	2.410	NS
1 & 4	0.1458, 0.0354	6.133	<0.05
1 & 5	0.1458, 0.0596	4.790	<0.05
2 & 3	0.1875, 0.1000	5.833	<0.05
2 & 4	0.1875, 0.0354	12.675	<0.001
2 & 5	0.1875, 0.0596	9.840	<0.001
3 & 4	0.1000, 0.0354	5.872	<0.05
3 & 5	0.1000, 0.0596	4.040	<0.05
4 & 5	0.0354, 0.0596	-3.025	NS

Both Holling (1966) and Hardman and Turnbull (1980) found a similar increase in response distance with 'hunger' for the mantis, <u>Hierodula crassa</u> and the wolf spider, <u>Pardosa vancouveri</u> respectively. In the case of the wolf spider, although the increase in reactive distance straight ahead of the spider ($\theta = 0$) was found to increase with hunger, the reactive distance directly behind the spider ($\theta = 180^\circ$) did not vary with 'hunger', remaining close to 5 mm from the spider's face. Hardman and Turnbull (1980) concluded that this suggested that the spider cannot see directly behind and reactions to prey in this position occur only when the prey touches the spider. Unlike the wolf spider, both Ranatra and the mantis (according to Holling's diagram, 1966, p.24) exhibit a similar increase in response distance with hunger behind the predator, although the responses are not as pronounced as those for the forward facing areas.

VERTICAL PLANE - Fig. 3:7B shows the shape of the arousal field in the vertical plane after 5 different periods of food deprivation. Observations on presentation path 225° proved extremely difficult to acquire without disturbing the subject; therefore these results have been discarded. The overall shape is almost circular with each field being essentially the same shape for each fasting period. (Unlike those found in the horizontal plane however, the shape of the fields are not symmetrical, in relation to the axis of the plane).

As the same two tendencies that were observed in the horizontal plane were again noticed ((1) Arousal distance increased with fasting time; (2) Distance was greatest anterior to the predator), a similar program of analysis was undertaken. The mean arousal distances were plotted against fasting time for each of the angles of presentation (Fig. 3:9 A to G). In all cases (except the 270°), slopes were significantly positive at the $\alpha = 0.05$. The t values, degrees of freedom and associated level of probability for the angles of presentation are shown in Table 3:8.

Fig. 3:9 Regressions of Arousal Distance (AD) against Fast Time (FT) for *R.dispar* when prey are presented along 7 different directional paths in relation to the longitudinal body axis of the predator in the vertical plane.

(A) Presentation path $\theta = 0^{\circ}$
(B) Presentation path $\theta = 45^{\circ}$
(C) Presentation path $\theta = 90^{\circ}$
(D) Presentation path $\theta = 135^{\circ}$
(E) Presentation path $\theta = 180^{\circ}$
(F) Presentation path $\theta = 270^{\circ}$
(G) Presentation path $\theta = 315^{\circ}$

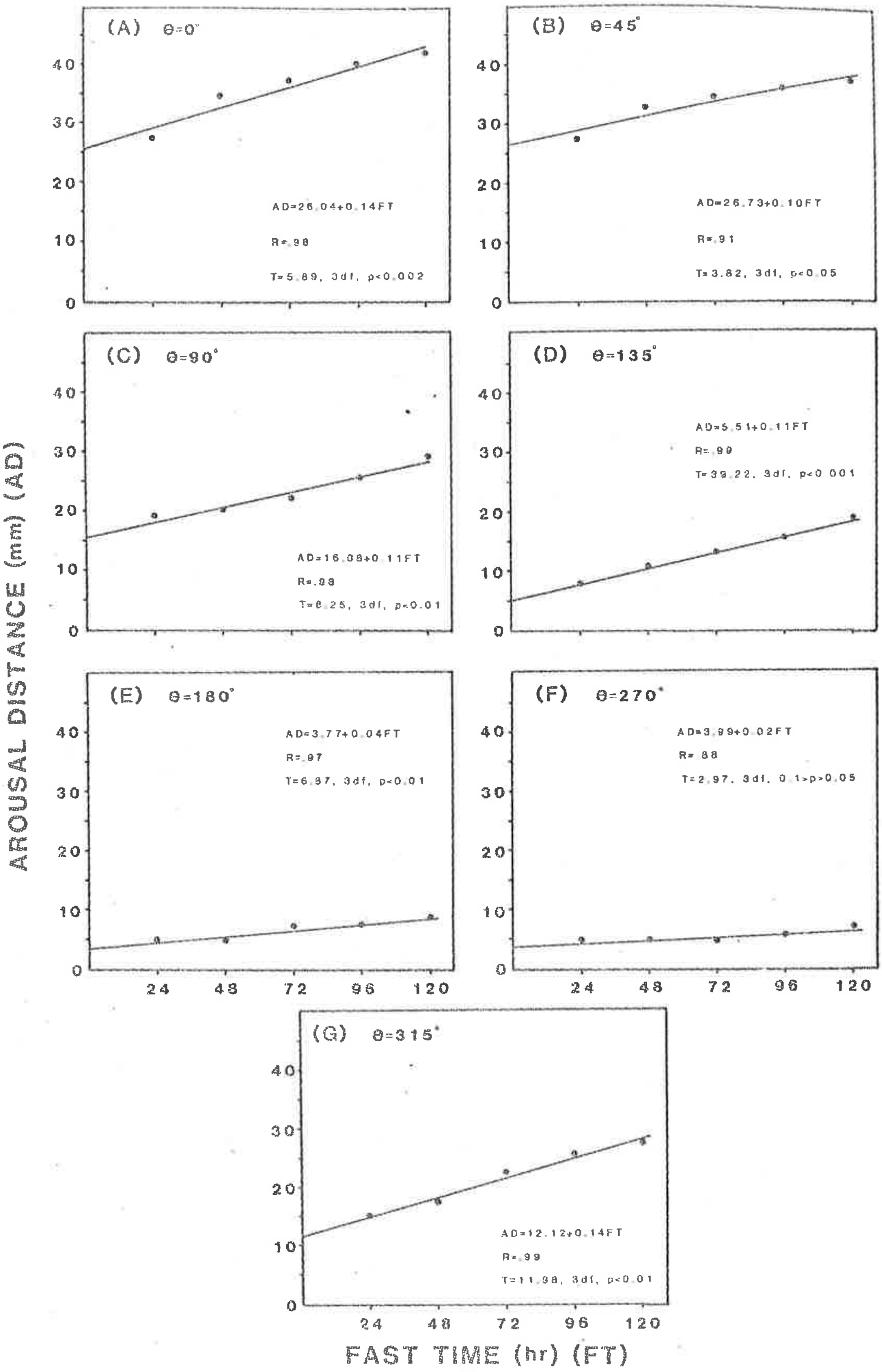

(A) θ=0°
AD=26.04+0.14FT
R=.98
T=5.89, 3df, p<0.002
(B) θ=45°
AD=26.73+0.10FT
R=.91
T=3.82, 3df, p<0.05
(C) θ=90°
AD=16.08+0.11FT
R=.89
T=6.25, 3df, p<0.01
(D) θ=135°
AD=5.51+0.11FT
R=.99
T=39.22, 3df, p<0.001
(E) θ=180°
AD=3.77+0.04FT
R=.97
T=6.87, 3df, p<0.01
(F) θ=270°
AD=3.99+0.02FT
R=.88
T=2.97, 3df, 0.1>p>0.05
(G) θ=315°
AD=12.12+0.14FT
R=.99
T=11.98, 3df, p<0.01
0
10
20
30
40
24
48
72
96
120
AROUSAL DISTANCE (mm) (AD)
FAST TIME (hr) (FT)

TABLE 3:8 Table of t-statistics, degrees of freedom, and associated level of significance for the regressions of mean arousal distance on fast time. (t-statistic test null hypothesis that the slope is not different from zero).

ANGLE OF PRESENTATION	t-value	df	Significance
0^o	5.89	3	$p < 0.01$
45	3.82	3	$p < 0.05$
90	8.25	3	$p < 0.01$
135	39.22	3	$p < 0.001$
180	6.87	3	$p < 0.01$
270	2.97	3	$0.1 > p > 0.05$
315	11.98	3	$p < 0.01$

These results support those found for the horizontal plane and likewise suggest that the arousal of Ranatra to a model prey increases as food deprivation time increases, irrespective of the angular position of the presentation.

Analysis of covariance to test the null hypothesis that the seven slopes are equal showed that a significant difference in the slopes did exist; $F = 6.13$, df. 5,19, $p<0.005$ and so the Student Newman Kuel MR Test was again used to test for differences. Table 3:9 shows the comparisons of each pair of β values with the calucated q statistic and associated probability level.

TABLE 3:9 Comparisons of each β values using the SNK Multiple Range Test. Table shows regressions compared, the calculated q statistic and level of probability (p).

Slopes to be Compared	b values	q statistic	p
1 & 2 (0^o vs. 45^o)	.1458-.1179	0.996	Not Significant (NS)
1 & 3 (0 vs. 90)	.1458-.1058	2.00	NS
1 & 4 (0 vs. 135)	.1458-.1113	2.03	NS
1 & 5 (0 vs. 180)	.1458-.0596	4.79	<0.01
1 & 6 (0 vs, 270)	.1458-.0229	6.83	<0.01
1 & 7 (0 vs. 315)	.1458-.1383	0.39	NS
2 & 3 (45 vs. 90)	.1179-.1058	0.50	NS
2 & 4 (45 vs. 135)	.1179-.1113	0.30	NS
2 & 5 (45 vs. 180)	.1179-.0596	2.53	0.1>p>0.05
2 & 6 (45 vs. 270)	.1179-.0229	4.32	<0.05
2 & 7 (45 vs. 315)	.1179-.1383	-0.89	NS
3 & 4 (90 vs. 135)	.1058-.1113	-0.61	NS
3 & 5 (90 vs. 180)	.1058-.0596	5.13	<0.05
3 & 6 (90 vs. 270)	.1058-.0229	8.29	<0.01
3 & 7 (90 vs. 315	.1058-.1383	-2.17	NS
4 & 5 (135 vs. 180)	.1113-.0596	8.62	<0.01
4 & 6 (135 vs. 270)	.1113-.0229	14.73	<0.01
4 & 7 (135 vs. 315)	.1113-.1383	-3.37	<0.05
5 & 6 (180 vs. 270)	.0596-.0229	4.59	<0.05
5 & 7 (180 vs. 315)	.0596-.1383	-7.89	<0.001
6 & 7 (270 vs. 315)	.0229-.1383	-11.54	<0.001

No significant differences were found between the slopes anterior to the predator suggesting that the effects were the same along those particular angles of presentation. However, the fact that significant differences were present between the slopes of the anterior and posterior presentation paths, and also a number of the slopes of the posterior presentation paths, indicate that the food deprivation effect was not the same in front as behind the predator.

Holling (1966) and Hardman and Turnbull (1980) formulated different functions which combined both the angular position of prey and the food deprivation time of the predator to describe the reactive field of the predator in the horizontal plane. Neither attempted such a description for the vertical plane, which to some extent is understandable for the wolf spider, in particular, is normally associated with a flat substrate on which any reaction between it and potential prey will take place. The same argument cannot be used in connection with the mantis however, for it is apparent that mantises respond to prey in the vertical plane, (this may of course be true for the wolf spider).

Before comparing the results of fitting Holling's model to the data obtained for Ranatra it is perhaps useful to reiterate his methodology briefly.

3:4.3.1 Holling's Model for Estimation of the Reactive Field of H.crassa.

Holling replotted the original polar co-ordinates of reactive distance and angular position of vestigal wing Drosophila when the mantid moved its head to fixate the fly, using Cartesian co-ordinates. The maximum distance of reaction declined in an S-shaped manner as the angle to the body axis increased. This pattern was found at 4 different hunger levels of the mantid (Fig. 3:10 Column A, Diagram 1). In order to produce linearity a double transformation was necessary. The first transformation, concerned the distance of reaction itself. This distance, Holling argued, must in part be a function of the size of the object viewed, since a larger object, he presumed, could be noticed at a greater distance than a smaller one. The important determinant of awareness is likely therefore to be the angle subtended by the object, since this angle is a measure of the number of ommatidia that are stimulated. This angle Holling termed 'the angle of vision' and defined the 'minimum angle of vision for awareness' as the angle subtending an object at the extreme boundary of the visual field (Fig. 3:10 Column A, Diagram 2). (It is considered that the term 'extreme boundary of vision' is regrettable in retrospect for we have no evidence that the object being subtended is indeed at the 'extreme boundary'. The mantid, as may other predators, may be quite capable of piercing objects at a far greater distance, but simply not 'reacting' to them in any identifiable way). If the size of the object and the maximum reactive distance are known then the minimum visual angle for awareness can be calculated from the expression :

$$\tan \alpha/2 = L/2\, r_a$$

or $\alpha = 2 \arctan (L/2\, r_a)$

where α = minimum visual angle for awareness

L = length of prey

and r_a = maximum distance of awareness.

This transformation changed the previously S-shaped curves to curves with slopes that change in one direction (Fig. 3:10 Column A, Diagram 3). Since the graphs so produced depicted angles of vision rather than distances, the relations were reversed, that is the minimum angle of vision increased as the angle to the body axis increased. This suggested to Holling that the effective size of the ommatidial angle may change in the same way from the front to the back of the eye, although no sections were taken to confirm this, and that the curvilinear form of the relationship found resulted from the architecture of the mantid eye. A second transformation, that of squaring the angle to body axis, was necessary to produce linearity. As a result the relation between α and, the angle to body axis could be expressed as :

$$\alpha = \alpha_o + m\,\theta^2 \qquad . . . (2)$$

where θ = angle to body axis

α_o = minimum angle of vision directly in front of the mantid ($\theta = 0^o$)

and m = the slope of function of field size or hunger.

Fig. 3:10 Summary of the various methods used in calculating the arousal fields of the mantid, *H.crassa*, (Column A, after Holling 1966) and *R.dispar* (Columns B to D).

Column A. Figs. 1 to 6. Summary of Hollings method to describe and model the reactive field of *H.crassa*.

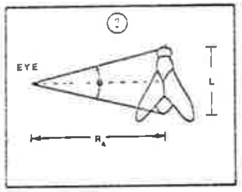
Column B. Figs. 1 to 5. The application of Holling's model in describing the arousal field of *R.dispar*.

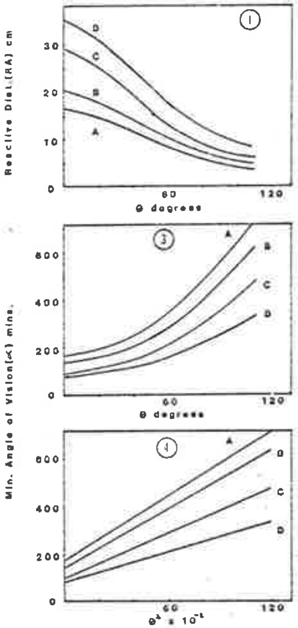
Column C. Figs. 1 to 3. The modified Hollings model (the use of θ instead of θ^2) to describe the arousal field of *R.dispar*.

Column D. The Multiple-regression method.

See text for full details.

Column A

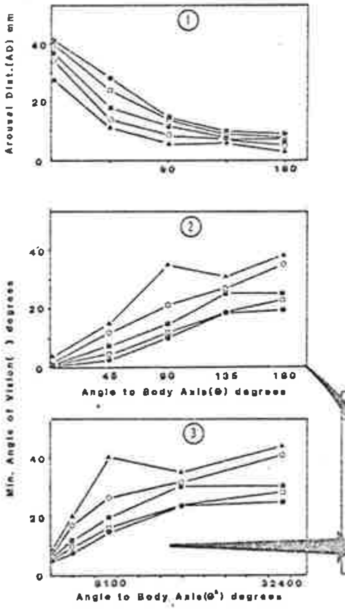




⑤

Fast Time	Intercept(∝)	Slope(m)	C (m/∝)
A	174.60	0.0446	0.000256
B	141.00	0.0415	0.000294
C	98.95	0.0323	0.000327
D	82.14	0.0219	0.000266
Av.	124.45	0.0350	0.000281

Column B



④

Fast Time	Intercept(∝)	Slope(m)	C (m/∝)
24 ▲	18.87	8.9×10^{-4}	6.9×10^{-6}
48 ○	13.22	9.1×10^{-4}	4.7×10^{-6}
72 ■	11.12	7.2×10^{-4}	6.5×10^{-5}
96 □	8.43	6.9×10^{-4}	8.2×10^{-5}
120 ●	8.10	6.1×10^{-4}	7.6×10^{-5}

Column C

Comparison of R Values for Θ & Θ²

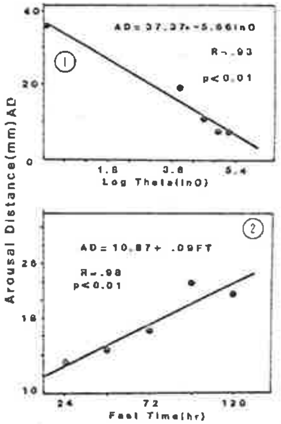
	Fast Time				
	24	48	72	96	120
Θ	.81	.98	.92	.98	.94
Θ²	.61	.86	.77	.92	.84

①

②

Fast Time	Intercept(∝)	Slope(m)	C (m/∝)
24	12.36	0.19	0.015
48	7.89	0.18	0.0231
72	6.62	0.15	0.0222
96	4.77	0.13	0.0281
120	4.61	0.12	0.0264

Column D



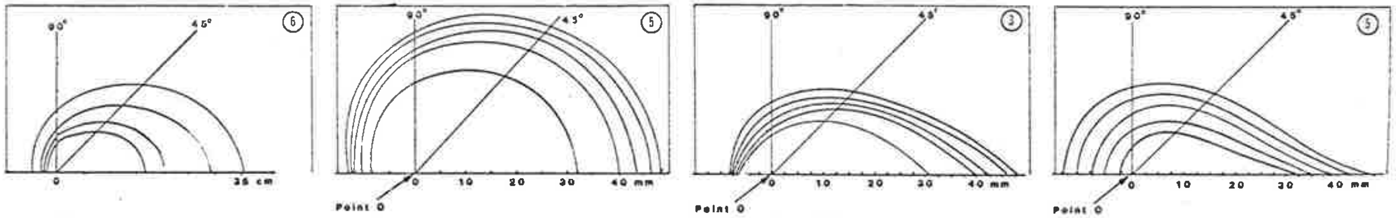
MULTIREGRESSION SUMMARY ③

Variable	B	F-ratio	Signif.	R
Natioang	-5.74	1687.26	P 0.01	.81
Fast	0.11	157.37	P 0.01	.99
Constant	29.78	1291.66	P 0.01	

④

$$AD = 29.78 + (\ln\Theta \times -5.74) + (FT \times 0.11)$$

for $24 < FT < 120$ hr



AROUSAL FIELDS

The equation was made more useful by expanding m, the slope. Since, Holling argued, the relation between θ and α is a function of the structure of the eye, and this structure is not subject to changes induced by hunger, it is likely that the minimum angle of vision at any angle θ bears a constant relation to α_o, irrespective of hunger. That is

$$\frac{\alpha_i}{\alpha_o} = K$$

where α_i = minimum angle of vision at $\theta = i$

and K = a constant.

In order to fulfil this condition, the slope m, in equation (2) must be a function of α_o such that

$$m = \alpha_o C$$

where C = a constant, independent of hunger, that describes the way effective ommatidial angles change from the front to the back of the mantid eye.

When C was calculated by dividing α_o into m, using values obtained from regression analysis of the data in Fig. 3:10 Column A, Diagram 4, the values obtained for C were reasonably constant (see Fig. 3:10 Column A, Diagram 5) and showed no consistent trend with field size. Therefore equation (2) was rewritten as

$$\alpha = \alpha_o + \alpha_o C\theta^2 \qquad \ldots (3)$$

It was now possible to describe the reactive field of the mantis. Holling used the previously derived expressing

$$\tan \alpha/2 = L/2r_a \quad \text{or} \quad r_a = \frac{L}{[2 \tan (\alpha/2)]}$$

which, taking α as small, was simplified to $r_a = L/\alpha$. . . . (4)

This equation, proposed Holling, had general application to any visual predator, since it simply involved the geometry of vision.

Equation (3), which described the specific way in which the minimum visual angle of mantids changed at various angles to the body axis, could now be substituted into (4). That is

$$r_a = \frac{L}{(\alpha_o + \alpha_o C\,\theta^2)}$$

or

$$r_a = \frac{L}{\alpha_o[1/(1 + C\,\theta^2)]}$$

From equation (4)

$$r_o = \frac{L}{\alpha_o}$$

where r_o = the maximum distance of reaction directly in front of the mantid where $\theta = 0^o$.

therefore

$$r_a = \frac{r_o}{(1 + C\theta^2)} \qquad . . . (5)$$

Equation (5) provided Holling with a description of the shape of the reactive field, independent of hunger, provided r_o and C are known. Fig. 3:10 Column A, Diagram 6) shows the response field for H.crassa based on this equation (5), using the empirically determined values for r_o and C (as shown in Fig. 3:10 Column A, Diagram 5) - after Holling 1966).

3:4.3.2 Models for the Estimation of the Arousal Field of R.dispar

In order to compare how well the Holling model fitted the data obtained for Ranatra, at least in the horizontal plane, the data was processed as outlined above. Figure 3:10 Column B shows a comparative summary of the results calculated from Holling's model.

Holling failed to provide any data on how precisely his model fitted the observed data, apart from indicating that 'the shape of each field size clearly is very well described by the lines' (Holling 1966 p.29). Using the Holling model for the R.dispar data the 'fit' appears to be good although the mean square residuals for all fast periods are quite large (Table 3:10). A better fit, in terms of smaller residuals, was achieved by using the untransformed angle to body axis term, θ, rather than θ^2. Comparison of the R^2 values in the regressions of α (minimum angle of vision) on either θ or θ^2 indicates a better linear relationship using θ, as shown in Fig. 3:10 Column C, Diagram 1.

The resultant calculated distances for each angular position of prey at each fast level of predator give significantly smaller MS residuals when compared with the observed data, as shown in Table 3:10. This improved 'fit' can also be observed in the re-plotted field shape for the predator as shown in Fig. 3:10 Column C, Diagram 2. Hardman and Turnbull (1980) constructed the shape of the reactive field of the wolf spider, Pardosa vancouveri, by following Holling's (1966) basic methodology (as outlined above) but then using a multiple regression equation which related the cosine of the angular position of the prey to the body axis of the predator and the fasting period.

The trends described by Hardman and Turnbull for P.vancouveri, in relation to the effects of food deprivation and angular position of prey, are very similar to those described for R.dispar here. This being so it seemed appropriate to examine their model in order to see if it

TABLE 3:10 Table of Calculated Arousal Distance (AD), Residual SS, and Residual MS, between the Observed and Calculated Arousal Distances at various angular positions of the prey and following 5 different periods of food deprivation for the predator. The calculated AD were arrived at from 3 different models that are described in the text.

FAST TIME	ANGLE OF PRESENTATION	HOLLINGS ORIGINAL MOD.					MODIFIED HOLLING MODEL					MULTIPLE REGRESSION				
		Calculated AD	Resid.SS	n	MS	DF	Calculated AD	Resid.SS	n	MS	DF	Calculated AD	Resid.SS	n	MS	DF
24	0°	27.5	62.5	10			27.5	62.5	10			28.2	742	10		
	45	23.8	1257	7			13.5	252.5	7			10.3	194.6	7		
	90	17.0	892	8	72.5	32	8.9	88.5	8	12.2	32	6.3	53.1	8	9.3	32
	135	11.5	211	4			6.7	11.6	4			4.0	4.0	4		
	180	7.9	42	5			5.3	0.5	5			2.3	36.4	5		
48	0	34.9	107	10			34.9	106.9	10			34.7	107.4	10		
	45	30.2	3074.8	10			17.1	384.9	10			12.8	256	10		
	90	21.5	1556.2	9	119	43	11.3	114.3	9	15.2	43	8.9	49.3	9	10.4	43
	135	14.5	460	8			8.5	52	8			6.5	44	8		
	180	10.0	179	8			6.8	24.1	8			4.9	9.7	8		
72	0	37.7	114	10			37.7	114.1	10			37.2	116.3	10		
	45	32.6	2369	10			18.5	240.5	10			15.4	299.9	10		
	90	23.2	1380	10	98	46	12.2	60.6	10	11.3	46	11.4	59	10	12.5	46
	135	15.7	706	9			9.1	78.5	9			9.1	78.5	9		
	180	10.8	144	9			7.3	50.2	9			7.4	50.4	9		
96	0	40.3	102	10			40.3	102.1	10			39.7	105.8	10		
	45	34.9	1380	10			19.7	376.9	10			18.0	552	10		
	90	24.8	1168	10	69	48	13.1	32.9	10	12.3	48	14	23	10	17.3	48
	135	16.8	594	10			9.8	34.6	10			11.7	76	10		
	180	11.6	205	10			7.8	67.9	10			10	111	10		
120	0	42.3	92	10			42.3	92.1	10			42.2	90	10		
	45	36.6	712	10			20.7	696.5	10			20.6	712.4	10		
	90	26.1	1345	10	59	48	13.7	30.5	10	17.6	48	16.6	62.4	10	25	48
	135	17.6	695	10			10.3	30.5	10			14.2	252.8	10		
	180	12.1	115	10			8.2	33	10			12.6	147.4	10		

was an improvement on the modified Holling model used for R.dispar.

Linear regressions seemed justified, on examining the data for R.dispar, between $\ln\theta$ (the natural logarithm of the angle to body axis) and the arousal distance of the predator (Fig. 3:10 Column D, Diagram 1), and Fast time with arousal distance (Fig. 3:10 Column D, Diagram 2). The multiple linear regression relating angular position of prey in relation to the predator body axis and the food deprivation time to the arousal distance of the predator is :-

$$AD = 29.78 + (\ln\theta . -5.74) + (\text{Fast Time}_{(hrs)} . 0.105)$$

$$\text{for } 24 < \text{Fast Time} < 120 \text{ hours.}$$

Full regression statistics are shown in Table 3:11. The calculated response fields for R.dispar deprived of food for 24, 48, 72, 96 and 120 hours are shown in Fig. 3:10 Column D, Diagram 5.

Examination of the MS residuals for each fast time (Table 3:10) indicates that the multiple regression model gave smaller residuals for the 24 and 48-hour fields, but larger residuals for the 72, 96 and 120 hour response fields when compared with the 'modified' Holling model. The overall mean MS for the modified model is some 10% less than the multiple regression model, and therefore indicates a better fit to the data.

TABLE 3:11 Summary of Multiple Regression Analysis of Arousal Distance of Predator (mm) on the natural logarithm of the presentation angle (^{o}) of model prey (in the horizontal plane) and food deprivation time of predator (h)

Multiple R	.94
R^2	.89
Adjusted R^2	.88
Std. Deviation	4.13

ANALYSIS OF VAR.	DF	SUM OF SQs	MEAN SQ.	F	Signif.
Regression	2	29925.3835	14962.691	874.62	$p < 0.0001$
Residual	224	3832.1319	17.108		

Coeff. of variability = 23.9%

VARIABLE	B	Std. Error of B	F-ratio	Signif.
Natloang	-5.7430	0.1410	1657.260	$p < 0.0001$
Fast	0.1051	0.0084	157.369	$p < 0.0001$
Constant	29.7782	0.8256	1291.548	$p = 0.01$

SUMMARY TABLE

VARIABLE	F-ratio	Significance	Multiple R	R^2	Simple R	Overall F	Signif.
Natloang	1657.256	$p < 0.0001$	.898	.807	-.898	874.616	$p < 0.0001$
Fast	157.369	$p < 0.0001$	.941	.886	.216		

Equation: $AD = 29.778 + (Natloang * -5.743) + (Fast * 0.105)$

for 24 hrs $<$FAST $<$ 120 hrs.

VERTICAL PLANE

Attempts to describe mathematically the vertical 'arousal' field, in the light of the Holling (θ^2) or modified Holling (θ) models were unsuccessful.

Examination of Fig. 3:11A, the change in 'arousal' distance at each angle to the body axis tested, shows a cyclic change over the 360^o examined. The sinusoidal nature of this curve suggests a cosine transformation of θ to produce linearity when regressed against 'arousal' distance (see Fig. 3:12A).

However, regressions of α (the minimum angle of vision) against $\cos\theta$, for each of the fast times examined, resulted in non-significant slopes in every case ($t<0.85$, $p>0.1$ in each case for testing observed slope is different from 0). When the 360^o field was divided into an upper 180^o and a lower 180^o section by bisecting along the $0/360^o$ axis (the predator's longitudinal body axis) (Fig. 3:7B) and separate regression analysis for $\cos\theta$ with α undertaken, significant slopes were observed for each fast period in both the upper and lower sections ($t>3.08$, $p<0.05$ in all cases). Table 3:12 shows the regression summary for both the upper and lower areas with the calculated constant, C, as described previously.

Fig. 3:11 (a) The change in Arousal Distance of *R.dispar* when model prey are presented at different angles to the body axis following 5 different food deprivation periods.

Fig. 3:11 (b) The minimum angles of vision of *R.dispar* following different food deprivation times, in relation to the angle to the body axis.

Only the 24 hr and 120 hr fast curves are shown. The remaining 3 intermediate fast periods follow the same pattern, but have been left out to avoid overcomplicating the figure.

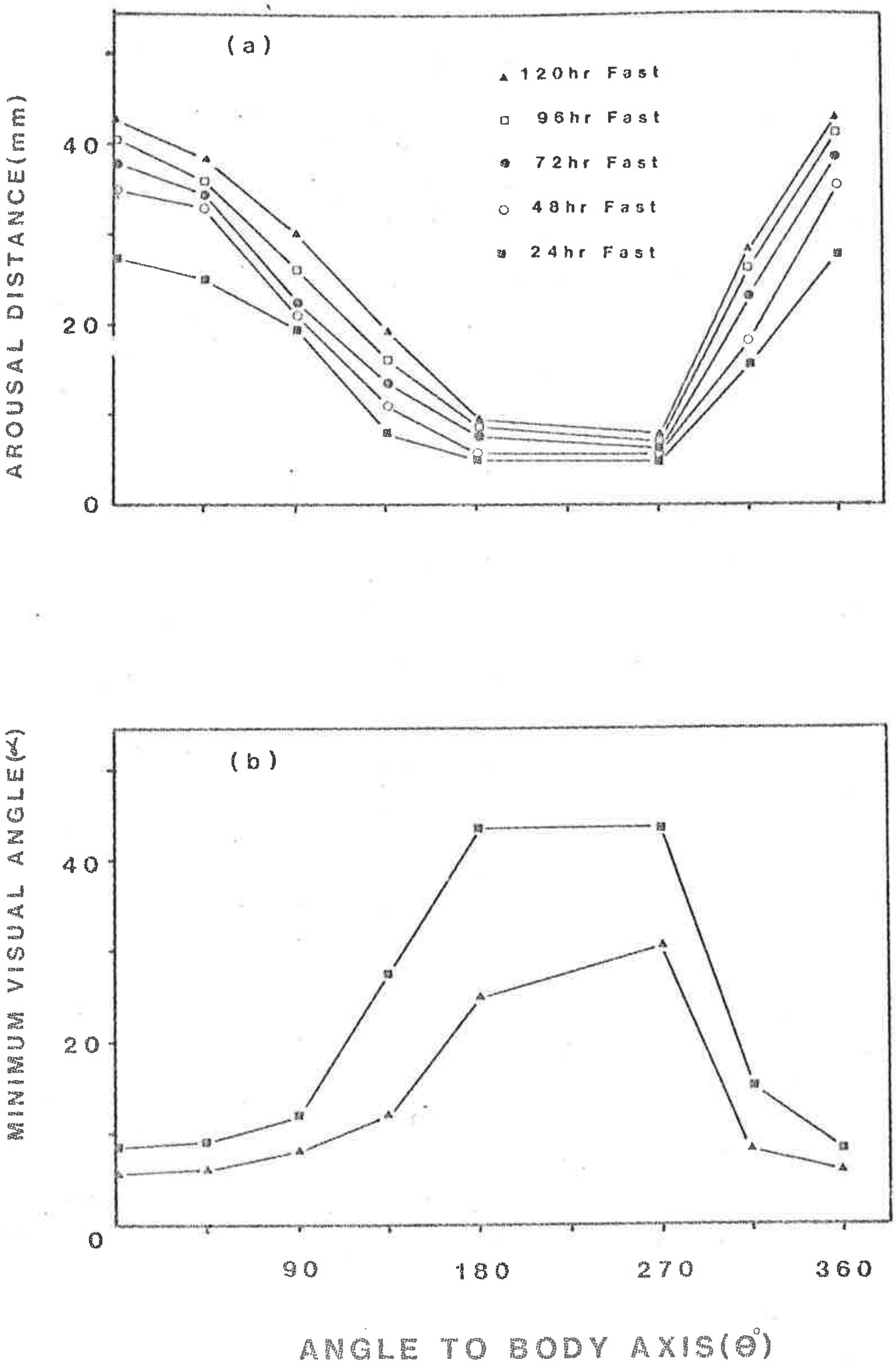
(a)
120hr Fast
96hr Fast
72hr Fast
48hr Fast
24hr Fast
AROUSAL DISTANCE(mm)
0
20
40
(b)
MINIMUM VISUAL ANGLE(α)
0
20
40
90
180
270
360
ANGLE TO BODY AXIS(θ°)

TABLE 3:12 Summary of Regression Statistics from plotting α (the minimum angle of vision) on Cosθ (where θ equals the angle to body axis on the model prey in the vertical plane). The 360° field has been divided into an Upper 180° and Lower 180° field through the predator's longitudinal body axis.

	Y-intercept (α_o)	Slope (M)	R	Constant ($C = \alpha_o/M$)
UPPER 180°				
24 h fast	24.18	-22.94	-.84	.94
48	17.15	-14.64	-.88	.85
72	13.83	-10.28	-.90	.74
96	12.71	- 9.50	-.87	.74
120	11.21	- 7.89	-.85	.70
				.79 = Average
LOWER 180°				
24	37.76	-28.77	-.98	.76
48	31.59	-18.97	-.76	.59
72	24.77	-13.72	-.69	.55
96	22.34	-12.93	-.75	.58
120	19.15	-10.87	-.78	.57
				.61 = Average

However, when the average constant values are substituted into Holling's equation for estimating the 'arousal distance' (AD), and solved, the results are both erroneous and self contradictory. It would appear therefore that the assumptions made by Holling, in formulating the equation concerning 'visual' continuity from the front to the back of the predator, when observed in the horizontal plane, do not hold true in moving from the top to the bottom as observed in the vertical plane, at least not for R.dispar. Possible reasons for this inconsistency will be discussed at the end of the chapter.

In order to describe the vertical 'arousal' field of R.dispar, with the obvious effect of food deprivation, a simple multiple regression equation was developed. This related the angular position of the prey to the predator's longitudinal body axis (θ) and the 'hunger' level of the predator (as measured by food deprivation time) to the resultant arousal distance.

As mentioned previously, the sinusoidal nature of the curve shown in Fig. 3:11, suggested a cosine transformation of θ to produce linearity when regressed with the observed arousal distance (see Fig. 3:12A). A second regression, that of fast time (hrs) with arousal distance (Fig. 3:12B) seemed to be justified (see also Hardman and Turnbull, 1980). The combined multiple regression is :-

$$AD = 13.393 + (\mathrm{Cos}\theta * 13.088) + (\mathrm{Fast\ Time}_{(hrs)} * 0.086)$$

$$\text{for } 24 < \text{FAST TIME} < 120 \text{ hrs.}$$

The full regression statistics are shown in Table 3:13 and the resultant calculated response fields for R.dispar deprived of food for 24, 48, 72, 96 and 120 hours are shown in Fig. 3:13B

Fig. 3:12 (a) Regression of the Arousal Distance (AD) of *R.dispar* against cosines of the angle of model prey presentation (θ) in the vertical plane. The cosine is 1.0 directly in front of the predator ($\theta = 0^o$), is 0 at $\theta = 90^o$ and is -1.0 directly behind the predator.

Fig. 3:12 (b) Regression of the Arousal Distance (AD) following different periods of fasting.

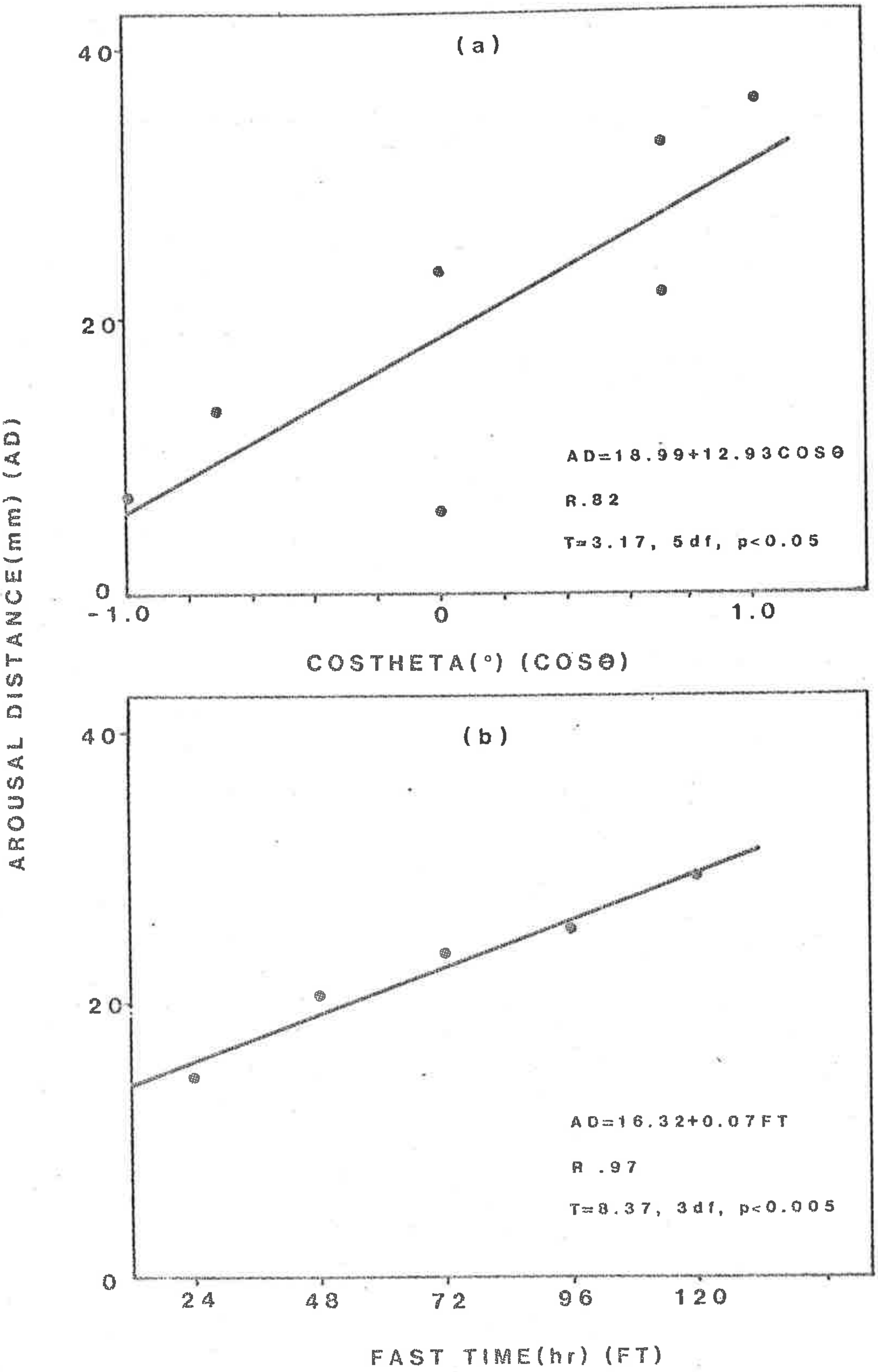

(a)
40
20
0
-1.0
0
1.0
AD=18.99+12.93COSΘ
R.82
T=3.17, 5df, p<0.05
COSTHETA(°) (COSΘ)
AROUSAL DISTANCE(mm) (AD)
(b)
40
20
0
24
48
72
96
120
AD=16.32+0.07FT
R .97
T=8.37, 3df, p<0.005
FAST TIME(hr) (FT)

TABLE 3:13 Summary of Multiple Regression Analysis of Arousal Distance (AD) of Predator on the cosine of the presentation angle (cosrang) of model prey (in the VERTICAL plane) and food deprivation time of Predator (hrs)

		ANALYSIS OF VAR.	DF	SUM OF SQs	MEAN SQ.	F	Signif.
Multiple R	.803	Regression	2	29405.043	14702.522	288.81	$p < 0.0001$
R^2	.645	Residual	317	16137.756	50.908		
Adjusted R^2	.643						
Std. Deviation	7.134	Coeff. of Variability = 33.0%					

VARIABLE	B	Std. Error of B	F-ratio	Signif.
Cosrang	13.088	.562	540.787	$p < 0.01$
Fast	0.862	.092	53.103	$p < 0.01$
Constant	13.393	.975	180.528	$p < 0.01$

SUMMARY TABLE

VARIABLE	F-ratio	Signif.	Multiple R	R^2	Simple R	Overall F	Signif.
Cosrang	540.687	$p < 0.01$	.76	.59	.76	288.807	$p < 0.0001$
Fast	53.108	$p < 0.01$	.80	.64	.20		

Equation: $Ad = 13.393 + (\text{Cosrang}.\ 13.088) + (\text{Fast}\ 0.862)$

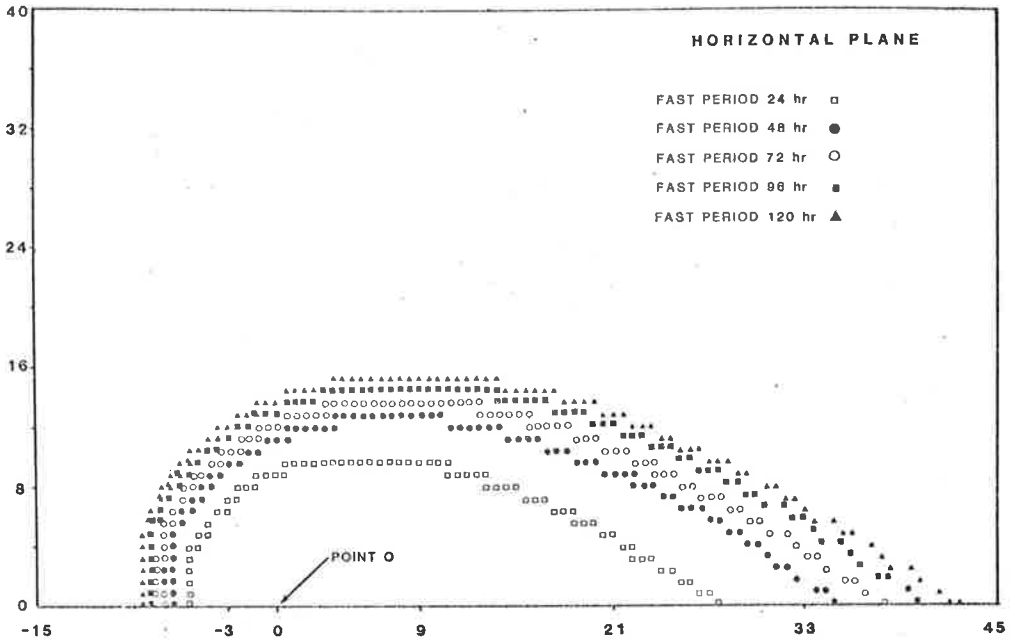
for $24 \text{ hrs} < \text{Fast} < 120 \text{ hrs}$

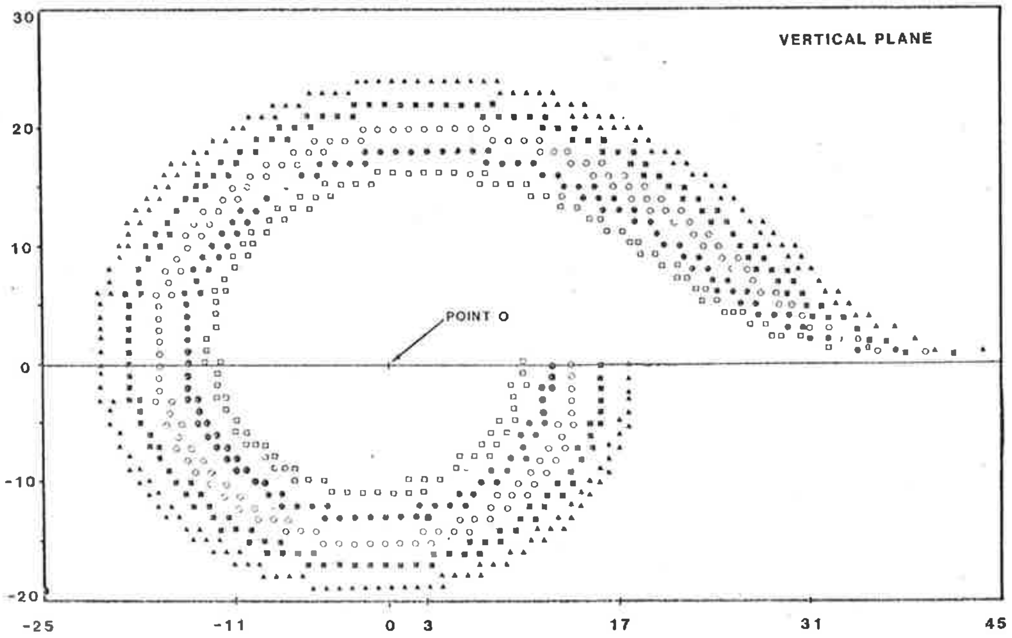
Fig. 3:13 (a) The predicted arousal field of *R.dispar* on the horizontal plane, following 5 food deprivation times as calculated using the modified (θ instead of θ^2) Holling's model.

(b) The predicted arousal field of *R.dispar* in the vertical plane following 5 food deprivation times as calculated using the multiple-regression technique.

Both axes are measured in mm.

(See text for details).


HORIZONTAL PLANE
FAST PERIOD 24 hr □
FAST PERIOD 48 hr ●
FAST PERIOD 72 hr ○
FAST PERIOD 96 hr ■
FAST PERIOD 120 hr ▲
POINT O
40
32
24
16
8
0
-15
-3
0
9
21
33
45


VERTICAL PLANE
POINT O
30
20
10
0
-10
-20
-25
-11
0
3
17
31
45

3:5 DESCRIPTION OF AND EFFECT OF PREDATOR FASTING ON THE 'CAPTURE SPACE'.

3:5.1 Methods

The experimental details outlined in Section 3:4 were repeated except as outlined below.

TEST PROCEDURE - the movement of the model prey was continued along the directional path after 'arousal movements' had been noticed until the predator attempted to capture the model, i.e. a STRIKE took place. The Strike Distance was defined as that distance from the mid point (o) between the predator's eyes to the anterior tip of the model prey when the strike took place, i.e. there was a rapid lowering of the femora on which the tibio/tarsi are closing.

A Strike was classified as :-

1. A HIT (+) - Contact was made between the femur/tibio tarsi and the model prey.
2. A MISS (-) - No contact was made.
3. CAPTURE - A successful Hit - contact was made and prey was held between the femur/tibio tarsi articulation.

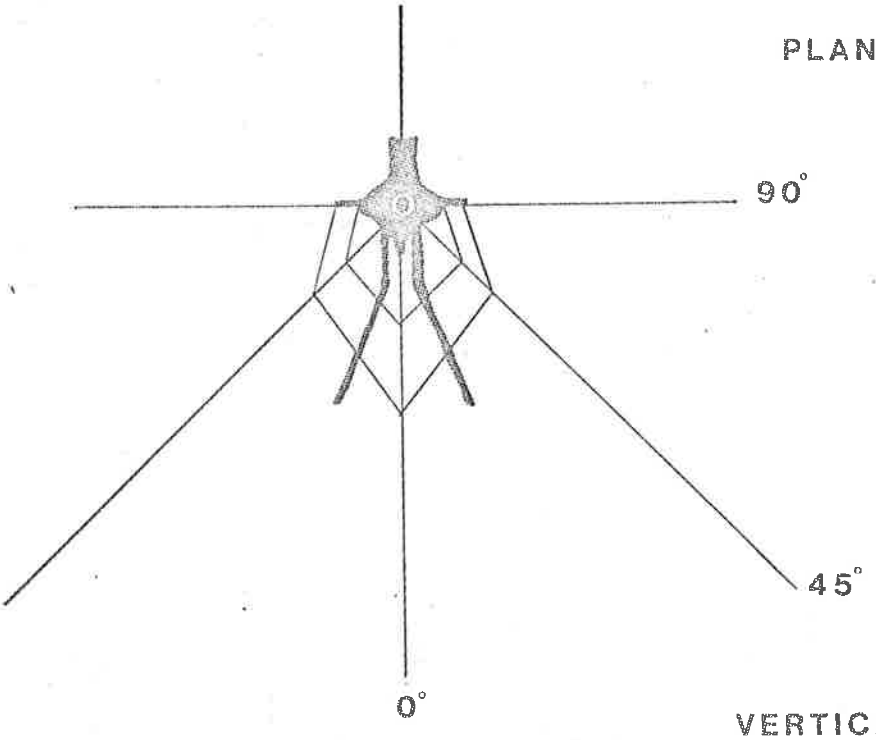
3:5.2 Results

Fig. 3:14 shows the shape of the strike field following 5 different periods of food deprivation of the predator. It is, as probably expected, restricted to the region anterior to the predator and is delineated by the $+90^{\circ}$ to -45° lines, in relation to the 0° line running through the longitudinal axis of the body, when viewing the predator in the vertical plane (see Fig. 3:14). In the horizontal plane the predator can strike (capture) only at prey 45° either side of the

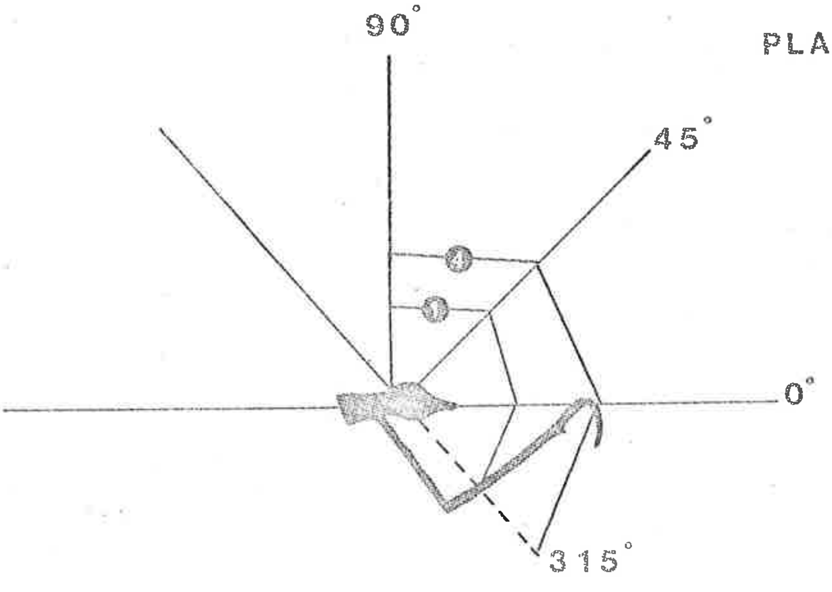
Fig. 3:14 The shape of the strike space in both the horizontal and vertical planes following 5 different food deprivation periods. For clarity only the 24 hr and 120 hr fasts have been shown (i.e. the shortest and longest).

(①) 24 hr fast

(④) 120 hr fast



HORIZONTAL PLANE



VERTICAL PLANE

body axis, although prey brought to within 5 mm along the 90° path evoke a strike which, however, is not directed at the prey. To test for a food deprivation effect a one way ANOVA, with repeated measures design, (SPSS, Statistical Package for the Social Sciences, Update 9), was performed for each of the angular paths of presentation where strikes occurred, in both the horizontal and vertical planes. In all cases except one (90°, Horizontal) significant effect of 'hunger' was observed (see Table 3:14).

The changes in the mean strike distance along the various paths of presentation are shown in Fig. 3:15 A to F. Comparison of means was carried out using the Student Newman Keuls Multiple Range Test, the results of which are also shown on Fig. 3:15.

TABLE 3:14 The effect of food deprivation on the distance at which *R.dispar* struck at a model prey when moved along a number of different angular paths of presentation in either the horizontal or vertical plane. Fast periods were 24, 48, 72, 96 and 120 hrs.

ANOVA TABLE

HORIZONTAL PLANE	SS	DF	MS	F	P
Presentation path					
0°	140.7115	4	35.1779	7.43	<0.05
45°	131.5626	4	32.8906	9.69	<0.05
90°	0	4	0	0	NS

.../(contd)

VERTICAL PLANE	SS	DF	MS	F	p
Presentation path					
0°	101.2791	4	25.3198	8.36	<0.05
45°	57.7200	4	14.4300	2.97	<0.05
90°	36.2761	4	9.0690	2.89	<0.05
315°	90.3512	4	22.5878	3.43	<0.05

For each of the different presentation paths in both vertical and horizontal planes the effect of 'hunger' was about the same, i.e. there was an increase of about 5 mm in the overall strike distance. ($\bar{x}$ = 5.6, SD = 1.2 mm in vertical plane; $\bar{x}$ = 5.5, SD = 1.4 in horizontal plane). There were some differences, depending on the angular path of presentation although they were not significant as Table 3:15 shows.

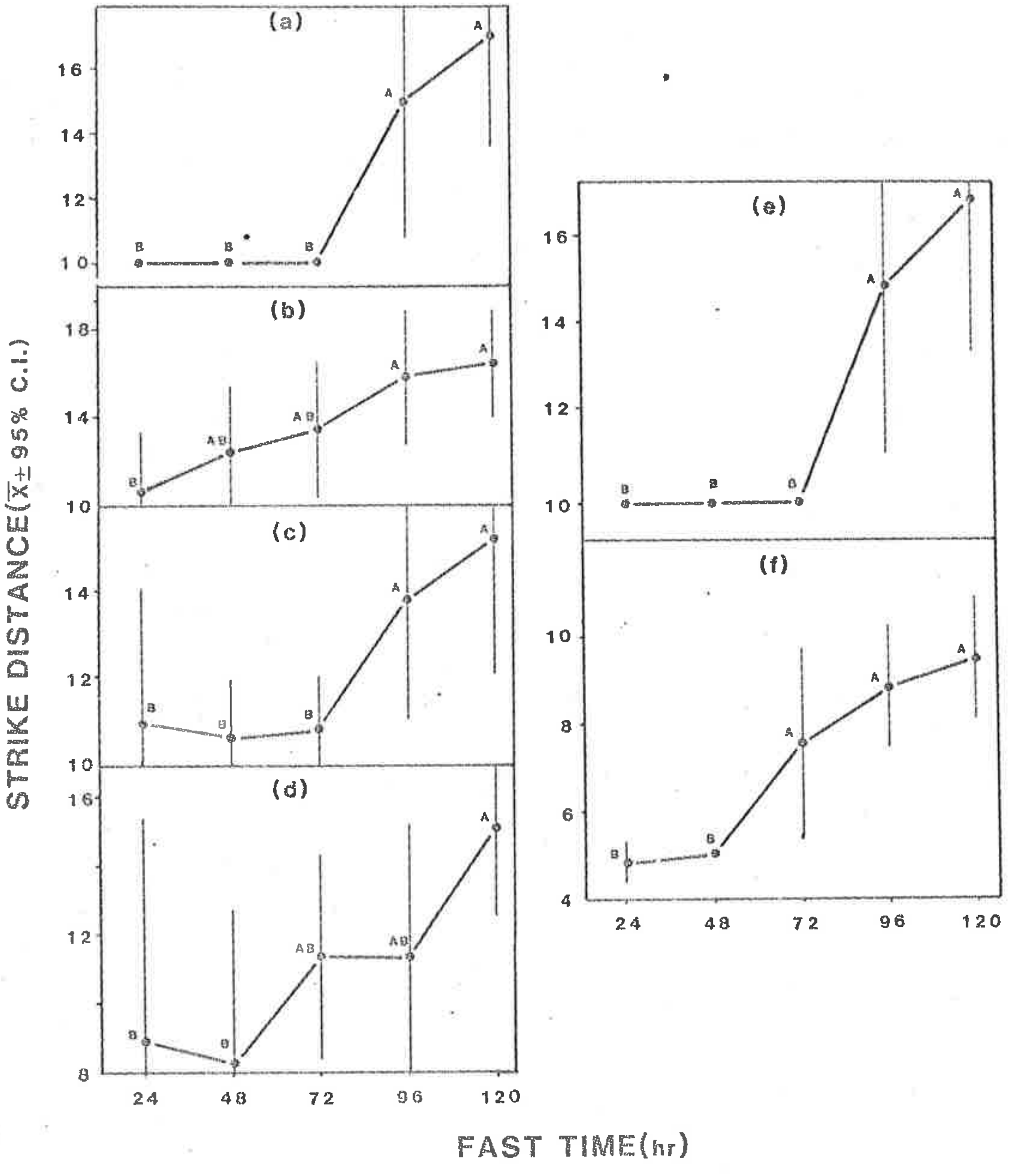
TABLE 3:15 The increase in strike distance of the predator for prey offered along various angular paths of presentation in both the vertical and horizontal planes following a 120 hour fast of the predator.

VERTICAL PLANE	ANGULAR PATH OF PRESENTATION ($^\circ$)							
	0°	45°	90°	315°	$\bar{x}$	SD	χ^2	p
Increase in Strike Dist.(mm)	+6.5	+5.9	+4.9	+6.2	5.6	1.2	.74	NS
HORIZONTAL PLANE								
Increase in Stirke Dist.(mm)	+6.5	+4.6			5.5	1.4	.35	NS

Fig. 3:15 The change in mean (± 95% Confidence Interval) strike distance along various angular paths of presentation of model prey in both the vertical (a to d) and horizontal planes (e and f) following 5 different fast periods.

(a)	0°	Vertical Plane
(b)	45°	Vertical Plane
(c)	90°	Vertical Plane
(d)	315°	Vertical Plane
(e)	0°	Horizontal Plane
(f)	45°	Horizontal Plane

Means with same letter on any one graph are NOT significantly different (SNK Multiple Range Test, $\alpha = 0.05$).


(a)
(b)
(c)
(d)
(e)
(f)
STRIKE DISTANCE($\overline{X}\pm$ 95% C.I.)
FAST TIME(hr)
24
48
72
96
120
4
6
8
10
12
14
16
18
A
B
AB

To describe the strike space _per se_ of a sit-and-wait predator is to identify only a minor, although significant, component of the predatory process. What is of paramount importance however, is the predator's strike success or capture efficiency within this dynamic space. In order to dissect this relationship two questions can be posed:

1. Are their particular regions within the strike space that, given an equal number of prey presentations, evoke a greater number of strikes or captures?
2. What is the effect of food deprivation on these regions?

In order to answer these questions the previous data were analysed in relation to the number of presentations, and subsequent strikes, hits and captures.

Because of the extreme difficulties in repeatedly identifying a point in a 3-dimensional space, the 5 angular paths of presentation were used to identify regions where strikes, hits and captures were highest. Fig. 3:16 A & B shows the differences in the proportion of either strikes, hits or captures when the prey were presented along these different angular paths in both the vertical and horizontal planes, following the 5 periods of food deprivation.

In the vertical plane (Fig. 3:16A) those prey presented along either 0° or 45° path appear to evoke the greatest response with respect

Fig. 3:16 The effect of angle of prey (to predator body axis) and food deprivation on the striking, hitting and capturing behaviour of *R.dispar*.

(A) Vertical Plane

(a) The number of strikes is expressed as a % of prey presentations.

(b) The number of hits is expressed as a % of strikes.

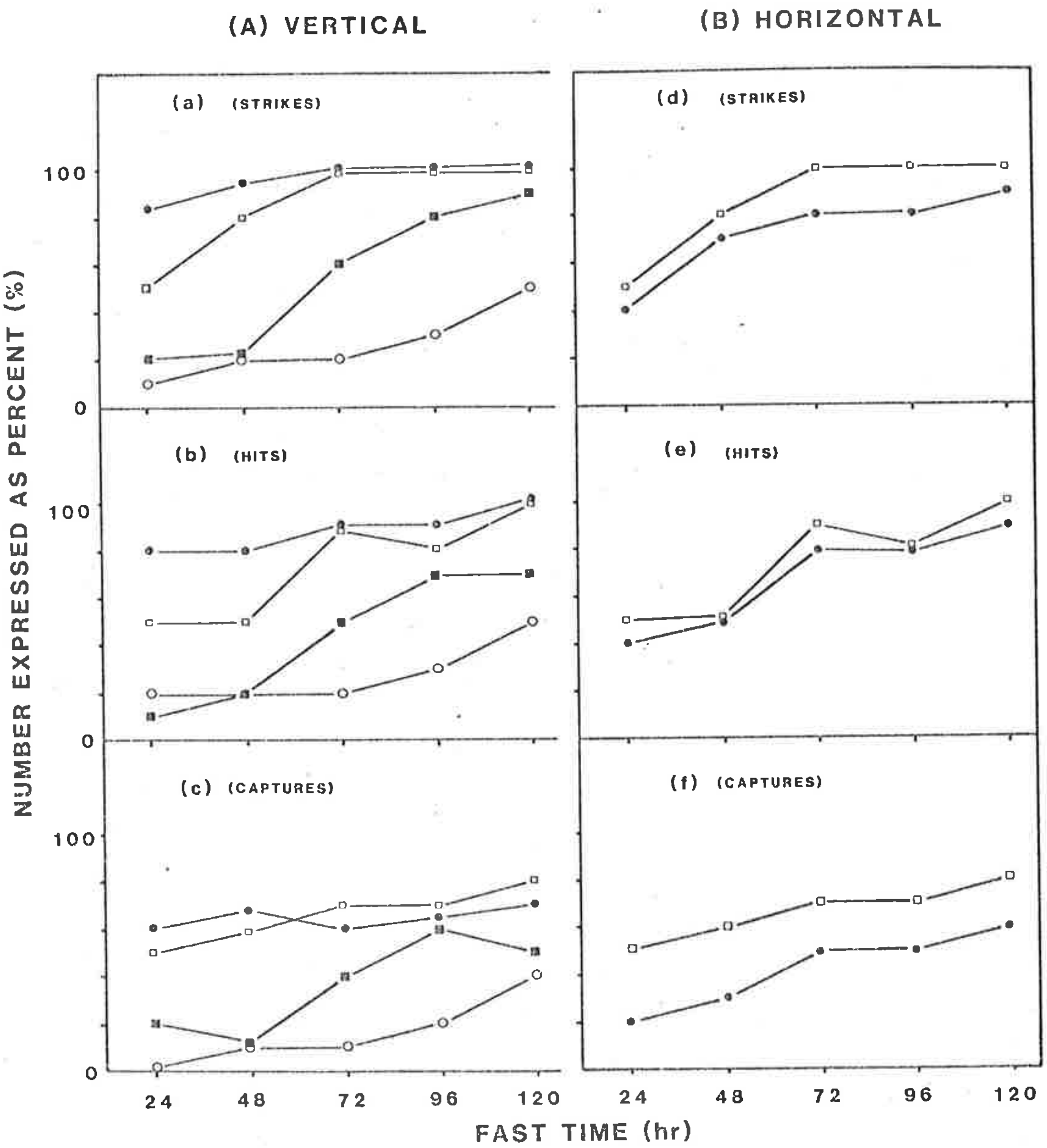
(c) The number of captures is expressed as a % of hits.

(B) Horizontal Plane

The number of (d) strikes, (e) hits and (f) captures expressed as in Vertical Plane (A) above.

Angle of Prey to Predator Body Axis.

(□)	0°
(●)	45°
(○)	90°
(■)	315°


(A) VERTICAL
(B) HORIZONTAL
(a) (STRIKES)
(b) (HITS)
(c) (CAPTURES)
(d) (STRIKES)
(e) (HITS)
(f) (CAPTURES)
NUMBER EXPRESSED AS PERCENT (%)
100
0
100
0
100
0
24
48
72
96
120
24
48
72
96
120
FAST TIME (hr)

to capture attempts. Those prey presented along the 45° path promote the largest number of strikes and hits whilst those moving directly towards the predator (0°) are captured more often. In the horizontal plane, Fig. 3:16B, prey presented along the 0° evoke the largest number of strikes, hits and captures. Prey moving in the horizontal plane greater than 45° to the predator's body axis are not captured, although at very close distances (e.g. 5 mm) they evoke occasional strikes. The results of 0° and 45° support the data from the vertical plane with respect to the number of captures. It would appear that prey moving within the 0° to 45° arc, in both the horizontal and vertical planes, evoke the greatest number of capture attempts following moderate fasting periods (e.g. 24 to 48 hours). However, following long periods of food deprivation (>72 hours) prey moving within the region up to 45° below the 0° axis (i.e. at 315°) evoke a similar level of capture responses. In fact the largest increase in the number of strikes (expressed as a percentage of presentation) as an effect of 'hunger' was from 20 to 90% for the 315° path between the fast periods 24 to 120 hours.

The same pattern is observed in the horizontal plane, with prey presented along the 0° path evoking the largest number of capture attempts. Again there is an obvious 'hunger effect' in both the 0° and 45° paths, increasing the proportion of strikes, hits and captures. Prey that are presented along the 90° path evoke a strike when they are 5 mm from the predator. There is no apparent 'hunger effect' for this presentation angle, even following the 120 hour fast; the model prey must still come to within 5 mm to evoke a strike and no capture was ever observed. As a measure of the level of success or strike efficiency for each angular path of presentation the 'capture efficiency'

$$CE = \frac{\# \text{ Captures}}{\# \text{ Strikes}} \times 100$$

was calculated for each path and fast period.

Table 3:16 shows the mean capture efficiency for each angle of presentation of prey and fast level of predator in both the vertical and horizontal plane. Analysis of variance reveals no highly significant effect of fast ('hunger') or angle of presentation.

TABLE 3:16 The x capture efficiency of *R.dispar* (# Captures/# Strikes x 100) for each angle of prey presentation and food deprivation time of predator in both the vertical and horizontal plane with the associated ANOVA Tables.

VERTICAL PLANE

ANGLE OF PRESENTATION	CAPTURE EFFICIENCY (%) FAST PERIOD 24h	48	72	96	120
0°	100	75	70	70	80
45°	71	72	60	64	70
90°	0	50	50	66	70
315°	100	50	66	75	55

ANOVA Source	SS	DF	MS	F	p
Total	8078.2000	19	425.1684		
Angle	2671.4	3	890.4667	2.0618	NS
Fast	224.2	4	56.05	0.1298	NS
Resid.	5182.6	12	431.8833		

.../(cont.)

Table 3:16(cont.)

HORIZONTAL PLANE

ANGLE OF PRESENTATION	CAPTURE EFFICIENCY (%) FAST PERIOD 24	48	72	96	120
0°	100	75	70	70	80
45°	50	43	62	62	66

ANOVA Source	SS	DF	MS	F	p
Total	2249.6	9	249.9566		
Angle	1254.4	1	1254.4	7.493	= 0.055
Fast	325.6	4	81.4	0.486	NS
Resid.	669.6	4	167.4		

The capture efficiency is not affected by food deprivation irrespective of the angle of presentation of prey. Although the ANOVA did not reveal a significant effect due to angle of presentation on the capture efficiency, in the vertical plane ($p = 0.15$) in the horizontal plane the effect was not quite significant ($p = 0.055$). With this, an examination of the mean capture efficiencies over all fast periods for each angle shows that the probability of capture is higher in some parts of the strike field than others.

Table 3:17 summarizes the mean capture efficiency for each of the angles of presentation in both vertical and horizontal plane, irrespective of fast time.

TABLE 3:17 The mean capture efficiency of *R.dispar* when the prey are presented along various angular paths to the predator in both the vertical and horizontal planes.

VERTICAL	ANGLE	$\bar{x}$ CAPTURE EFFICIENCY (%) ± Std.Dev.
	0	79 ± 12.0
	45	67 ± 8.2
	90	47 ± 28.0
	315	69 ± 20
HORIZONTAL		
	0	79 ± 12.0
	45	56 ± 10.0

Clearly then the angular position of prey relative to the predator has a profound influence on the capture probability. In addition to the angular position one would intuitively expect a 'distance' effect on the strike and capture parameters, due to the physical limitations of the raptorial legs. However, due to the design of this experiment (and the small sample sizes) no correlation analysis between the distance of the strike and subsequent capture success was undertaken at this point, although the data and experimental observations suggested a strike distance capture success relationship to exist (see Section 3:6.2).

In summary it can be seen that the overall strike/capture space of R.dispar is restricted to the space anterior to the predator and bounded by approximately the 45° axes either side of the horizontal plane and the 90° to -45° (315°) axes in the vertical. The level of food deprivation (as a measure of predator 'hunger') significantly affects the distance between the predator and prey when a strike takes place. The longer the fast period the greater the distance from which the strike takes place, up to a maximum of about 30 mm for a 120 hour fasted predator. Presentation along some paths evokes more strikes, hits and captures than presentation along others, indicating that there is an optimum region within the strike space where the capture efficiency is highest. In particular, prey moving along the 0° path in the horizontal plane or either the 0° or 45° path in the vertical plane, evoke the highest number of strikes, and hits, while the highest capture efficiency occurs when prey are moved on the 0° path. Following long periods of fasting (>72 hours) prey moved in the region below the 0° axis (Vertical Plane) along the -45° (315°) presentation path evoke a similar level of strikes as both the 0° and 45° paths.

Clearly then, for a predator like R.dispar, both the position of the prey (in relation to the predator's longitudinal body axis) and the time since the predator last fed significantly influence not only the proportion of encounters that will result in a capture attempt but the distance at which the attempt will be made. However, another important variable (as mentioned in the introduction) in examining predatory behaviour, is that of prey size. Therefore to investigate the combined influence of prey size and predator 'hunger' (as measured by food deprivation time) additional experiments were carried out, the results of which are presented in Section 3:6.

3:5.3 Disucssion

The sequence of behavioural events leading from initial arousal to prey capture and finally prey discard that were observed in *R.dispar* are similar to those of *R.linearis* (Cloarec 1969b). They follow the predatory pattern that has been previously reported, for example in mantids (Holling 1966), salticid spiders (Gardner 1964), *Chaoborus* larva (Pastorok 1980), a number of orb-weaving spiders (for example Jackson 1979; Robinson and Mirick 1971; Lubin 1973) and ant-lion larva (Wilson 1974; Griffiths 1980a).

The similarity in overall shape of the arousal field of *R.dispar* and *R.linearis* (Cloarec 1969b, 1976) tends to suggest that, as in *R.linearis*, both visual and mechanoreceptors (located on the prothoracic tibial spur) are involved in perceiving prey. In addition Cloarec (1976) reported that both these sensory structures combined to elicit a strike. The size of the strike space is believed to reflect the relationship between the length of the raptorial legs, the strike path and the overall functional morphology of the legs. The shape of the strike field for *R.linearis* was not reported and so a comparison cannot be made, although one would imagine it to be similar to *R.dispar*.

The effect of food deprivation or 'hunger' in increasing the reactive or arousal fields of predators has been reported for a variety of animals, for example mantids (Holling 1966), wolf spiders (Hardman and Turnbull 1980) and paradise fish (Mathavan, Muthukrishnan and Heleenal 1980), although no suitable mechanism of how this should happen has been proposed.

In *R.dispar*, food deprivation increases the distance of arousal along all directions of prey presentation in both the horizontal and vertical plane, although the results tend to indicate that the effect is not as pronounced for presentation paths coming from behind the predator. The strike distance also increases with fasting, but not so dramatically as that observed for the arousal distance.

Attempts to describe the shape of the arousal field and effect of 'hunger' using the model designed by Holling (1966) proved reasonably satisfactory, after slight modification, for the field viewed in the horizontal plane, but totally unsatisfactory for the vertical plane. This was probably due to the structure of the eye of *Ranatra*, with its two distinct regions (see Cloarec 1971c, 1976; Pellerano and Carlo 1977; Carlo and Pellerano 1977), and the effect this has on the assumptions of Holling's model in calculating α, the minimum angle of vision, and perhaps more significantly, C, the constant, which independ~~a~~ent of hunger, describes the way the effective ommatidial angle changes from the front to the back of the eye. It would appear that these assumptions cannot be met in moving from the top to the bottom of the eye.

Holling (1966 p.27) assumes that the structure of the eye is not subject to changes induced by food deprivation; thus it is likely that the minimum angle of vision (α) at any angle of prey presentation (θ) is constant. If this is so what causes the mantid, or any other predator, to react to prey at a greater distance when 'hungry'? It is thought by the majority of workers (for reviews see Barton Browne 1975; Bernays and Simpson 1982; Dethier 1976) that the sensitivity of the sense organ(s) themselves change with the 'motivational' state. Although the suggestion that selective attention is mediated by centrifugal control of activity in the sensory pathways is not well substantiated (see Hinde 1970 pp 120-144) the long-term changes in 'hunger' arousal could still depend on sensory structures. The evidence, however, is against such a view. In the blowfly, the time relations involved in the adaptation of the taste organs are quite different from those of hunger itself (Dethier and Bodenstein 1958). In mammals, more direct evidence is available. Meyer (1952) found that 34 hours of starvation produced no changes in the salt, sweet or bitter thresholds of human subjects. Nachman and Pfaffmañ (1963) concluded that taste preferences are governed by a central mechanism although the possibility that there is a change in the patterning of the peripheral discharge, even when the overall frequency remains constant, remains open. In addition, in the case of visual stimuli, where shape, size or pattern relevant to many different types of behaviour are received through the same sensory organs, motivational changes in responsiveness can hardly depend on the changes in the sense organs themselves. In general, therefore, the effect of motivational factors on changes in responsiveness to particular stimuli is usually described as a sensitization of particular stimulus-response relations (Hinde 1970). A food-deprived predator responds to a potential prey when a satiated one ignores it. Sensitization of stimulus-response relations implies that there is an inverse relationship between the strength of the motivational factors and the strength of the stimulus required to elicit a response of a given strength. Such relationships have been found by Baerends, Brouwer and Waterbolk (1955) and Heiligenberg (1965a, b, 1966) (see also Barton Browne 1975; Barton Browne, Moorhouse and Gerwen 1975; Dethier 1976; Dethier and Hanson 1965; Dethier, Solomon and Turner 1965; Nelson 1977). Often the motivational factor influences not just one response but a group of functionally related ones (see examples cited in Hinde 1970 pp 604-632). The results observed in R.dispar are consistent with this theme for, in addition to increasing the response and strike distance, food deprivation also affected the other components of prey capturing behaviour; it increases the proportion of arousals, attempted captures (strikes) and successful captures per unit encounters with prey (see also Chapter 7).

The ramification of the 'hunger' effect have been reported in a number of different ways and for different organisms. Beukema (1968) reported that 'hunger' caused an increase in the range of objects recognized or accepted as food, while Swynnerton (1919) discussed the relationship between palatability and hunger. When hungry, predators accepted a variety of over thirty insect species indiscriminantly, but with satiation only the most palatable. Similarly, search behaviour has been found to be affected by food deprivation (see for example, Mech 1970; Schaller 1972; Sandness and McMurtry 1972; Banks 1957; Dixon 1959).

For a sit-and-wait predator like R.dispar, where searching for prey is not important, the effect of food deprivation influences those components of predatory behaviour that will increase its likelihood of capturing a prey. Selection will act on those components that will increase overall the fitness of the organism. However, there must be a compromise or trade-off in the energetics of prey capture between, for example, the distance at which a strike is made or the number of strikes and the relative success of the outcome. Thus given a certain 'hunger' motivational level there will exist an optimum predatory response incorporating the strike distance and the number of capture attempts.

Clearly then food deprivation time ('hunger') has a significant effect on the predatory behaviour of R.dispar, in a way that will maximise the overall capture efficiency of this predator.

Cloarec (1969b) showed that both shape and size of prey affected the predatory behaviour of R.linearis. Therefore, it would appear that, as in other predators, a combination of internal (hunger) and external (prey size) stimuli are necessary for the sequential ordering of components of the prey capture behaviour. Section 3:6 sets out to investigate the interrelationships between food deprivation, prey size and predatory behaviour.

3:6 EFFECT OF PREY SIZE AND FOOD DEPRIVATION ON PREDATORY BEHAVIOUR

3:6.1 Effect of Prey Size and Food Deprivation on Prey Capturing Behaviour

3:6.1.1 Material and Method

The pre-experimental procedure was adopted as outlined in Section 3:4.1.1 for 20 adult female R.dispar. On Day 1 of the experiment 5 animals were allocated to each of four treatments (T1 - T4), each treatment being a proposed different fasting time as outlined below.

TABLE 3:18

	TREATMENT 1	T2	T3	T4
FASTING PERIOD (hrs)	0 to 6	24 to 30	48 to 54	>240

Model Prey:- A collection of model prey were made as outlined in Section 3:4 and were 2, 4, 6, 8, 15 and 20 mm in length. This range was decided on as it covered the size of the common prey that R.dispar encounter in their environment.

Procedure:- Predators were observed by closed circuit video T.V.(see Fig. 3:1). Each model prey was presented to each predator a total of ten times over the entire experimental period (normally 6 hours). The predator and order of prey presentation was chosen at random for each series of presentations and a model prey was presented only twice to any particular predator during a series. This enabled the total of 10 presentations of any model size for any predator to be staggered over the entire experimental period. Individual predators were allowed a minimum 15 minutes to acclimatize on transferring to the observation tank, normally whilst a second predator was being tested.

All prey were presented along the directional path 45° to the predator's body axis in the vertical plane. This path was chosen in order to promote the greatest number of clearly measurable behavioural responses (see Section 3:4).

The outsome of each presentation was categorized as follows :-

1. Predator 'AROUSAL' to prey i.e. An Arousal
2. Predator 'STRUCK' at prey i.e. A Strike
3. Predator made contact with prey i.e. A Hit
4. Predator grasped prey i.e. A Capture
5. The predator-prey distance when an arousal took place i.e. Arousal Distance
6. The predator-prey distance when a strike took place i.e. Strike Distance

A one-way Analysis of Variance for each of the behavioural categories at each hunger level showed no significant effect of time in relation to the duration of each experiment (about 6 hours) and therefore the results from each individual predator were treated as a continuous data set and a mean proportion or mean distance was calculated for each prey size presented.

Statistical Analysis

Statistical procedures were completed using SPSS (Statistical Package for the Social Sciences Update 9). Data analysis for the effect of hunger and prey size on each of the six behavioural categories followed the design procedure of MANOVA with repeated measures. Due to the binomial rather than normal distribution that proportions normally follow, the deviation from normality being particularly great for small or large proportions, an arcsine transformation was performed on the raw mean data.

Comparisons between means was performed using the Student Newman Keuls Multiple Range Test (Zar 1974).

3:6.1.2 Results and Discussion

The arousal of the predator to the model prey is significantly affected by the time of food deprivation but not the size of the prey model (Fig. 3:17A). Following a short period of fasting (0 to 6 hrs) the predator is aroused to about 50% ($\bar{x}$ = 41.3, SD = 7.5) of prey presentations. No significant difference in the percent arousal was found between the three other fasting regimes, the mean responses being 86%, 94.7 and 99.6 for the 24, 48 and 240 hour fasts respectively.

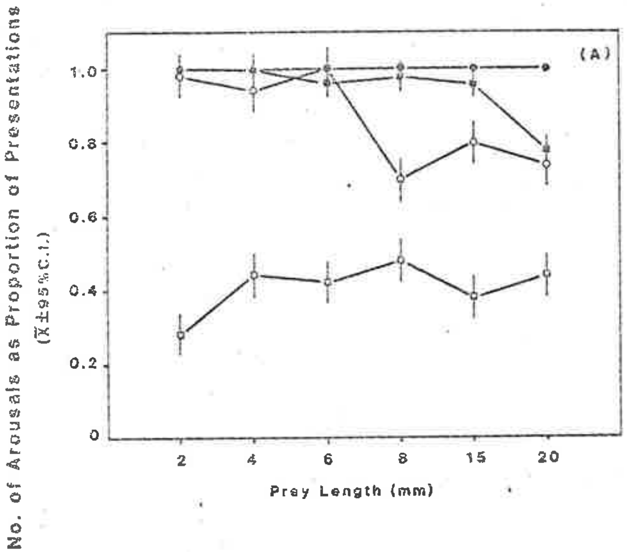
Whereas prey size had minimal effect in determining whether the predator was aroused to the model prey it had a highly significant effect in influencing the proportion of these arousals that led to the predator striking at the prey. Fig. 3:17B shows that prey size in addition to fast period both influenced this behaviour although the significance of the interaction term suggests that they do not act

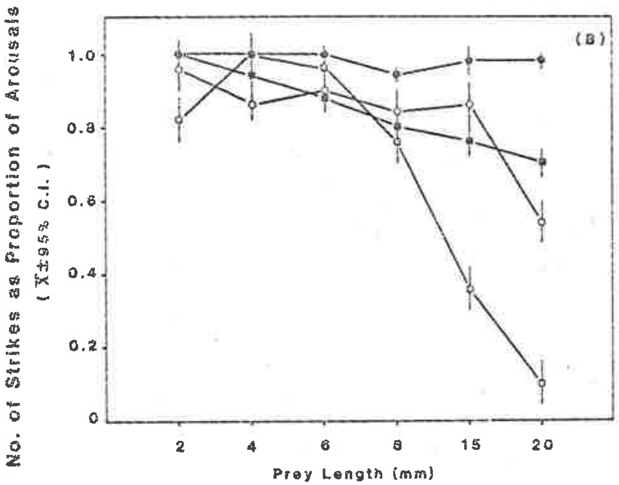
Fig. 3:17 (A) The effect of prey size on the number of arousals expressed as a proportion of presentation after 4 different food deprivation periods. Value given is the mean (± 95% Confidence Interval).

Fig. 3:17 (B) The effect of prey size on the number of strikes expressed as a proportion of arousals after 4 different food deprivation periods. Value given is the mean (± 95% Confidence Interval).

In the comparison of Means they are ranked from the lowest (Rank 1) to the highest (Rank 4 or 6). Subject means underlined by common line are not significant.

(□) 0 to 6 hr fast
(○) 24 to 30 hr fast
(■) 48 to 54 hr fast
(●) 240 to 246 hr fast





Source of Variation	Sum Squares	DF	MS	F	Sig.
Constant	187.27	1	187.27		
Error 1	3.36	16	0.20		
Hunger	16.02	3	5.34	25.46	P < 0.001
Error 2	3.77	80	0.04		
Prey size	0.53	5	0.10	2.23	P = 0.06 NS
Hung. by P.size	1.23	15	0.08	1.73	P = 0.06 NS

Comparison of Means :- SNK Multiple Range Test ($\alpha = 0.05$)

	Rank of Sample Mean					
	1	2	3	4	5	6
Fast period	1	2	3	4		
Prey size	F-ratio not significant.					

Source of Variation	SS	DF	MS	F-Ratio	Sig.
Constant	190.71	1	190.71		
Error 1	2.13	16	0.13		
Hung.	3.67	3	1.22	9.18	P=0.001
Error 2	5.24	75	0.07		
Prey size	4.37	5	0.87	12.50	P=0.0001
Hung. x Prey size	4.23	15	0.28	4.04	P<0.05

Comparison of Means :- SNK Multiple Range Test ($\alpha = 0.05$)

	Rank of Sample Means					
	1	2	3	4	5	6
Fast Period	1	2	3	4		
Prey size	20	15	8	6	4	2

independently. The trend of the larger the prey the less likely that the predator would strike at it was present over all fasting conditions, being particularly obvious in the 0 to 6 hour fast. However as the food deprivation time increased there was a corresponding increase in the proportion of strikes at the larger prey, until for the longest fast time (>240 hrs) the proportion of strikes was about the same for all prey sizes; almost 100% of arousals ($\bar{x} = 98$, SD = 2.5). As in the 'Arousal' category the x number of strikes was significantly less for the shortest fast period, over all prey sizes, whereas no such differences were observed between the other three fast periods. Across all food deprivation times there were significantly fewer strikes at the larger prey model (20 mm) than the other models.

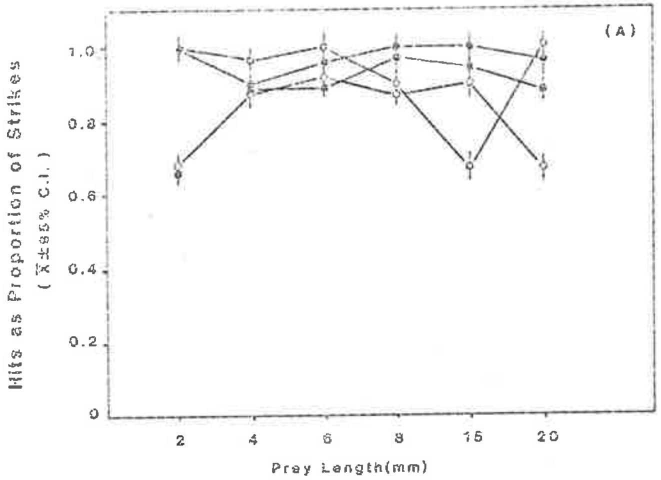
Of paramount importance to the predator in any encounter with a potential prey item, is whether contact is made with the prey and more importantly that contact leads to a successful capture. Fig. 3:18A shows that although both fast time and prey size have a significant effect, no differences between the mean proportions could be identified using the Student Newman Keuls MR Test. In all likelihood the probability of the predator making contact with the prey once a strike has been initiated is very much dependent on the characteristics of the prey itself. Factors such as swimming speed, movement patterns and evasion efficiency will all play a vital role in determining whether a hit occurs. Fig. 3:18B shows that whereas the prey size has a significant effect in the proportion of prey capture, hunger has no significant effect on the capture efficiency of this predator. The x capture efficiency for the smallest prey, over the 4 fast periods, is significantly less than the 5 remaining sizes. No such differences were

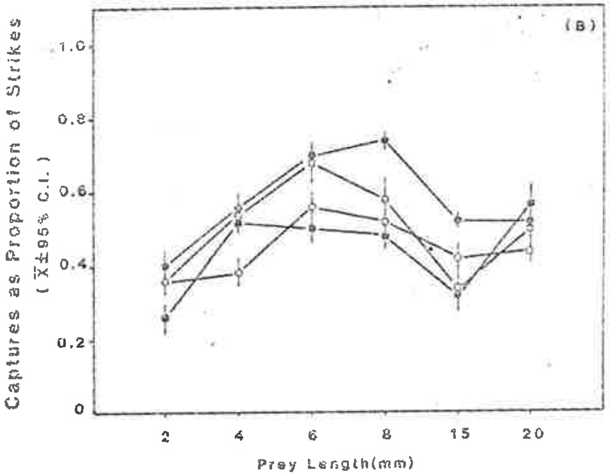
Fig. 3:18 (A) The effect of prey size on the number of hits expressed as a proportion of strikes after 4 different food deprivation periods. Value given is the mean (± 95% Confidence Interval).

Fig. 3:18 (B) The effect of prey size on the number of captures expressed as a proportion of strikes after 4 different food deprivation periods. Value given is the mean (± 95% Confidence Interval).

As Fig. 3:17

(□) 0 to 6 hr fast
(○) 24 to 30 hr fast
(■) 48 to 54 hr fast
(●) 240 to 246 hr fast





Source of Variation	SS	DF	MS	F-Ratio	Sig.
Constant	283.39	1	203.39		
Error 1	1.09	16	0.07		
Hung.	1.51	3	0.50	7.38	P < 0.005
Error 2	3.09	71	0.04		
Prey size	0.49	5	0.10	2.24	P = 0.05
Hung x Prey size	2.17	15	0.14	3.32	P = 0.005

Source of Variation	SS	DF	MS	F-Ratio	Sig.
Constant	68.38	1	68.38		
Error 1	3.24	16	0.20		
Hung.	0.30	3	0.10	0.50	P=0.62 NS
Error 2	6.04	71	0.08		
Prey size	1.53	5	0.31	3.6	P= 0.005
Hung. x Prey size	1.29	15	0.09	1.0	P=0.45

Comparison of Means :- SNK Multiple Range Test

Rank of Sample Means

	1	2	3	4	5	6
Fast Period	2	3	1	4		
Prey size	2	20	15	4	8	6

Comparison of Means :- SNK Multiple Range Test (α = 0.05)

Rank of Means

	1	2	3	4	5	6
Hung	F- ratio not significant					
Prey size	2	15	20	4	8	6

observed over these 5 means, although it is to be remembered that the proportions for the 15 mm and more particularly the 20 mm prey size are based on a very small sample and thus the variability of these numbers is high. The *Ranatra* struck at the larger prey significantly less than the other prey models (see Fig. 3:17B) although it appears that for those few strikes the proportions of captures is quite high. Fig. 3:19 shows the number of captures as a proportion of the initial number of arousals of the predator to the model. Although not a true measure of capture efficiency, it better emphasizes the trend of the effect of prey size on capture efficiency. In addition it clearly shows the greater proportion of captures of the 6 mm model prey.

As shown in Section 3:5, food deprivation time had a significant influence on the distance at which *Ranatra* was aroused to and struck at a prey. Figs. 3:20A and 3:20B show the additional effect of prey size on these distances.

There was a significant effect of both food deprivation time and prey size on the distance at which the predator was aroused to the model prey. A comparison of the fast period distance means across all prey sizes revealled that animals that had fasted longest was aroused at a significantly greater distance than the other 3 fasting periods. No difference was found between the two intermediate fasting periods (24 and 48 hrs) or the satiated/short fast and the 24 hr fasting time. Over all hunger levels the predators were aroused to the smallest prey model (2 mm) at a significantly shorter distance than the other 5 models. Although the conservative multiple range test used did not identify any significant differences in arousal distance between the remaining 5

Fig. 3:19 The effect of prey size on the number of prey captures expressed as a proportion of predator arousals after 4 different food deprivation periods.

Value given is mean ± (95% Confidence Interval).

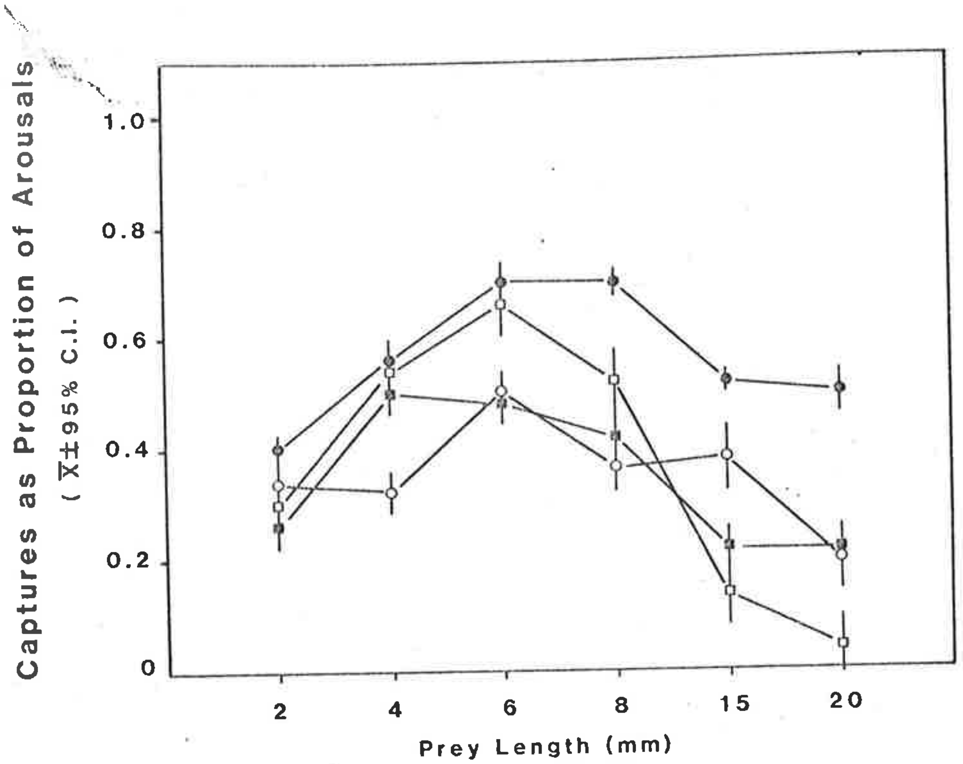
As in Fig. 3:17

(□) 0 to 6 hr fast

(○) 24 to 34 hr fast

(■) 48 to 54 hr fast

(●) 240 to 246 hr fast



SOURCE OF VARIATION	SS	DF	MS	F-RATIO	SIG.
CONSTANT	53.59	1	53.59		
ERROR 1	2.44	16	0.15		
HUNG.	1.32	3	0.44	2.89	P=.07 NS
ERROR 2	4.61	75	0.06		
PREY SIZE	1.98	5	0.39	6.43	P<0.05
HUNG BY PREY SIZE	2.18	15	0.14	2.37	P=0.008

COMPARISON OF MEANS :- SNK MULTIPLE RANGE TEST (α=0.05)

	RANK OF MEANS					
	1	2	3	4	5	6
HUNG - F - RATIO NOT SIGNIFICANT						
PREY SIZE	20	15	2	4	8	6

models, what is of particular interest is the rank order of the means. The predators were aroused to model size 6 at a greater distance than any of the others, even though it is less than a third the length of the largest model used (20 mm).

The trend of responding at a greater distance to model size 6 was repeated over the first three fast periods (0 to 6, 24 to 30 and 48 to 54 hrs). When subjected to the longest (>240 hrs) fast the response distance increased linearly with prey size.

The duration of the fast period had a significant effect on the distance at which the predator struck at the prey, i.e. an attempted capture took place. No such effect was observed for the size of model prey offered. The predators struck at prey at a significantly greater distance after the >240 hr fast and significantly shorter distance when subjected to a minimal fast (<6 hrs). There was no significant differences observed in the strike distances between the 2 intermediate fast periods (24 and 48 hr fasts).

Having identified the significant effects that both food deprivation time and prey size have on the arousal and strike distances of the predator, the next obvious question to ask concerns the possible relationships between arousal and strike distance and the subsequent capture success of the predator.

Figs. 3:20A and 3:20B show the significant correlation between the arousal distance and the strike distance. That is, those predators that were aroused to a model prey at a greater distance tended to strike

Fig. 3:20 (A) The effect of prey size on the arousal distance of *R.dispar* following 4 different food deprivation periods. Value given is mean (± 95% Confidence Interval).

Fig. 3:20 (B) The effect of prey size on the strike distance of *R.dispar* following 4 different food deprivation periods. Value given is mean (± 95% Confidence Interval).

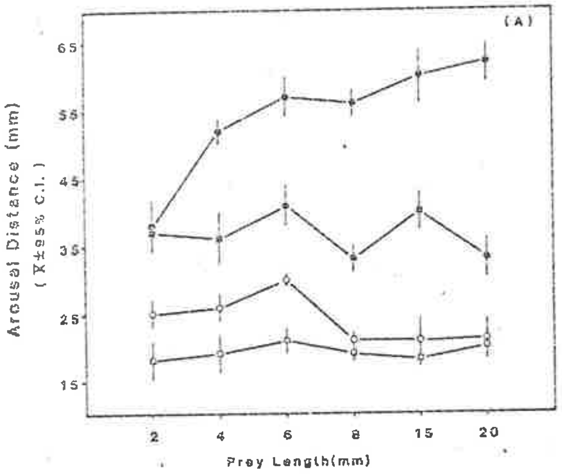
As Fig. 3:17

(□) 0 to 6 hr fast

(○) 24 to 34 hr fast

(■) 48 to 54 hr fast

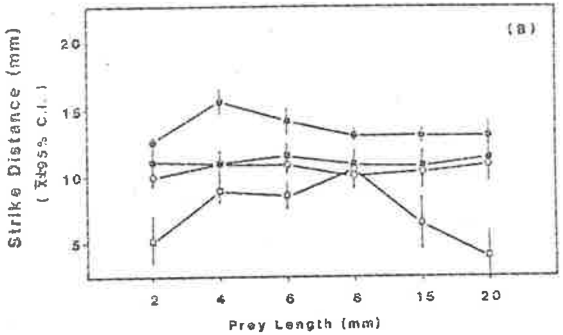
(●) 240 to 246 hr fast



Source of Variation	SS	DF	MS	F-Ratio	Sig.
Constant	129882.62	1	129882.62		
Error 1	6204.97	16	425.16		
Hung.	24081.93	3	8027.31	18.88	P=0.005
Error 2	3048.12	80	38.10		
Prey size	776.75	5	155.35	4.08	P=0.002
Hung. x Prey size	1845.00	15	123.00	3.23	P=0.004

Comparison of Means :- SNK Multiple Range Test

Rank of Means	1	2	3	4	5	6
Hung.	1	2	3	4		
X̄ value (mm)	19.8	24.3	36.8	54		
Prey size	2	8	4	15	20	6
X̄ values	27.89	32.27	32.81	33.876	34.69	35.96



Source of Variation	SS	DF	MS	F-Ratio	Sig
Constant	13459.89	1	13459.89		
Error 1	227.23	16	14.20		
Hung.	597.70	3	199.23	14.23	P=0.004
Error 2	525.15	80	6.56		
Prey size	66.79	5	13.16	2.00	P=.08 NS
Hung. x Prey size	12443	15	8.29	1.26	P=.24 NS

Comparison of Means :- SNK Multiple Range Test (= 0.05)

Rank of Means	1	2	3	4
Hung. Rank	1	2	3	4
X̄ values	7.27	10.24	11.14	13.52

Prey size F - Ratio Not Significant.

at the prey at a greater distance. Table 3:19 shows the trend remained significant even when allowing for both the fast period and prey size effects in the correlation equation.

TABLE 3:19 Correlation coefficients of Arousal distance with Strike distance allowing for the time of food deprivation and size of prey presented to the predator.

	Corr. Coeff.	Signif.
A.Dist. with S.Dist.	0.66	0.00001
Controlling for fast	0.37	0.001
Controlling for p.size	0.67	0.001
Controlling for both	0.39	0.001

In relation to this trend one should therefore pose two questions:-

1. Do those predators that are aroused to a prey at a greater distance increase the proportion of successful captures; and
2. Do those predators that strike at a prey at a greater distance increase the proportion of successful captures.

Table 3:20 shows the resultant correlation coefficient matrix of the arousal and strike distance with either the proportion of successful captures or the capture efficiency (No. of successful captures/No. of Strikes x 100) taking into account the fast period and prey size used.

TABLE 3.20

	AROUSAL DISTANCE			
	CAPTURES		CAPTURE EFF.	
	R value	Sig	R value	Sig
Simple	.54	.001	.13	.20
Controlling for fast	.28	.003	.08	.38
Controlling for prey size	.56	.001	.12	.20
Controlling for both	.30	.002	.07	.46
	STRIKE DISTANCE			
Simple	.40	.001	.11	.25
Controlling for fast	.15	.116	.06	.53
Controlling for prey size	.39	.001	.11	.25
Controlling for both	.15	.121	.06	.51

It would appear from Table 3:20 that those predators that are aroused to prey at a greater distance catch a greater proportion of the prey that are encountered. This trend is still significant even after taking into account the obviously important food deprivation effect and the size of the prey. Although this relationship appears to exist for strike distance the significance of the correlation disappears when controlling for fast time. Neither arousal distance nor strike distance appear to be correlated with overall capture efficiency as measured by number of captures/number of strikes, however the design of the experiment did not permit conclusive statements to be made because distance, like other parameters measured, was a dependant variable. To investigate the effect of distance between the predator and prey model on the prey capturing parameters, the following experiment was carried out.

3:6.2 The Effect of Distance between Prey Model and Predator on the Prey Capturing Behaviour

3:6.2.1 Methods

Twenty five adult, non-reproductive female R.dispar were fed abundant prey and then fasted for 48 hours. The prey stimulus used was model size 6 mm used in the preceding experiments. As before the model was presented by hand along either of two directional paths, 0^o or 45^o to the predator's body axis in the vertical plane. Animals were observed in large glass aquariums fitted with a vertical dowelling rod at one end, on which the predator rested. A graduated (in mm) glass rod fixed to a moveable clamp was fixed at right angles to the piece of dowelling to aid in positioning the prey. However, estimation of distance was not without error (see below).

Each trial consisted of 50 presentations of the model (2 per subject) at 5, 10, 15, 20, 25, 30, 35, 40, 45 and 50 mm distance from the predator. The shorter distances, 5 to 10 mm, proved difficult to use as the predator often responded before the prey was in position. Cloarec (1976, 1979) experienced the same problem in a similar series of experiments with R.linearis. A number of presentations were recorded by use of video T.V. as outlined in Section 3:5, to enable an estimate of error associated in the distance estimation to be calculated. Table 3:21 shows the degree of error associated with the estimated distance and the subsequent range of distances that may have been used.

TABLE 3:21 Estimation of Error in Distance Estimation.

ESTIMATED DIST.(mm)	ACTUAL DIST.(mm)	ERROR (%)	POSSIBLE RANGE (mm)
5	4.0	20	4 to 6
10	8.5	15	8.5 to 11.5
15	12.5	17	12.5 to 17.5
20	23.2	16	16.8 to 23.2
25	27.5	10	22.5 to 27.5
30	32.0	7	28.0 to 32.0
35	36.2	5	33.8 to 36.2
40	42.0	7.5	38 to 42
45	43.1	5	43 to 47
50	52.6	5	47 to 53

At each presentation the following behaviours were scored if they occurred:

1. Predator aroused to prey model	i.e. AROUSAL
2. Predator struck at the prey model	i.e. STRIKE
3. The predator's strike hit the prey model	i.e. HIT
4. The strike resulted in a capture	i.e. CAPTURE

(See Section 3:6 for definition if required).

3:6.2.2 Results and Discussion

Fig. 3:21 a and b shows the reactivity of the predator as measured by arousal (response) movements, strikes and associated hits, elicited by a given number of presentations of a model prey at a different distance from the predator along two different directional paths. A similar trend is observed in both, although the overall level of reactivity of the predator is grerater when prey are presented along the directional path, 45° to the predator's body axis. The figures show the probability, expressed as a percentage, of a predator responding to, striking at, and hitting a prey at various distances. The nearer the prey comes the more likely the predator is to respond to it, strike and hit it, although the probability of striking and hitting starts to decrease when the prey comes closer than about 10 mm. The greatest number of strikes is found to occur at 20 mm in both the 45° and 0° presentation paths, although little difference is observed in the number of strikes occurring between 15 and 25 mm from the predator in the 45° presentation path.

STRIKE EFFICIENCY:- Strike efficiency (# Captures/# Strikes x 100) is expressed in terms of captures and strikes for 50 presentations of the model prey at each distance from the predator. The strike efficiency is shown in Fig. 3:21 for both the 0° and 45° presentation paths, and is the probability that a strike elicited by the model prey presented at that distance will be successful.

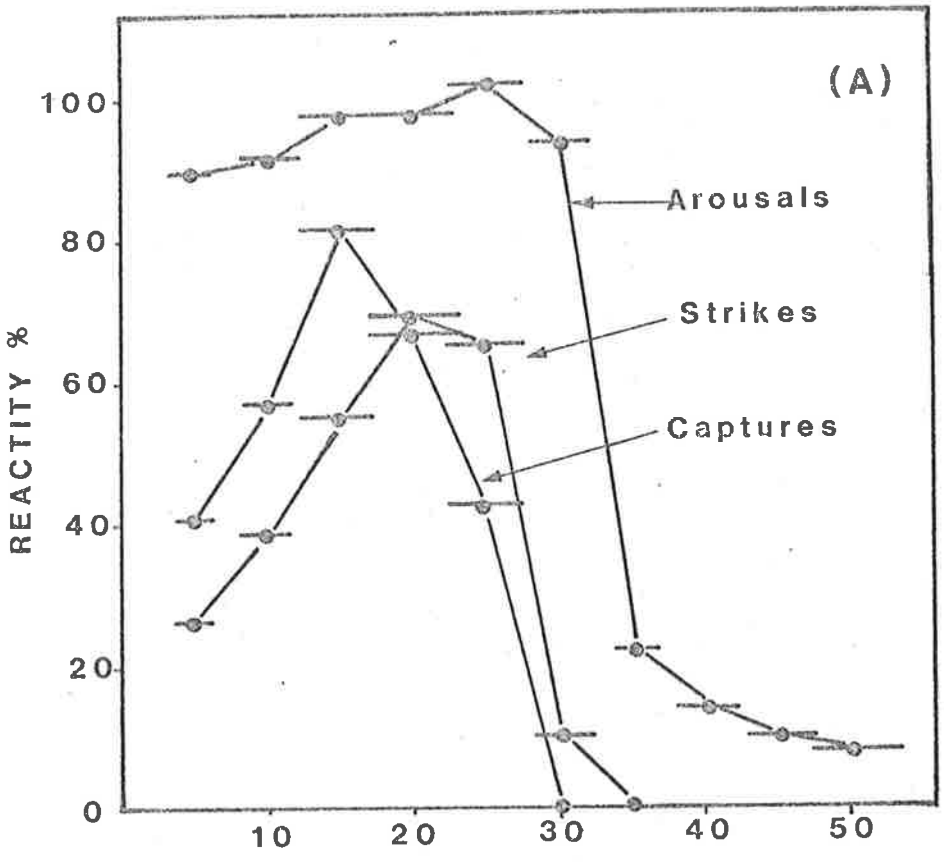
As Fig. 3:21 shows the probability of capture is low at first (where closer to predator), increases to a maximum at 15 mm from the

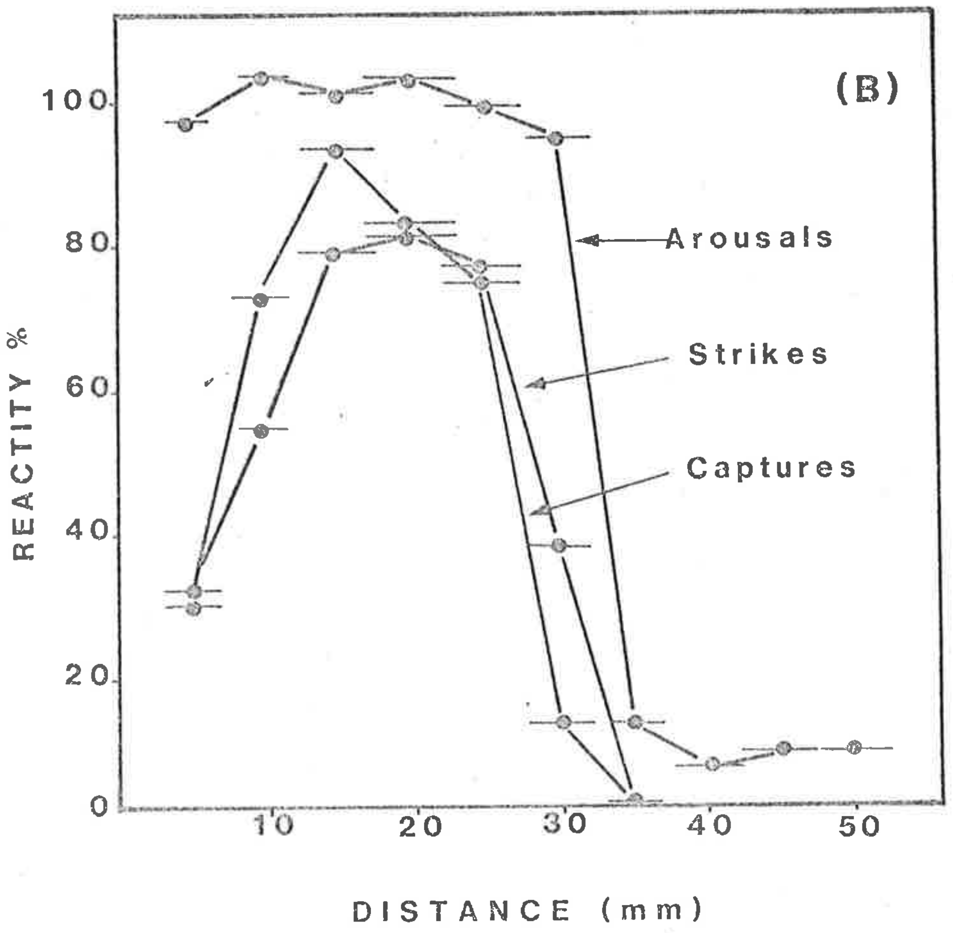
Fig. 3:21 The effect of distance of prey on the % reactivity of *R.dispar*. Reactivity was measured by the number of arousals, strikes and captures elicited by a given number of presentations of model prey at different distances from the predator along the different directional paths

(A) 0^o, (B) 45^o,

to the predator body axis in the vertical plane. The horizontal bars indicate associated error in distance estimation.

See text for additional details.


(A)
REACTITY %
100
80
60
40
20
0
10
20
30
40
50
Arousals
Strikes
Captures


(B)
REACTITY %
100
80
60
40
20
0
10
20
30
40
50
Arousals
Strikes
Captures
DISTANCE (mm)

predator and then decreases abruptly at 25 mm. Although still able to successfully capture prey at a distance of 5 mm the lower probability is believed to reflect the morphology and related mechanism of the grasping action rather than visual acuity. R.dispar is particularly efficient in capturing prey of the 6 mm size class at distances between 10 and 20 mm when presented along the 0° path (i.e. coming head on), and between 10 and 25 mm for prey approaching along the 45° path above the longitudinal body axis.

MAXIMUM MOTIVATION DISTANCE AND MAXIMUM EFFICIENCY DISTANCE:-

An additional way of expressing strike efficiency is to examine the distribution of strikes and captures in relation to distance. The term 'maximum motivation distance' was first used by Maldonado, Levin and Barros-Pita (1967) and later by Cloarec (1979), and was defined as the distance at which prey items elicits the most strikes. It is an unfortunate term because there is no way of knowing (from the term itself) whether 'maximum' refers to motivation or distance. A better term would be perhaps 'the distance of maximum motivation'. Examination of the 'strike' curves in Fig. 3:21 shows that the maximum number of strikes occurred at 20 mm distance. Therefore, 20 mm is the distance of maximum motivation of adult R.dispar. Similarly, the 'maximum efficiency distance' or as argued above perhaps better stated as 'the distance of maximum efficiency', is the distance at which most captures occur. The curves labelled 'captures' in Fig. 3:21 show that the maximum number of captures occurs at 15 mm, therefore the distance of maximum efficiency of adult R.dispar is 15 mm.

3:7 DISCUSSION

The previous Section (3:5) showed the significant effect that food deprivation had on :-

1. increasing the distance that both R.dispar was aroused to and struck at a model prey; and
2. increasing the number of initial arousals, strikes and, as a result, the number of captures.

Section 3:6 set out to demonstrate the added effect of prey size on predator behaviour in order to see if, as in other predators (see for example Connell 1961; Farmer and Beamish 1973; and numerous references in Curio 1976), prey size is a significant capture eliciting stimulus in R.dispar, and if so what components of the prey capturing sequence are affected. In addition, the data collected permit the overall effect of 'hunger' on the subsequent size of prey captured when given a range of different prey sizes, to be examined and discussed. For R.dispar it appears that the initial 'arousal' or 'preparation' for prey capture is significantly affected by an internal of 'hunger' state. Prey size, apparently, has no effect on the proportion of animals that are aroused. However, for those predators that are aroused, both 'hunger' and prey size significantly affect the distance of arousal, the significant F-ratio of interaction implying that they do not act independently. In all likelihood this reflects the visual capacity of R.dispar and the fact that larger objects can be seen at a greater distance (but see also Maiorana 1981). Of course the possibility of a combination effect between visual and mechanoreceptors cannot be ruled out, although Cloarec (1976) did show that mechanoreception was restricted to areas close to the predator, especially below the front legs. As the prey moves closer to the predator both 'hunger' and prey size determine whether or not a strike will take place. This is brought about, it is proposed, by the prey organism moving into both the visual binocular (and mechanoreceptor?) field where, depending on the number, position and frequency of ommatidia and mechano-sensilla stimulated and their relative intensities, a size/distance estimation can be made (see Frantsevich and Pichka 1975). Whether the strike takes place or not depends on the observed size of prey and the internal 'hunger' state. Clearly a relatively complex decision making process takes place incorporating, not only the obviously important prey size component, but also the influence of the 'hunger' motivational level and the associated prey size/risk factor (see also Cerri and Fraser 1983; and Griffiths 1980b). The outcome of the strike, i.e. whether or not it is a success, is dependent on prey size and not on the internal state of the predator. This is thought to reflect the relationship between size (and shape) of the prey and the predator's leg morphology. However, prey size has no effect on the strike distance, this being determined by the internal or motivational state of the predator. On reflection this seems reasonable for, as mentioned previously, R.dispar has a restricted capture field, determined overall by leg length and no pursuit or lunge component (see Copeland and Carlson 1979) in their predatory repertoire.

Holling (1966) reported the absence of a hunger threshhold of the 'awareness' response in the mantid, and interpreted it (op. cit. p.23) to be adaptive, "for while it is only necessary that hungry predators be aware of prey, it is extremely important that both hungry and satiated predators be aware of potentially dangerous objects". In my work with R.dispar it was possible to differentiate between predatory arousal and 'awareness' or evasion behaviour as reported in Section 3:3. The lack of an 'awareness' response occurring in the model prey experiments is probably due to the range and maximum size of model used. The range was chosen to cover the size of prey items that R.dispar had been seen to catch in natural (and laboratory) situations. As mentioned in Chapter 2 of this thesis, adult R.dispar catch and consume prey ranging in size from small water fleas (Daphnia spp.$\bar{x}$ 2.0 mm in length) (see also Blois and Cloarec 1983) to tadpoles (Limnodynastes tasmaniensis, $\bar{x}$ 25 mm in length) although, obviously movement and speed, amongst other things, will have a pronounced influence on capture success.

Holling (1964) predicted the optimum prey size for the mantis, H.crassa, from analysing the geometry of the mantid limb and relating this with the size of prey that it can grasp. By offering model prey of various sizes and recording the percentage of strikes provoked, Holling apparently confirmed, quite impressively, his predictions. Recently, however, Loxton and Nicholls (1979) have critized Holling's model on the basis of Holling's suggested mechanism of the functional morphology of the limb. Loxton and Nicholls (op. cit.) proposed a new mechanism and argued that Holling's original equation gives a predicted prey size which is largely determined by the length of the tibia. However, this does not necessarily negate the idea of leg morphology being highly correlated with an 'optimum' prey size that can be caught. In addition Loxton and Nichols (op. cit.) provided a number of examples of different species of mantises whose leg morphology, they suggested, were related to the type and size of prey they would probably catch. In addition, Gittleman (1977) discussed the leg segment proportions of some aquatic bugs in terms of their adaptive advantages in capturing prey of different sizes, and suggests, in analysing the relationship between prey size and ease of capture, that the mechanism lay in the mechanics of grasping (Gittleman 1978).

Clearly, as shown in Fig. 3:21, the greater the strike distance the less likely the prey will be captured (probability of capture will eventually be zero). As discussed earlier the strike distance is clearly affected by food deprivation (and the associated motivational state (Hinde 1970)), and therefore the greater the internal or hunger level the more likely the predator is to strike when the prey is further away, thus increasing the possibility that a capture will occur (although the probability of capture is reduced) when the prey is at that position rather than 'wait', the prey possibly moving away from the predator and therefore be completely out of range.

Some similar ramifications of the 'hunger' effect in predatory behaviour have already been discussed in Section 3:5. Additional related examples that are more pertinent to this section include Kniprath's (1969) study of Kingfishers (Alcedo atthis). He found that when starved, these diving birds attacked fish that were longer and swam at a greater depth than they normally would. Beukema (1968) found that 'hungry' sticklebacks (Gasterosteus aculeatus) snapped at, grasped and ate a greater proportion of encountered prey, and that they swam more actively than satiated fish and therefore had more prey encounters. 'Hunger' has also been shown to increase the intensity of pecking in young chicks (Hogan 1971), and a mantis will actively pursue flies only when they have been starved for longer than is necessary to exhibit any other component of predatory behaviour (Holling 1966). This is what, in functional terms, would be expected from an ambush predator compared with one that actively searches for prey.

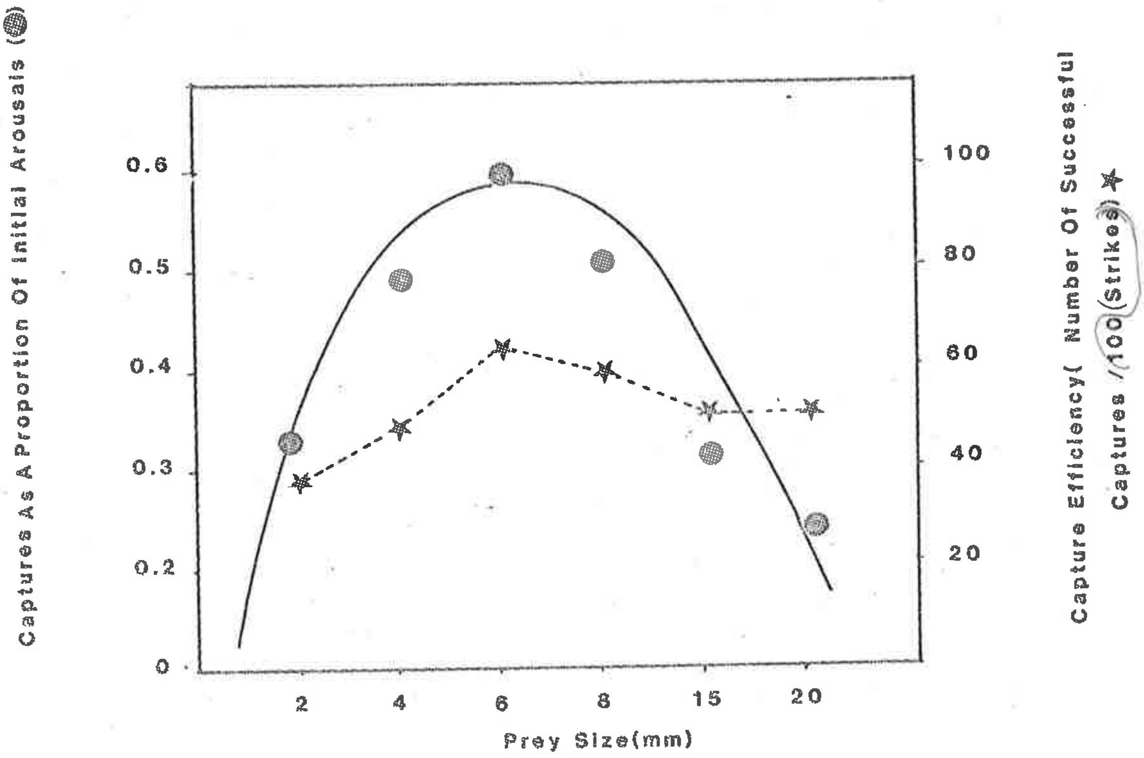
The data set collected in these experiments allows some tentative comments to be made on the effect of hunger on the resultant relationship with prey size as measured by a number of predatory behaviours. From this it was hoped to identify either a particular size or range of prey sizes that, as a result of particular 'selective' behaviours, would be caught in the natural setting.

Food deprivation clearly extends the size range of model prey that R.dispar respond to (Fig. 3:17A) and will strike at (Fig. 3:17B). Irrespective of hunger the highest proportions of 'arousals' that led to a strike were directed at the smallest prey size, and linearly decreased towards the largest. Although not significantly different the trends identified in Figs. 3:18A and 3:18B are, it is thought, important. Firstly, when one examines the number of resultant hits as a percentage of strikes the smallest (2 mm) model, although initiating the highest number of strikes, records the lowest number of hits. This is followed by the two largest models, that evoked few strikes so the values presented are associated with large variance (see Fig. 3:18A). What is of particular interest however, is the final rank ordering of the prey size means for capture. Significantly less Prey Size 2 were caught compared with the other prey sizes. In addition, although the conservative multiple range test did not identify individual differences, the ordering of prey size models is considered important with more Prey Size 6 being successfully caught than any of the others, this being followed by Prey Size 8 then Prey Size 4. Again, the smallest model used, Prey Size 2, was caught significantly less than the other models.

As the food deprivation level of R.dispar increases, so the upper size limits of model prey increase. Drees (1952) found a similar result for the jumping spider, Epiblemum (Salticidae), when black, round, flat dummies of increasing size elicit capture movements with increasing food deprivation, until finally the model size extended into a range which, in normal spiders, releases flight responses (see also Hoppenheit 1964 quoted in Curio 1976 for a comparable study on Aeschna cyanea (Odonata) larvae). Irrespective of 'hunger' level, about the same number of strikes were directed at the four smallest prey sizes (PS2, PS4, PS6, PS8), while as food deprivation increased so the predators struck at progressively larger prey. More successful hits and, more importantly from a predation perspective, captures were associated with prey sizes 6, 8, 4, 15, 20, 2 decreasing in that order. It is suggested that the four smallest prey sizes (2 to 8) evoke about the same number of attempted captures from R.dispar but due to the interrelationships between structure of grasping leg of predator, prey size and closeness of the prey, the observed capture success was PS6, PS8, PS4 and PS2 in that descending order.

This chapter has demonstrated the significant effect of both 'hunger' and prey size on the subsequent components of predatory behaviour of a sit-and-wait predator, Ranatra dispar. In addition, from the results obtained on capture success and model prey size, once could tentatively hypothesize a relationship such as that shown in Fig. 3:22. Similar relationships have been suggested for mantids (Holling 1964) and

Fig. 3:22 A hypothetical relationship between prey size and capture success based on either the number of successful captures as a proportion of initial predator arousals (●) or number of captures per 100 strikes (★).


Captures As A Proportion Of Initial Arousals (●)
0.6
0.5
0.4
0.3
0.2
0
Capture Efficiency(Number Of Successful Captures /100 Strikes) ★
100
80
60
40
20
2
4
6
8
15
20
Prey Size(mm)

Chaoborus larva feeding on Daphnia (Pastorok 1981).

In addition to prey size, the resultant capture success will also be related to the frequency with which the prey encounter the predator. The next chapter sets out to investigate the effect of both size and encounter frequency on the predatory behaviour of R.dispar by examining the functional responses of all developmental stages of the predator, R.dispar, with the complete range of sizes of its common naturally occurring prey, Anisops deanei.

3:8 SUMMARY

In summary, this chapter has described the sequence of behavioural components involved in the predatory behaviour of a typical sit-and-wait predator, R.dispar, paying particular attention to the effect that food deprivation and prey size has on the various identified components. The results idnicate that -

1. The sequence of behaviour follow the previously described predator pattern, i.e. Initial Precapture Posture, Arousal, Orientation, Capture, Consolidation of Grip, Exploration, Injection of Venon/Enzymes, Feeding, Discard, although much variation and interrelation between components exist.

2. Both the 'Arousal' and 'Strike' space surrounding the predator increase with food deprivation, although the 'capture' space is restricted to the morphology and reach of the raptorial legs, there being no lunge or pursuit component.

3. The internal hunger or motivational level determines whether R.dispar will initially be aroused or not but the distance at which the arousal takes place is influenced by the size of the prey. This is believed to reflect the capacity and interrelation between visual and mechanoreceptor, sensory organs.

4. Once additional, more accurate, assessment of prey can take place the decision to strike at a prey is, although again influenced by hunger, significantly affected by prey size. The distance of the prey when the strike takes place is affected by the 'hunger' state not the size of the prey.

5. The outcome of the strike is determined by the size of the prey struck at, not the 'hunger' level of the predator. This is believed to reflect the relationship between strike trajectory, leg morphology and prey size.

6. 'Hunger' apparently affects all components of predatory behaviour leading up to prey capture, by increasing not only distance of 'response' but the number of strikes, hits and captures per unit presentation of prey. It does not increase capture efficiency however which remains at about 70-80%. Hunger also increases the range of prey sizes that R.dispar responds to and attempts to capture.

7. The effect of food deprivation is considered to reflect a motivational change in responsiveness to particular prey stimuli usually described as a sensitization of particular stimulus-response

relations, rather than the food deprivation affecting the sensory mechanism. There being an inverse relation between the strength of the stimulus and the strength of the motivational factors required for a given response.

8. The predatory success in relation to size of model prey suggested an 'optimum' size that could be captured, irrespective of predator motivational level, which is based primarily on the relationship between the shape of the grasping leg and size of prey.

CHAPTER 4

THE EFFECT OF PREY DENSITY ON THE NUMBER OF PREY EATEN

4:1 INTRODUCTION

A sit-and-wait predator is one that, by definition (see Chapter 1) is normally dependent on the movement of its prey rather than its own searching movements, to bring about an encounter with the prey. The outcome of an encounter will depend, amongst other things, on the current motivational state and capturing efficiency of the predator (see Chapter 3) and the evasive or escape efficiency of the prey. Both of these variables are the result of a number of different selection pressures operating on them. The previous chapter examined the effects of predator 'hunger' and prey size on the various components of the predatory behaviour of R.dispar. This Chapter sets out to examine the effect of prey density on the capture success as measured by the number of prey killed. In addition, by observing all developmental stages of the predator and the range of prey sizes that would naturally be available, it is hoped that changes in capture success in relation to the age structure of the populations of both the predator and prey will be identified.

The density of the prey in the predators' vicinity will directly influence the frequency of encounters (see also Chapters 6 and 7) and clearly then will influence the number of prey that can be successfully captured by a sit-and-wait predator. It is therefore logical in an analysis of predatory behaviour to examine in detail the effect of prey density on the subsequent number of prey killed.

Solomon (1949) first acknowledged the twofold nature of the response of predators to changes in prey density. He applied the term 'functional response' to the change in the number of prey killed by individual predators, and the term 'numerical response' to the change in the density of the predators. The term functional response has come to be used to describe how individual predators respond to changes in the density of a single prey species that occur within a time interval that is short relative to the predator's life span. Such functional responses reflect changes in the attack rate of a predator whose physical characteristics (e.g. size and age) remain essentially constant during the interval (Murdoch and Oaten 1975), and which search at random for a homogeneous prey population, itself distributed at random (Holling 1959a, b, 1965, 1966; Hassell et al.1976).

Intuitively, one would expect a functional response to take the form of an increasing number of prey eaten per predator as prey density increases, at least up to some limiting value representing maximum prey consumption within the prescribed time interval.

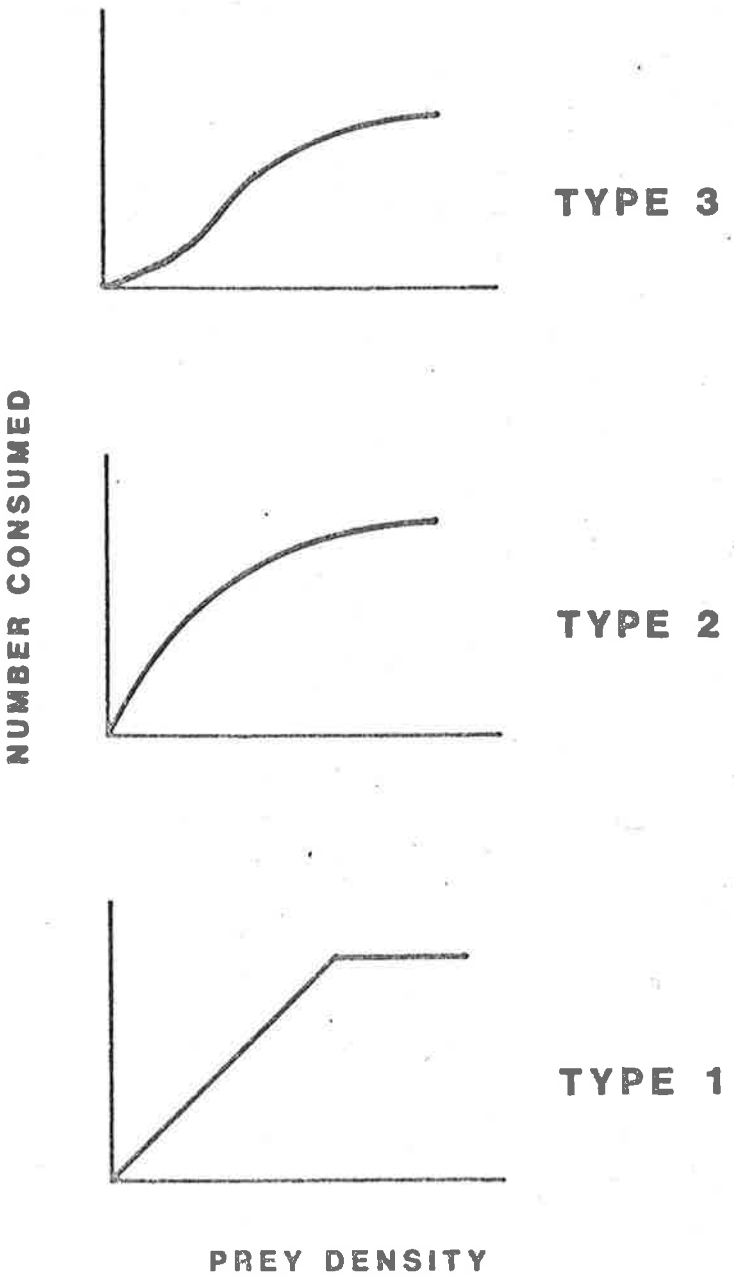
Holling (1959a) discussed three basic types of functional responses (see Fig. 4:1). All three possible responses level off at high prey densities, because the predator becomes satiated and/or has no more time in which to eat more prey. In the Type 1 curve the response rises linearly to a plateau and produces density-independent mortality of the prey up to satiation; Type 2, the response rises at a continually decreasing rate to an upper asymptote producing inversely density-dependent mortality over the entire range, while in Type 3 the response is sigmoid and this produces density-dependent mortality over the lower part of its range (Begon and Mortimer 1981; Hassell 1978).

Fig. 4:1 Holling's three basic fundamental response curves :-

the number killed (or eaten) by a single predator per unit time.

HOLLING'S three basic functional response curves:-

the number killed by a single predator per unit time



The usual response for arthropod predators is the Type 2 curve (though Hassell et al. (1977) have evidence which suggests that sigmoid functional responses may be more frequent than was once thought). Hassell et al. (1976) reviewed these 'typical' Type 2 arthropod functional responses for a variety of predators and parasitoids, while Hassell (1978) modelled all three responses in a general way and then considered their effects on the outcome of predator-prey models by considering each of the three types of response in turn.

Several factors, notably the developmental state of the predator and prey (Thompson 1975; McArdle and Lawton 1979), the predator's mode of search (Akre and Johnson 1979), hunger and satiation (Nakamura 1974; Mills 1982), the availability of prey refuges (Hildrew and Townsend 1977) and temperature (Messenger 1968; Thompson 1978a; Gresens et al. 1982) are known to influence the functional response of invertebrate predators.

The object of this chapter is twofold. To determine the form of the functional response of a sit-and-wait predator using a range of densities that it normally encounters in the field (in many previous determinations with other predators it would appear that unnaturally high densities of prey have been used, which may lead to artificially high encounter rates (see also Hassell et al. 1977)). Second, to examine various aspects of, and identify any alterations in, the functional response in relation to temperature and developmental stage of both predator and prey.
Section 4:2 describes the statistical techniques used to derive the

parameters which characterize the functional response, together with some of the possible errors that can arise in so doing, while Section 4:3 describes the basic experimental procedure. The effect of temperature (Section 4:3) and predator and prey size (Section 4:4) are dealt with next.

4:2 THE PARAMETERS OF THE FUNCTIONAL RESPONSE

4:2.1 Review of Functional Response Equations.

Models which purport to describe the response of predators to changes in prey density have become familiar in the behavioural and ecological literature (e.g. Thompson 1924; Nicholson and Bailey 1935; Holling 1959b; Watt 1959). The most important in the present context is the 'random predator equation' of Rogers (1972) used to describe the functional response. Detailed reviews of models for predation can be found in Royama (1971), Hassell and May (1973), Murdoch and Oaten (1975) and Hassell (1978).

Holling (1959b) made the biologically reasonable assumption that a predator's searching efficiency was dependent upon prey density. He pointed out that predators always require some time to consume their prey and this time would not be available for searching. This so-called handling time progressively reduces the time available for searching as more prey are encountered. Holling argued that as prey density increases 'search' becomes trivial, and handling takes up an increasing proportion of the predator's time. Thus, at high densities the predator effectively spends all of its time handling prey, and the predation-rate reaches a maximum, determined by the maximum number of 'handling-times' that can be fitted into the total time available.

Thus he derived the now familiar 'disc' equation (equation 4.3) (Holling 1959b):

$$T_s = T_t - T_h N_e \qquad \ldots 4.1$$

$$N_e = a N_t T_s \qquad \ldots 4.2$$

where T_s = time spent searching for prey,

T_t = total time that prey and predator are together,

T_h = handling time

a = attack coefficient (or attack rate)

N_t = prey density

and N_e = number of prey eaten

Combining equations 4.1 and 4.2, we obtain

$$N_e = \frac{a N_t T_t}{1 + a T_h N_t} \qquad \ldots 4.3.$$

This equation is an 'instantaneous equation' and as such makes no allowance for any reduction in the prey numbers during the course of the experiment (i.e. exploitation). Consequently, it should be used only when an experiment is run for a very short period (see, for example, Visser 1982), or where the predator's search is systematic, so that areas that have been searched are not re-visited, or when a prey item is replaced as soon as it is eaten. In the present work, the prey were not replaced during the course of the experiment and the total time that predator and prey were together was reasonably long (24 hours), so that the 'disc' equation was considered not strictly applicable. The most appropriate equation to describe the functional response under these conditions is the random predator equation of Rogers (1972) which can be derived from the disc equation as follows:

$$\frac{d\,N_t}{d_t} = \frac{-\,a\,N_t}{1 + a\,T_h\,N_t.} \qquad \ldots\ 4.4$$

This is the instantaneous rate of change of the population at time t.

Let N at time 0 = N_o and N at time T = N_T

Then:

$$\int_{N_o}^{N_T} \frac{1 + a\,T_h\,N}{a\,N}\,dN = -\int_{o}^{T} dt \qquad \ldots\ 4.5$$

Integrating, we have

$$\left[\frac{1}{a}\log_e N + T_h\,N\right]_{N_o}^{N_T} = -\,[t]_0^T \qquad \ldots\ 4.6$$

and solving within limits gives :

$$\frac{1}{a}\log_e N_T + T_h N_T - \frac{1}{a}\log_e N_o - T_h N_o = -T \qquad \ldots 4.7$$

which simplifies to

$$\log_e \left[\frac{N_T}{N_o}\right] = -aT-aT_h (N_T-N_o) \qquad \ldots 4.8$$

where N_T is the number of prey left after T, and N_o is the initial prey number at time 0.

N_e, the number of prey eaten is simply $N_o - N_T$. With the substitution of $N_e = N_o - N_T$, elimination of logarithms and some rearrangement, equation (4.8) becomes the random predator equation :

$$N_e = N_o (1 - \exp (-a (T-T_h N_e))) \qquad \ldots 4.9$$

4:2.2 Random Predator Equation

Equation (4.9) allows for exploitation and can easily be amended to include a predator density term (Rogers 1972).

Most workers who use the random predator equation for estimating a (Attack Rate) and T_h (Handling Time) have done so using a linear regression model based on equation 4.9 (Rogers 1972; Evans 1973; Hassell et al. 1976).

$$\log_e \frac{N - N_e}{N} = -a\,T_t + a\,T_h\,N_e \qquad \ldots\ 4.10$$

This method however, is statistically incorrect as the term N_e occurs on both sides of the regression equation (see equation 4.10), and one of the basic assumptions of regression, i.e. Model I, analysis is that the independant variable (which is N_e in this case) should be without error, which N_e obviously is not.

If this incorrect method is adopted the estimates of $\underline{a}$ in particular and $\underline{T_h}$ may be unrealistic due to two factors. First, in a normal Type 2 functional response which rises with an ever decreasing slope towards an asymptote, there is a prey density beyond which the predator eats a constant number of prey. In the regression of the logarithms of the proportion of the survivors against the number of prey eaten, any points beyond this prey density merely provide more variance about the plateau, resulting in an increase in the slope of the line and the lower intercept. This will lead to an increase in the estimate of $\underline{a}$ (attack rate). Since the slope of the regression line is $\underline{a}$ times $\underline{T_h}$, the estimate of $\underline{T_h}$ (handling time) will be correspondingly reduced. This first type of discrepancy however does not greatly alter the relative values of $\underline{a}$ and $\underline{T_h}$ provided that only a few points are on the plateau of the functional response curve. This can be allowed for by careful design of the experiment.

The second type of discrepancy (which results by invalidating this statistical procedure) may be of greater importance. If the level of exploitation is too high at any prey density, the logarithm of the number of survivors becomes very small; at complete exploitation it is of course the logarithm of zero. High exploitation has the effect, as discussed previously, of increasing the estimate of a and reducing that of T_h. (Thompson (1978a) has shown by simulation that any exploitation greater than about 75% causes a significant bias in the estimate of a and T_h).

Glass (1970) pointed out that a logarithmic or similar transformation may produce a bias in the results because logarithms give greater emphasis to data points near the origin than to those further away. In addition, such a transformation is only valid if it results in homogeneity of the error variance, which is a necessary requirement for regression analysis. If the error term is additive then a non-linear model such as equation 4.9 should be fitted by an iterative least-squares parameter estimation procedure, such as that described by Glass (1967, 1970) or Conway, Glass and Wilcox (1970). In the least-squares method, values of the constants in the equation are found that minimized the sum of the squared deviations of the observed values from those predicted by the equation (Daniel and Wood 1971).

To avoid the errors discussed above a non-linear weighted least-squares procedure has been adopted throughout. This involves viewing equation 4.9 as expressing the number of prey eaten (N_e) as a non-linear function of prey density (N) and the two parameters a and T_h (attack rate and handling time), plus the experimental error.

i.e. $N_e = f(N; a, T_h) + \text{error}$ ... 4.11

Given values of the parameters a and T_h, a value of the function, corresponding to any value of N, can be calculated by solving equation 4.9 for N_e. This equation can be rearranged as :

$$N_e - N + N^{*}\exp(-a(T - N_e T_h)) = 0 \qquad \ldots 4.12$$

This can then be solved by the standard Newton-Raphson iterative method using the observed number eaten as the initial approximation.

Following the method of Visser and Reinders (1981) to compensate for the variability of the error in equation 4.11, the function to be minimized is defined as :

$$\chi^2 = \sum \left[\frac{N_{e(fit)} - N_e}{\text{S.E. } N_e} \right]^2 \qquad \ldots 4.13$$

where the summation extends over the prey densities used, and N_e and $N_{e(fit)}$ are respectively the observed and the calculated values for the number of prey eaten at each of the prey densities. ($N_{e(fit)}$ is the function specified in equation 4.11.) By including the standard error (S.E. N_e) in the denominator of 4:13 the correct weight is given to each point.

To start the iteration process initial estimates of the two parameters a and T_h were obtained from the linearised form of equation 4.9 (see equation 4.10). The iterations continued until the relative change in the weighted residual sum of squares, χ^2, (see equation 4.13) was less than 0.01.

The final estimates of a and T_h can then be used to estimate the final values for the fitted number of prey eaten ($N_{e(fit)}$) at the given densities.

The computations were carried out using the GENSTAT (General Statistical Program) (Alvery et al. 1977) on the CYBER 173 computer at the University of Adelaide computing centre.

4:3 BASIC EXPERIMENTAL PROCEDURE

The functional responses in the following experiments were measured by placing single predators in containers with different densities of their prey. The predators were allowed to feed for no more than 24 hours, after which the numbers of prey killed and eaten were noted. The number of additional dead prey was also recorded if necessary, although, due to experimental design (see later this chapter) this occurrence was very uncommon.

Previous work (e.g. see references in Bernays and Simpson 1982) has shown that moulting can significantly influence the feeding behaviour of insects. In addition Cloarec (1969b, 1980b, 1981) has shown that the predatory behaviour and performance of *Ranatra linearis* is also altered by moulting behaviour. To overcome this difficulty, only individuals of *R.dispar* that had moulted at least 48 hours previously were used in the experiments. This ensured that they had recovered from the moult and settled down to the normal steady feeding rate. Prey were *A.deanei*.

On day 1 of an experimental run, the *R.dispar* were removed from the holding tanks and provided with an excess of mixed natural prey (*Anisops deanei*, other Notonectidae, Corixidae, ostracods (Ostrecoda : Crustacea) and *Daphnia* spp. (Daphniidae : Crustacea)). Following 24 hours of feeding the predators were removed and fasted for 24 hours. During the fast period animals were housed in the experimental containers. These were 1 litre plastic beakers filled with 800 ml of filtered, dechlorinated tap water, with a length (about 15 cm) of 2 mm diameter wooden cocktail stick weighted at one end with a lead sinker embedded in bees wax, which acted as an ambush site.

Prey animals were fed abundant water fleas (*Daphnia* spp.) or mosquito larvae, up to the size grading (as outlined in Chapter 2) and counting immediately prior to the beginning of an experiment, in order to reduce any cannibalism that may occur (see Fox 1975c). Any prey individuals that appeared damaged due to the sorting or counting procedure were replaced. The prey animals were transferred to the experimental containers, the water level made up to 1000 ml and the predator allowed to feed for 24 hours. All experiments were performed at either a constant temperature of 22 ± 2.0°C or in more closely controlled constant temperature rooms under a light regime of 14L:10D (lights on 0600 h, off 2000 h). The experiments started between 1700 and 1800 h. At the end of the 24 hour feeding period the predators were removed and the *Anisops* recounted. Both the number of live and dead *Anisops* were recorded. Dead *Anisops* could have died naturally, been killed but not eaten (see Chapter 3, Section 3), or killed and eaten. Control containers of various prey densities were run at intervals throughout the entire experimental program. The results showed the incidence of natural mortality or cannibalism to be less than 1% and it was therefore ignored in the analysis. The number of *Anisops* eaten during the experiment was obtained by counting the number of discoloured 'husks'. *Ranatra*, like other Heteroptera, is an exterodigester, and sucks out the prey's liquidified tissues. The very characteristic discolouration caused by enzymatic activity permits the eaten prey to be readily distinguishable from the occasional naturally dying *Anisops*.

4:4 THE EFFECT OF TEMPERATURE ON THE FUNCTIONAL RESPONSE OF ADULT *R.dispar*.

4:4 1 Introduction

Very little is known about the changes of the key parameters of the functional response, a and T_h, with respect to changes in the physical conditions of the environment, despite the obvious importance of, for example, temperature. Only a few investigators have examined this relationship between temperature and functional response, (Mack *et al.* 1981; Messenger 1968; Thompson 1978; Gresens *et al.* 1982). Since temporal synchronization is necessary if predators are to exert an effect on their prey, seasonal differences, especially temperature, can alter the magnitude of predation (Thompson 1978a). The fact that adult R.dispar are relatively long-lived and overwinter as adults means that they experience highly variable environmental temperatures, especially in the shallower or surface water layer. The following section therefore sets out to describe the effect of temperature on the functional response of R.dispar adults and its prey, A.deanei.

4:4.2 Method

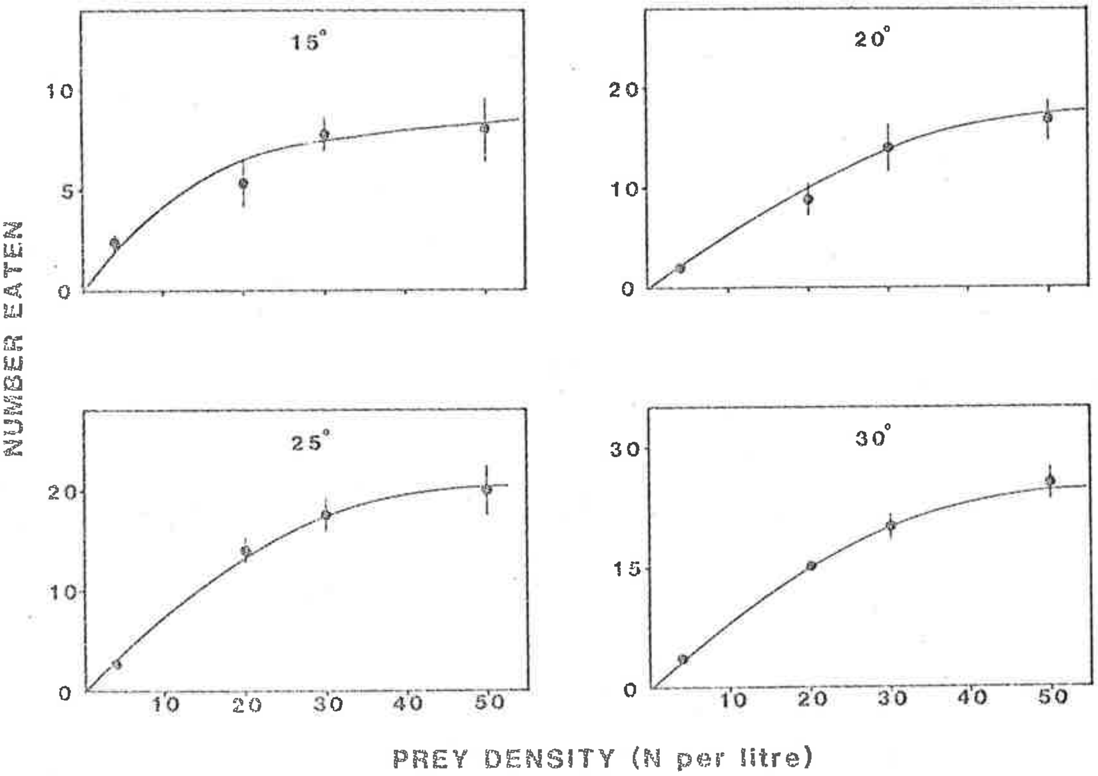
The basic experimental procedure has been described above. Eight replicates were used at each of four prey densities ranging from 4 to 50 Anisops/litre. The experiments were performed at four temperatures, namely 15.5 ± 1.0, 20.0 ± 1.0, 25.0 ± 0.5, and 29 ± 1.0, in constant temperature rooms. Both predators and prey were acclimatized at the appropriate experimental temperature for two days before the start of the feeding period and Ranatra were satiated and then fasted at the experimental temperature.

4:4.3 Results:

Following examination of the results of this section and those referred to in the following Section 4:5 the most generally applicable response seemed to be the Type 2, although a Type 3 curve may have been fitted in some cases (see in particular 15° Curve of Fig. 4:2). Accordingly, the Type 2 response model was fitted to the data, as outlined in Section 4:2. The observed and fitted data are shown in Fig. 4:2. The curves all show a typical Type 2 response and the degree of fit of the data is good as shown in Table 4:1. The asymptote increases from 8.2 at 15.0°C to 25.0 Anisops eaten at 29.0°C, with intermediate values of 16.4 and 20.2 at 20.0°C and 25.0°C respectively. The

<u>Fig. 4:2</u> The functional response of adult female *R.dispar* to changes in prey density of prey size class 5, *A.deanei* at four different water temperatures.

Means, 95% confidence intervals and fitted curves are plotted.


15°
20°
25°
30°
NUMBER EATEN
PREY DENSITY (N per litre)
0
5
10
0
10
20
0
10
20
0
15
30
10
20
30
40
50

attack-rate (a) and handling-time (T_h) parameters are shown in Fig. 4.3. Over the temperature range investigated the attack-rate changes in an almost linear fashion.

The handling-time curve shows a dramatic decrease from 15°C to 20°C from which it appears to reach a constant value between 20°C and 30C.

TABLE 4:1 Values of the functional response parameters, attack rate (a) and handling-time (T_h) that provided the best fit to the model, with the associated χ^2, and df.

Temp	a	Std.Err. of a	T_h	Std.Err. of T_h	χ^2	df.	Sig.
15°	.05	.01	2.50	.34	1.55	3	NS
20°	.03	.005	0.69	.14	0.48	3	NS
25°	.08	.02	0.76	.16	2.45	3	NS
30°	.11	.007	0.71	.04	0.34	3	NS

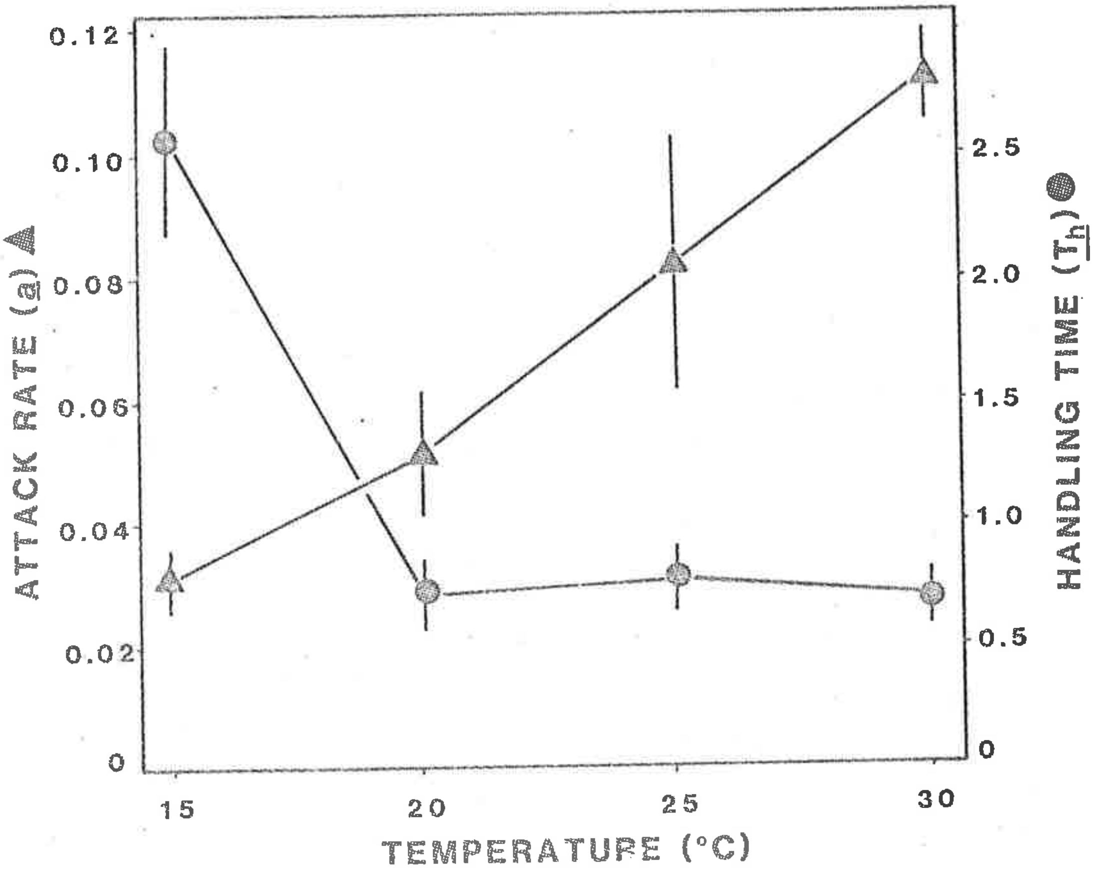
(The probability level on the chi-square distribution was set at $\alpha = 0.05$). A non-significant χ^2 value indicates that no significant difference was observed between observed and fitted values.

4:4.4 Discussion

The constant handling time between 20 and 29° suggests that at these temperatures R.dispar was feeding at its maximum possible rate at the higher prey density and that the processes which limit the speed at

Fig. 4:3 The effect of water temperature on the attack-rate (a) and the handling time (T_h) of adult female *R.dispar* feeding on size-class 5 *A.deanei*.

Means and Standard Error plotted.


ATTACK RATE (a) ▲
HANDLING TIME (T_h) ●
TEMPERATURE (°C)
0.12
0.10
0.08
0.06
0.04
0.02
0
2.5
2.0
1.5
1.0
0.5
0
15
20
25
30

which the prey individuals are "processed" (direct handling of the captured prey during consumption, the extraction process, digestion, gut clearance, etc) were not apparently speeded up above 20^{o}C. The mean gut-clearance time for R.dispar at 22^{o}C was about 3 hours ($\overline{x}$ = 3 h 16 m, SE = 27 m, N = 5) following a 5 day fast. No other data on gut clearance rates are available for R.dispar. Lawton (1970) showed that for larvae of the damsel fly, Pyrrhostoma nymphula gut clearance times increased significantly from 5 to 15^{o}C, but above this temperature the rate of increase became greatly reduced. Whether a similar pattern exists for R.dispar is of course unknown, although the constant handling-times observed between 20 and 29^{o}C is consistant with this possibility. The asymptote increases dramatically (Fig. 4:2) from 15^{o}C to 20^{o}C but thereafter increases almost linearly, which shows itself in the increased values of a with temperature. One would expect that at higher temperatures the attack rate, a, should also plateau off as the water becomes unnaturally warm and lies outside the normal range of R.dispar. It was believed that 30^{o}C would have been warm enough to show this, but it is not uncommon for the upper surface water layers in the farm ponds to approach 30^{o}C and slightly higher in shallower regions. Thus it may be necessary to subject R.dispar to higher temperature to see if the attack rate reaches an asymptote. There are signs of this happening at the lower (15^{o}C) end of the curve as shown in Fig. 4:3. Handling times should behave in a reciprocal manner, decreasing with temperature and then increasing under stressful conditions. Messenger (1968) reported such a pattern variation in the parasitic wasp, Praon exsoletum, while Thompson (1978) reported that handling time of a damsel fly, Ishnura elegans, decreased exponentially, levelling off at 16^{o}C, while the attack rate (a) increased sigmoidally, levelling off at

27.5°C. In retrospect, the temperature range that R.dispar was subjected to does not fully cover the natural upper and lower limits experienced in the field, although 29.5°C is very close to the upper limits.

The dramatic increase in handling-time observed at 15°C probably reflects the lower metabolic rate of Ranatra at this temperature and the associated influence on the 'hunger' level of the predator. The results in Chapter 6:3 show that increasing the temperature from 15 to 25°C does not significantly increase the activity level of the prey while increasing it to 30°C does. Therefore it is proposed that the observed increase in the number of prey eaten shown in the functional response results for 15 to 25°C indicate an increase in the metabolic activity of R.dispar (with the associated increase in 'hunger' motivation) rather than an increase in prey activity and therefore encounter rate. However, at 29°C, the additional prey eaten may have resulted from both predator metabolic and prey activity effects.

4:5 THE EFFECT OF AGE STRUCTURE OF BOTH PREDATOR AND PREY ON THE FUNCTIONAL RESPONSE

4:5.1 Introduction.

All size classes of both R.dispar and A.deanei are found together during the summer and autumn periods in farm ponds. The functional responses (with the associated $\underline{a}$ and $\underline{T_h}$ parameters) will vary markedly, depending on the stage of the predator development and the size of the prey taken (Murdoch 1971; Hassell, et al. 1976). Identification of these changes permits the incorporation of age structure into population models, which in turn provides a more dynamic predator-prey model

(Hassell 1978). The identification also allows changes in the behavioural strategies employed by the predator in all stages of its development to be identified. To do this we must first know how the parameters of $\underline{a}$ and $\underline{T_h}$ (assuming Type 2 responses) vary among successive developmental stages of the predator when they encounter the same size of prey, and how they vary within the same predator stage, but encountering different sizes of prey (Hassell op. cit.).

Despite the undoubted importance of such age structure effects (Auslander, Oster and Huttaker 1974; Oster and Takahashi 1974) very few studies present us with such information, gathered for a single predator species. Notable exceptions are provided by Thompson (1975) working with nymphs of the damselfly Ischnura elegans and Fernando (1977) with the predatory mite Phytoseiulus persimilis. Thompson (1975) obtained functional responses for a number of the nymphs feeding on water fleas (Daphnia) of different sizes, and from each response he abstracted values of $\underline{a}$ and $\underline{T_h}$ which were found to depend upon predator and prey size. Although his results are incomplete because he did not examine small predator instars, they indicate a clear tendency for $\underline{a}$ to decline and $\underline{T_h}$ to increase as prey becomes larger or predators smaller. These trends are also largely supported by Fernando (1977) and by several other experiments, reviewed by Hassell, et al. (1976), where predator or prey size alone have been varied.

The only study which I am aware of that reports changes over all instars of a predator feeding on a full range of prey size classes is that of McArdle and Lawton (1979). Working with the Notonecta/Daphnia system they were able to show that the changes in both attack rate and handling time were far more complicated than those documented by Thompson (1975) for the *Ishnura/Daphnia* system, with maximum attack rates for small predators attacking small prey, and large predators attacking large prey. Adult *Notonecta* had lower attack rates than the two previous juvenile instars (4 and 5). From their data and those of other workers, which they reviewed, they suggest that small predator instars will usually compete with large instars for food, unless there is spatial or temporal separation between them. In addition, where predator and prey sizes are plotted against either a or T_h, complex surfaces are to be expected wherever a wide range of prey and predator sizes is involved.

The following section sets out to describe the changes in the functional responses and their associated attack rate (a) and handling time (T_h) parameters for all instars of *R.dispar* feeding on a full range of size classes of *A.deanei* under controlled conditions in the laboratory. As such it constitutes the first complete surface to be described for a sit-and-wait predator.

4:5.2 Method

The basic experimental procedure has been outlined in Section 4:2, while the collecting, size grading and pre-experimental holding period for both predators and prey are given in Chapter 2. (Additional experimental details are given, where appropriate, below).

Originally the experiment was designed to permit each *A.deanei* instar to be viewed as a separate prey size class. However, due to difficulties in both capturing and maintaining sufficient numbers of first-instar prey to allow this, Prey Size 1 is a combination of both Instar 1 and 2.

The experimental design, as shown in Fig. 4:4, was treated as a 7 x 5 x 5 randomized block with normally 5, but in some cases 8 replicates.

Only those predators that had moulted at least 48 hours before the experiment were used. The first instar predators were observed for moulting for 48 hours after they were used but this never occurred. On rare occasions predators died during the experimental period. These individuals' results were discarded. Individual predators were used only once during any particular instar but some were used a second time in an older instar.

4:5.3 Results

As outlined in Section 4:3 the most appropriate response model to fit to the data seemed to be a Type 2. However, as before, it would appear that a Type 3 response may have been just as easily fitted in some cases (see for example Figs. 4:5a (Prey Size 1); 4:5b (Prey Size 1); 4:5c (Prey Size 5); 4:5d (Prey Size 4 and 5); 4:5f (Prey Size 5)). The functional response curves obtained for each of the predator instar (adult)/prey size combinations are shown in Figs. 4:5 a-g. Generally the degree of fit of the data to the model is good, as shown by Table 4:2. The majority of curves obtained follow the typical Type 2 pattern although several exceptions are worth noting. Figs. 4:5 e-g show that the functional response obtained for the 5th instar and both the male and female predators with the two smallest prey sizes follow a

Fig. 4:4 Randomized block experimental design for effect of age structure of both predator and prey on the functional responses of *R.dispar*.

			PREDATORS							
			INSTAR I	INSTAR II	INSTAR III	INSTAR IV	INSTAR V	ADULT FEMALE	ADULT MALE	
REPLICATE No. 1 2 3 4 5										
PREY	PREY SIZE 1	4								
		12								
		20								
		30								
		50								
	PREY SIZE 2	PREY DENSITY (N/litre)								
	PREY SIZE 3									
	PREY SIZE 4									
	PREY SIZE 5									

Figs. 4:5 A-G The functional response of each developmental stage of *R.dispar* feeding on 5 size class of *A.deanei*.

Graph (A) is for I instar *R.dispar*,

(B) II instar, (C) III instar, (D) IV instar,

(E) V instar, (F) Adult female, and

(G) Adult male.

Means, 95% confidence interval and fitted curves are plotted.

PS1 = Size class 1, PS2 = Size class 2,

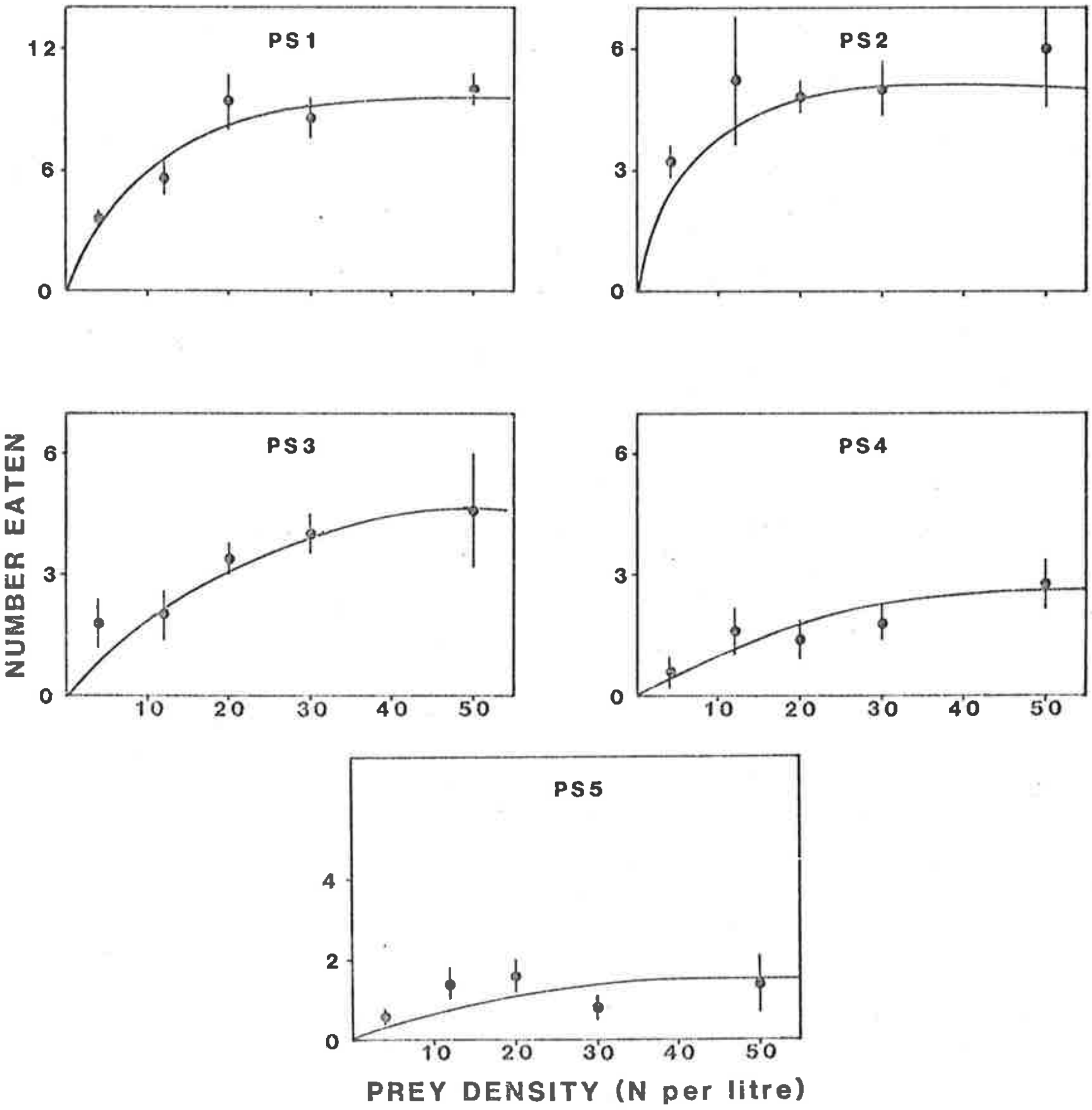
PS3 = Size class 3, PS4 = Size class 4

and PS5 = Size class 5 of *A.deanei*.

Note the changes in the vertical axes.

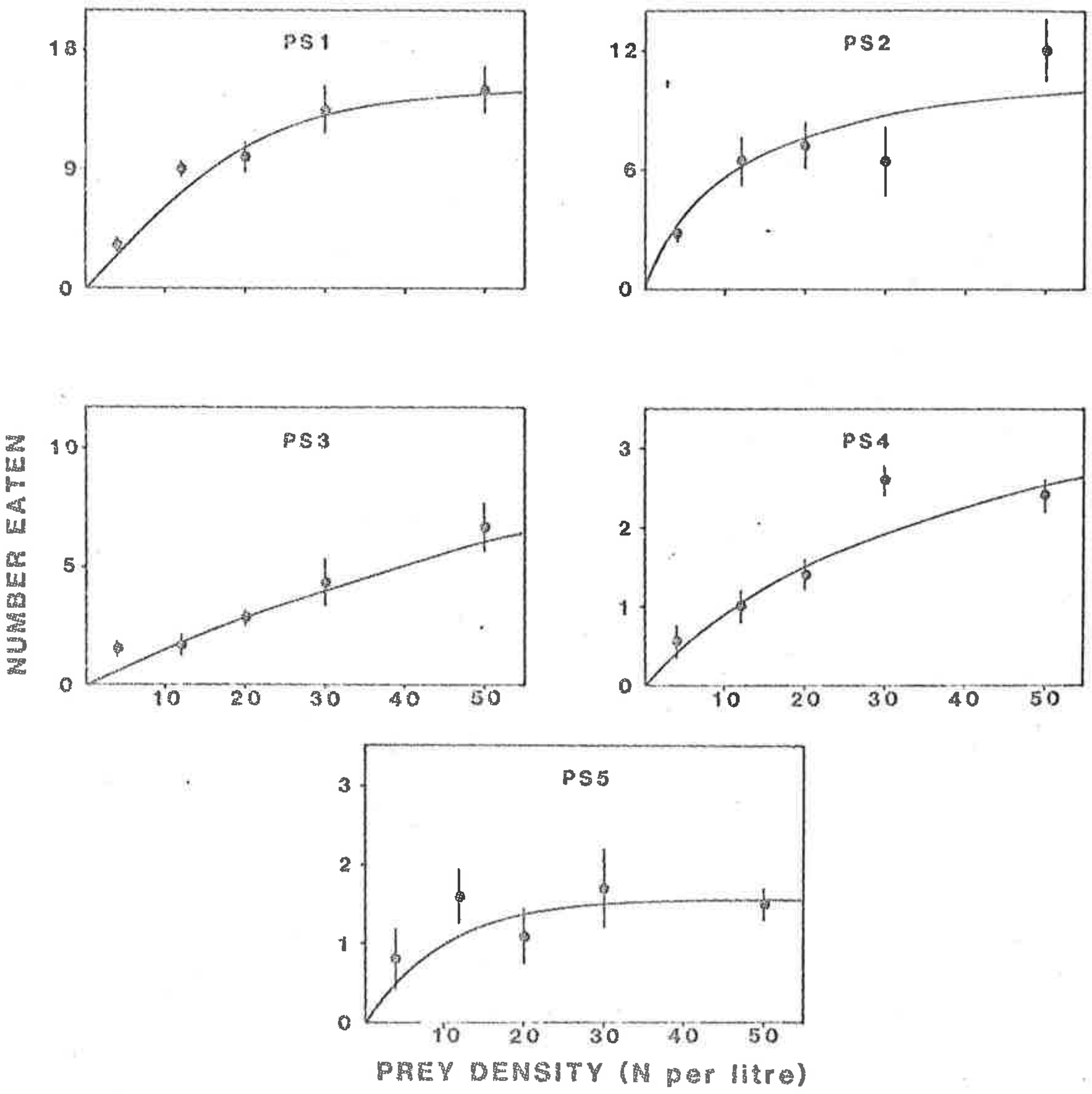
(A)

I INSTAR


PS1
12
6
0
PS2
6
3
0
PS3
6
3
0
PS4
6
3
0
PS5
4
2
0
NUMBER EATEN
10
20
30
40
50
PREY DENSITY (N per litre)

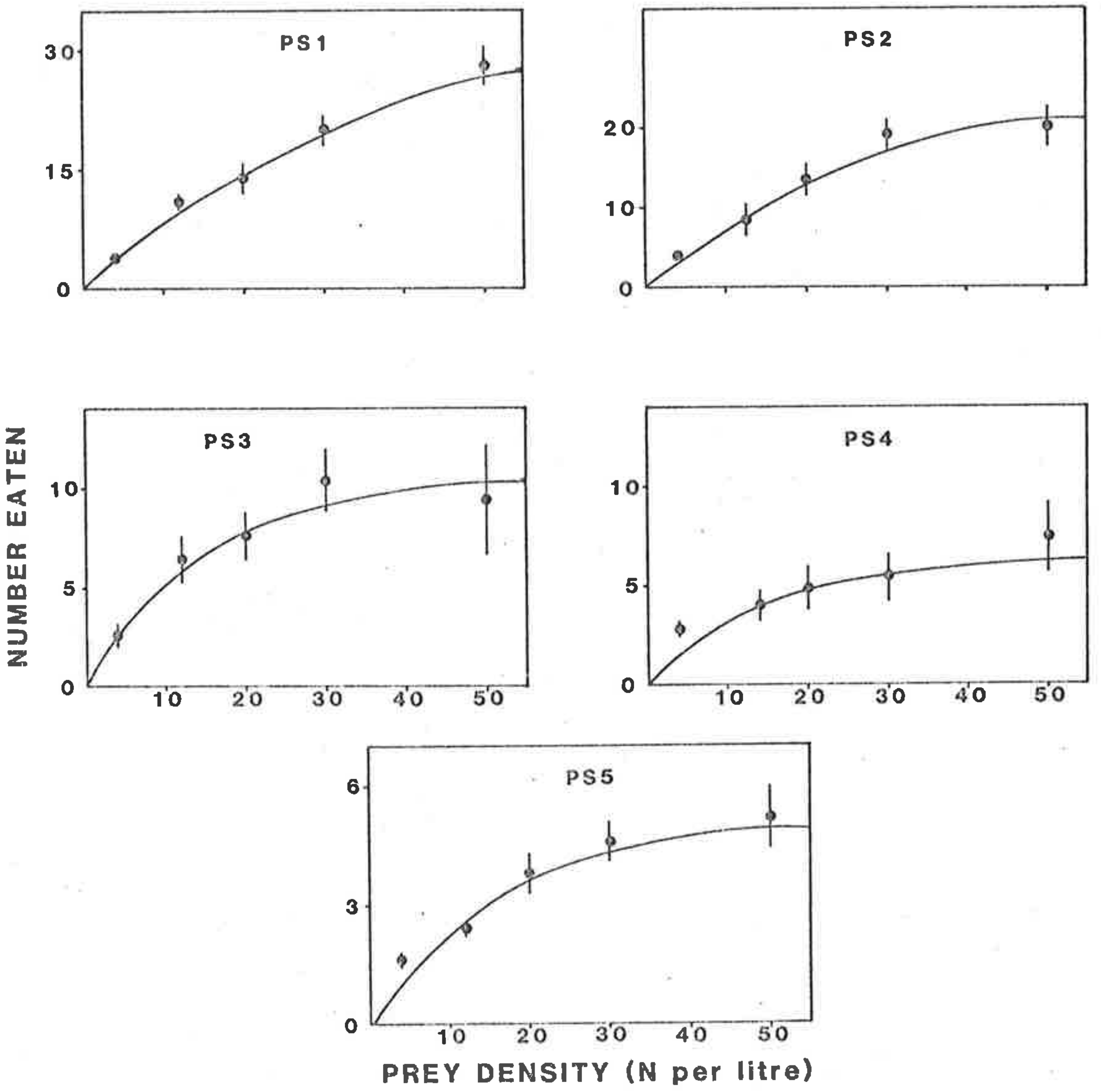
(B)

II INSTAR


PS1
18
9
0
PS2
12
6
0
PS3
10
5
0
PS4
3
2
1
0
PS5
3
2
1
0
10
20
30
40
50
NUMBER EATEN
PREY DENSITY (N per litre)

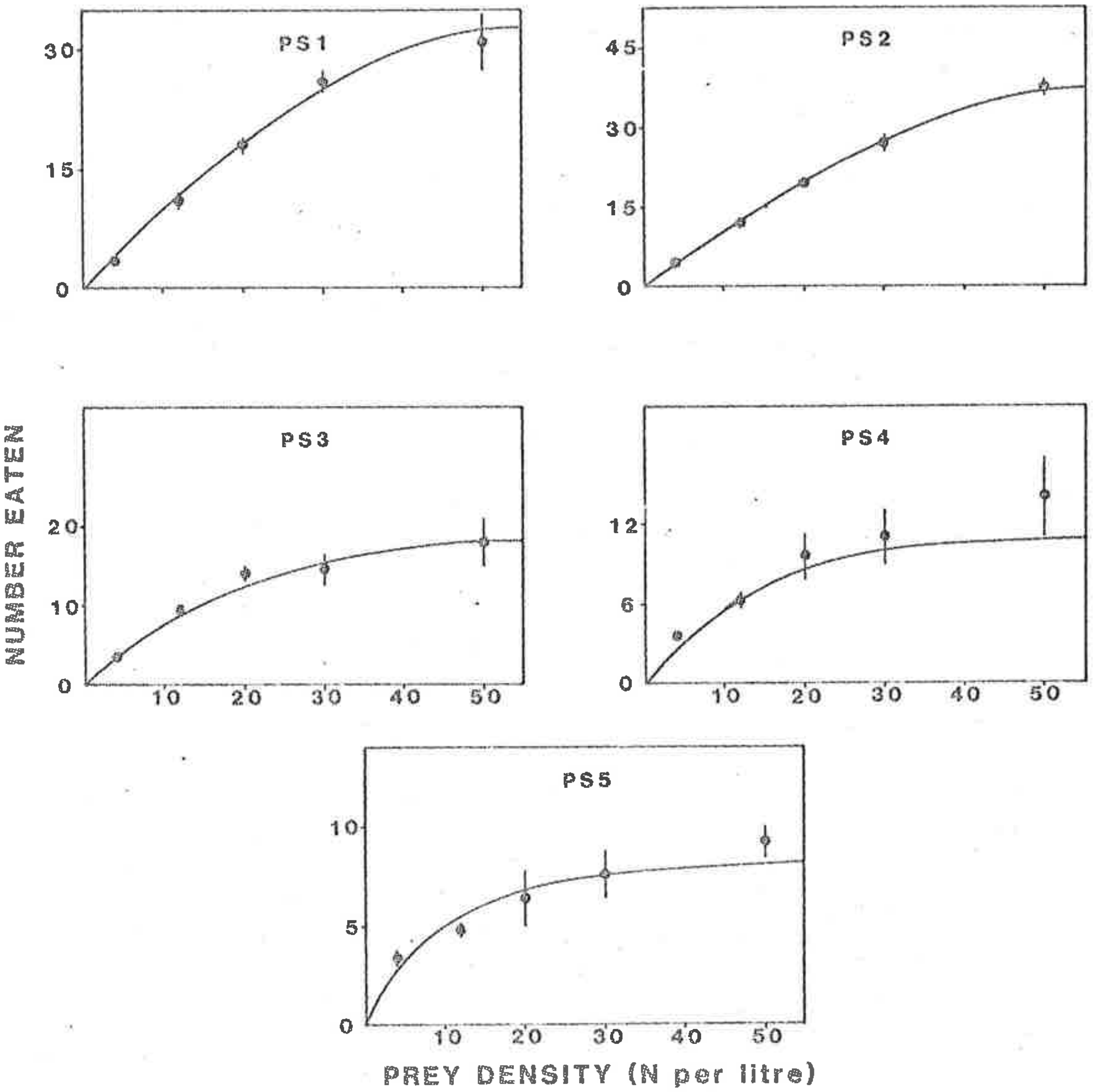
(C)

III INSTAR


PS1
30
15
0
PS2
20
10
0
PS3
10
5
0
10
20
30
40
50
PS4
10
5
0
10
20
30
40
50
PS5
6
3
0
10
20
30
40
50
NUMBER EATEN
PREY DENSITY (N per litre)

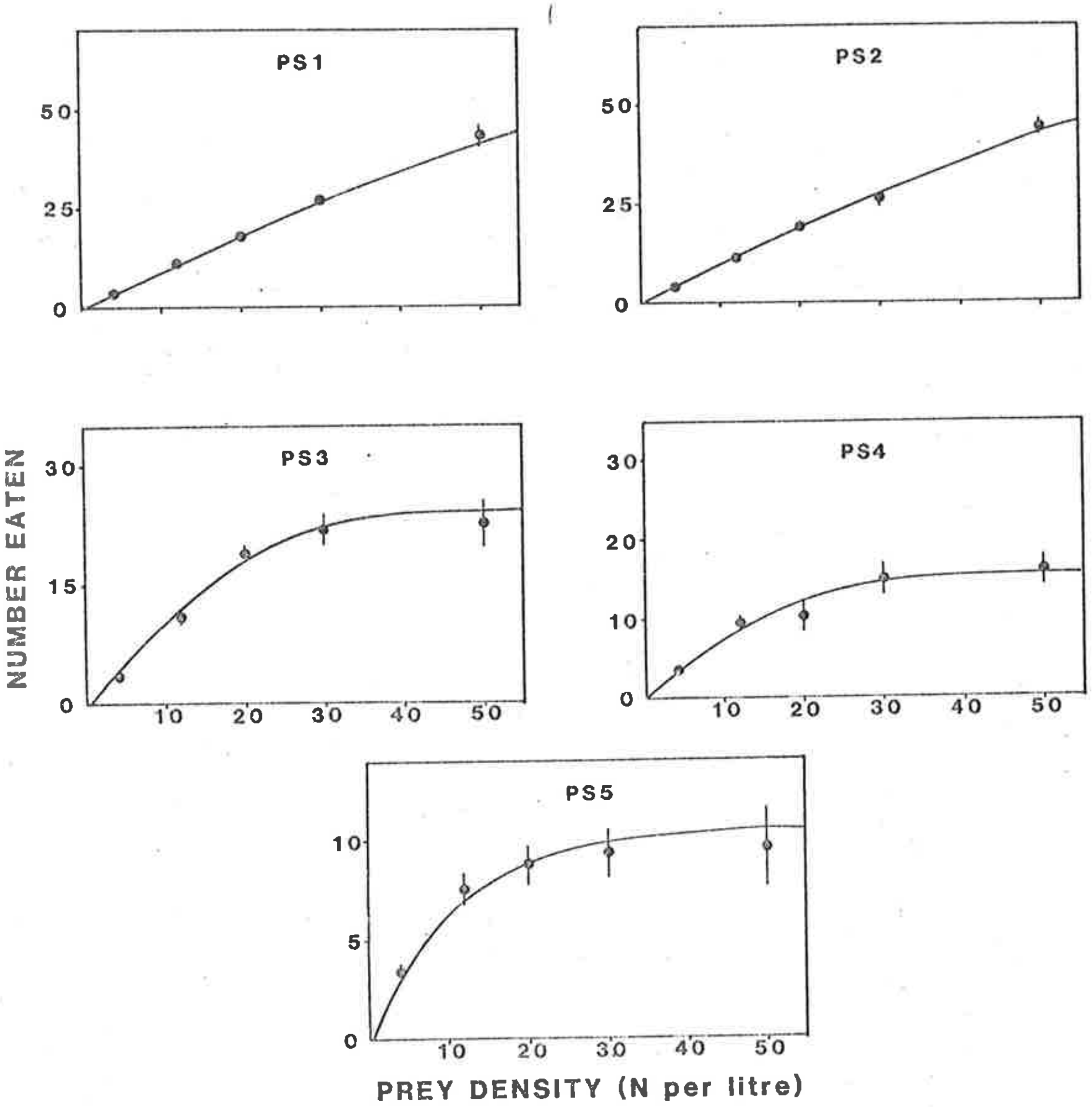
(D)

IV INSTAR


PS1
30
15
0
PS2
45
30
15
0
PS3
20
10
0
10
20
30
40
50
PS4
12
6
0
10
20
30
40
50
PS5
10
5
0
10
20
30
40
50
NUMBER EATEN
PREY DENSITY (N per litre)

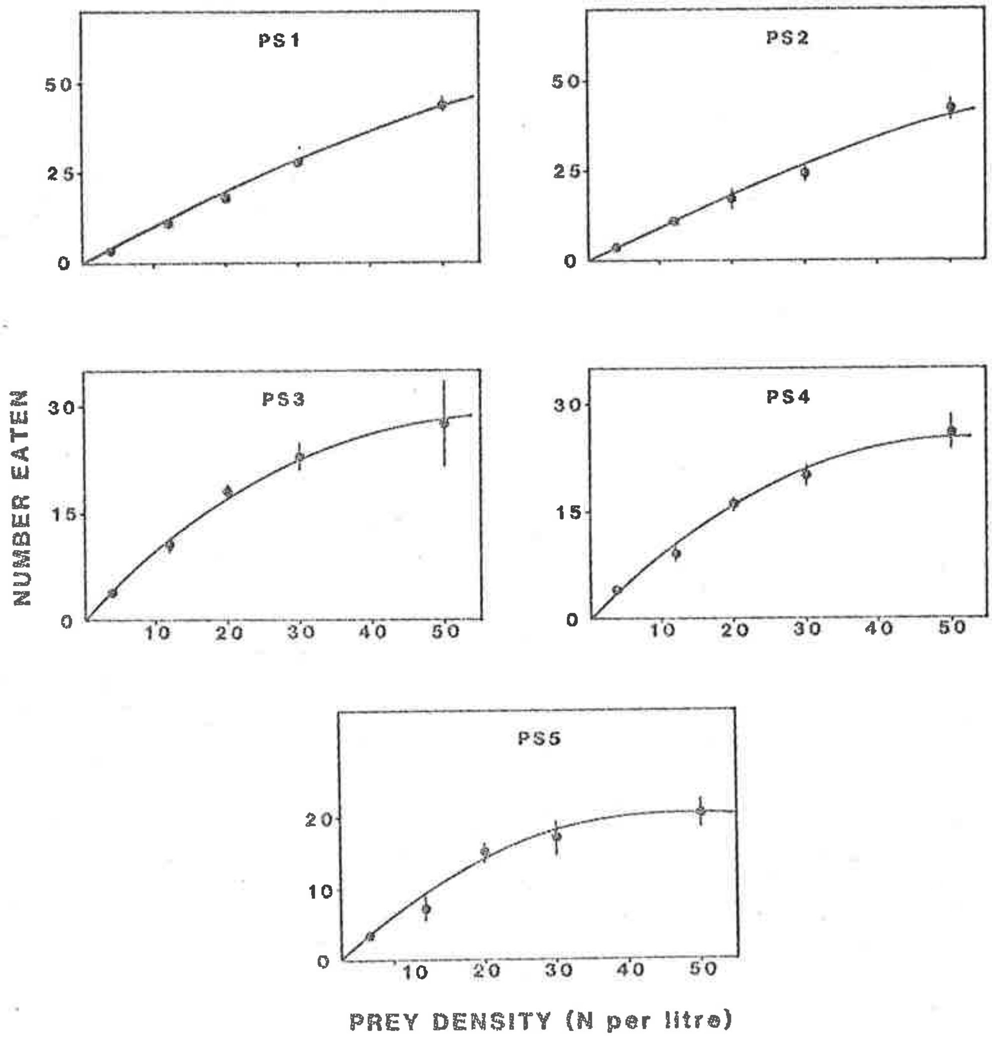
(E)

V INSTAR


PS1
50
25
0
PS2
50
25
0
PS3
30
15
0
10
20
30
40
50
PS4
30
20
10
0
10
20
30
40
50
PS5
10
5
0
10
20
30
40
50
NUMBER EATEN
PREY DENSITY (N per litre)

(F)

ADULT FEMALE



(G)

ADULT MALE

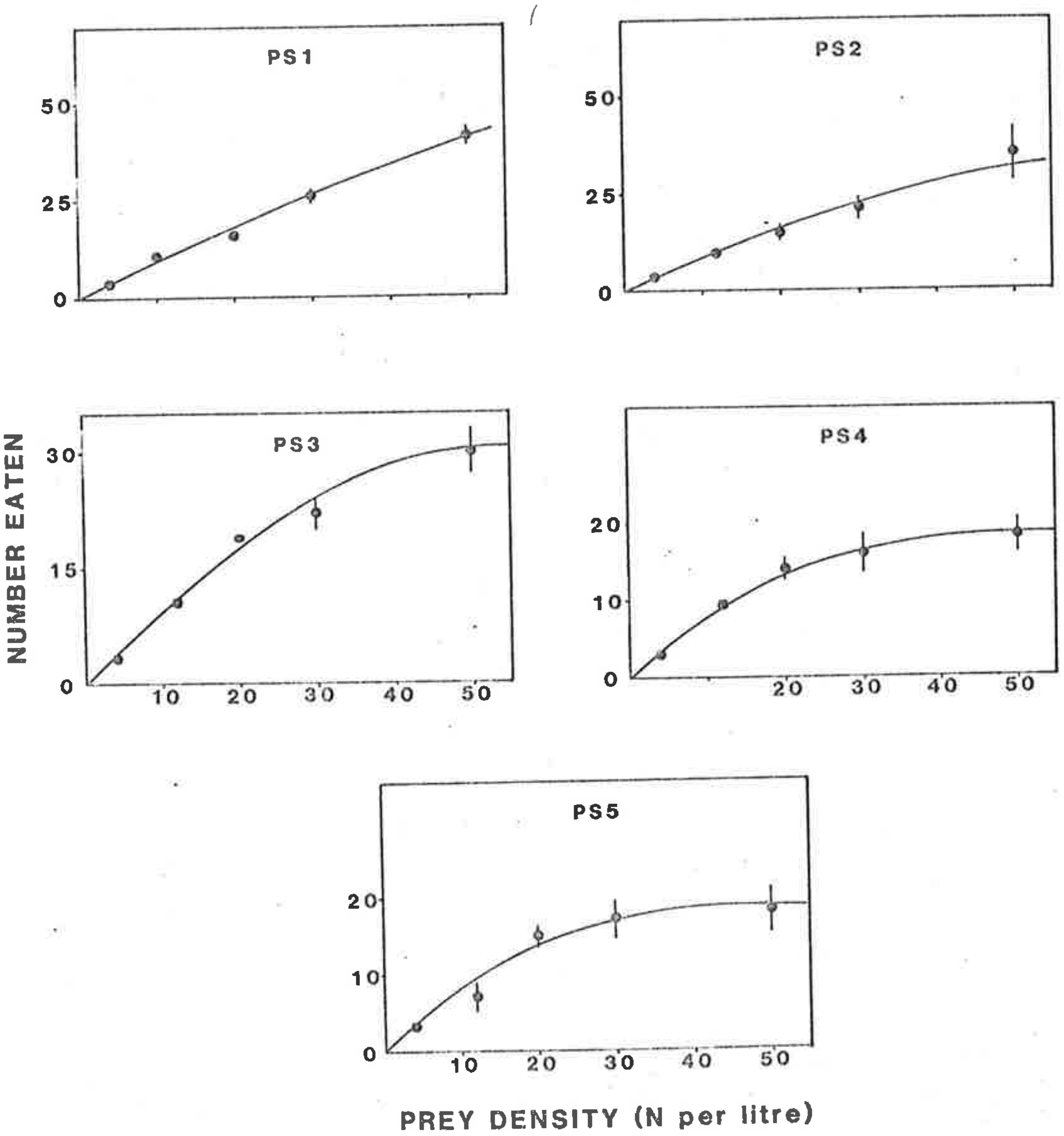

PS1
50
25
0
PS2
50
25
0
PS3
30
15
0
10
20
30
40
50
PS4
20
10
0
20
30
40
50
PS5
20
10
0
10
20
30
40
50
NUMBER EATEN
PREY DENSITY (N per litre)

TABLE 4:2 Values of the attack rate (a) and handling time (T_h) parameters that provided the best fit to the Type 2 Functional Response Model, as shown by the associated $\chi^{2\,A}_{3}$ values.

PREY SIZE CLASS	PREDATOR STAGE I			II			III			IV			V			ADULT			ADULT		
	a[1]	T_h[2]	χ^2	a	T_h	χ^2	a	T_h	χ^2	a	T_h	χ^2	a	T_h	χ^2	a	T_h	χ^2	a	T_h	χ^2
1	.17 .03	2.4 .24	4.97	.10 .02	1.4 .2	3.62	.13 .02	.7 .90	1.94	.14 .03	.5 .11	2.85	.15 .01	.2 .05	0.75	.10 .01	.17 .06	4.83	.10 .01	.1 .1	1.38
2	.12 .03	4.6 .16	3.29	.06 .02	2.0 .4	2.36	.13 .02	1.0 .09	2.24	.22 .02	.5 .04	1.89	.19 .02	.3 .05	1.40	.11 .02	.22 .14	4.01	.11 .01	.5 .17	0.54
3	.02 .007	4.1 1.1	2.27	.01 .003	1.0 1.5	8.26[B]	.06 .01	1.8 .24	0.83	.17 .03	1.3 .13	1.69	.32 .04	.9 .21	9.42[B]	.20 .05	.68 .11	6.71	.22 .08	.6 .17	1.42
4	.01 .002	6.6 2.5	1.21	.01 .002	5.8 2.3	7.39	.08 .02	3.9 .53	1.55	.07 .03	1.6 .88	5.37	.15 .02	1.4 .1	1.04	.14 .03	.76 .11	.75	.11 .01	1.0 .09	2.28
5	.01 .01	16.8 5.2	3.46	.01 .004	15.6 2.6	3.59	.02 .01	4.8 1.5	9.71[B]	.07 .03	2.6 .55	11.18[B]	.13 .01	2.2 .06	0.16	.13 .03	.99 .11	2.61	.14 .03	1.1 .16	2.48

1. Attack Rate value given, standard error underneath.
2. Handling Time value given, standard error underneath.

A. A Chi-square value lower than 7.815 ($\alpha = 0.05$) implies no significant difference between observed and fitted values.

B. $0.01 < p < 0.05$

linear slope, the asymptote not being reached even at the highest prey density given.

Values for the handling time ($\underline{T_h}$) and attack rate (a) for all predator/prey combinations are given in Table 4:2 and Figs. 4:6 and 4:7. It is obvious from Fig. 4:6 that, in general, the handling time increases as prey size increases and decreases as predator size increases. This pattern supports that of Thompson (1975) who also reported handling time changing monotonically in the opposite direction for dragonfly nymphs feeding on Daphnia. The attack-rate surface however, is very different from that obtained by Thompson (1975). As the predator size increases the attack rate surface changes in a complex way (Fig. 4:7). For the first two predator instars (I and II) the maximum attack rate occurs on the smallest prey sizes (1 and 2). As the predator size continues to increase so the attack rate on each of the prey sizes increases. Unlike the previously published attack rate surface of McArdle and Lawton (1979), where the surface 'rolls over', i.e. the maxima are found in opposite corners with small predators attacking small prey and large predators attacking large prey, no such change is observed here. In the present study the maximum attack rate, rather than 'rolling' completely over, stops mid-way, i.e. at prey size 3.

Examining the surface in greater detail reveals that the maximum attack-rate for predator instar III is almost the same for prey size 1 and 2, that of predator instar IV is greater for prey size 2, while in the three largest predator sizes (instar V, adult female and male) the maximum attack-rate is found for prey size 3. As in the McArdle and

Fig. 4:6 The effect of predator and prey size on the handling time of R.dispar feeding on A.deanei. Exact numerical values are given in Table 4:2.

HANDLING TIME SURFACE

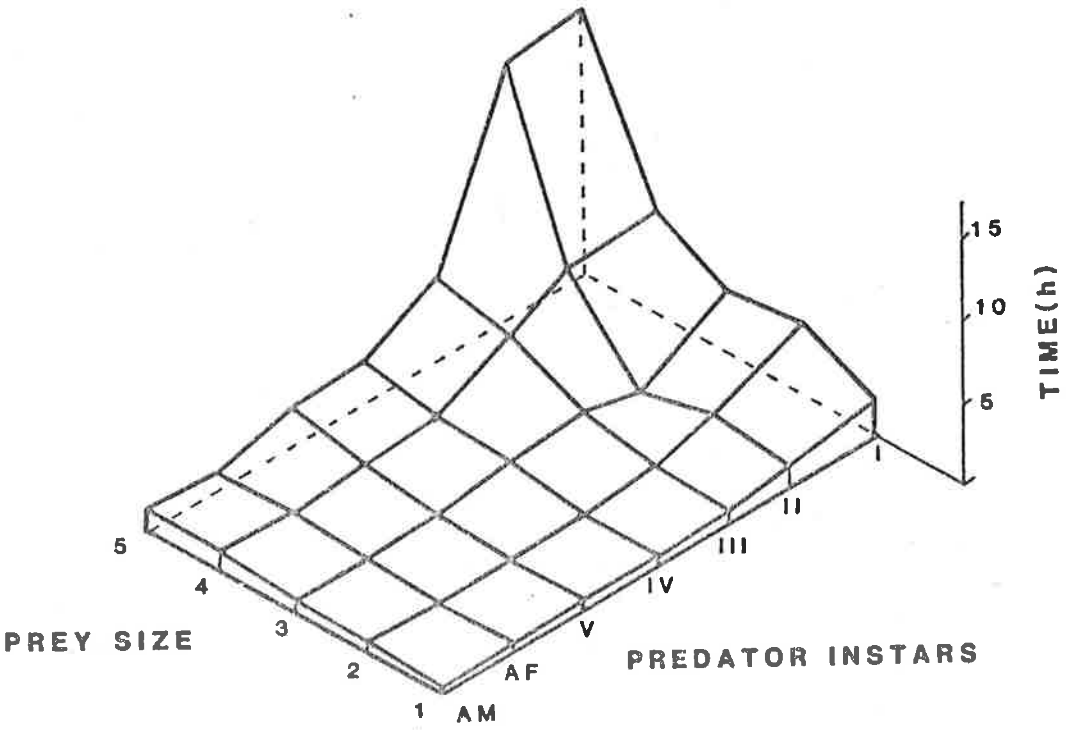
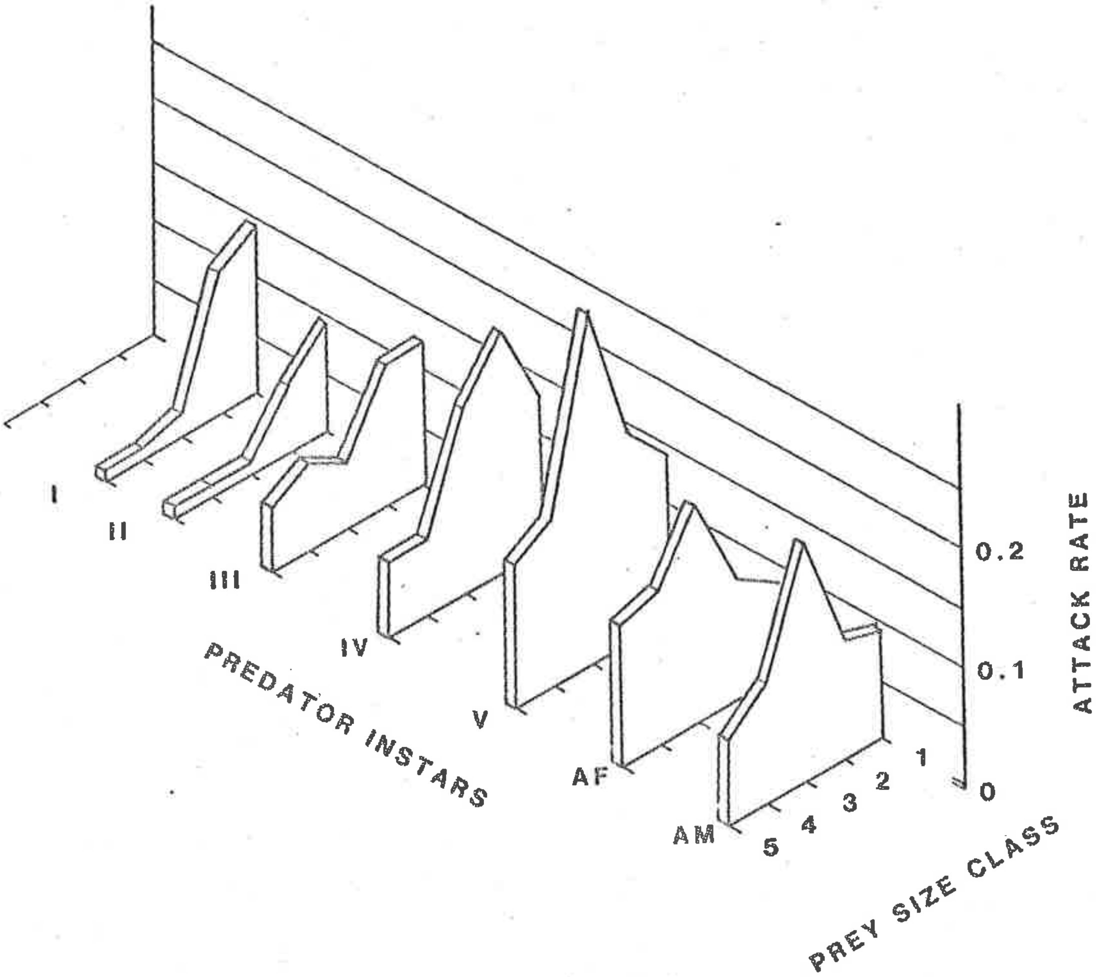


Fig. 4:7 The effect of predator and prey size on the attack-rate (a) of *R.dispar* feeding on *A.deanei*. Exact numerical values are given in Table 4:2.


I
II
III
IV
V
AF
AM
PREDATOR INSTARS
5
4
3
2
1
PREY SIZE CLASS
0
0.1
0.2
ATTACK RATE

Lawton (1979) study, predator instar V has the largest attack rate values over all prey sizes and the adult Ranatra have noticeably lower attack-rates for various prey sizes than instars V, IV and to some degree III.

4:5.4 Discussion

The apparently linear functional responses obtained for the fifth instars and adult Ranatra, feeding on the smallest prey sizes, requires comment before considering the overall changes in the attack-rate and handling-time for the various predator/prey combinations. It is interesting to note that for these larger predators exposed to the various prey densities that are found in the field (including the very dense aggregations) no plateau is reached in the response curve, and in fact resemble a Type 1 functional response.

The Type 1 response, much less common than Type 2, is not normally associated with insect predators, usually being characteristic of filter feeders. In a Type 1 response the predation-rate is directly proportional to the food concentration up to a particular concentration value which is a function of the predators handling efficiency. At low prey concentrations the handling component of the predator's behaviour does not interfere with the predation-rate, because it happens sufficiently quickly to remove all the food accumulated. Above a certain prey density however, the predator is unable to process the prey any faster. At such densities, therefore, it ingests food at a maximum rate, limited by its handling time. The Type 1 response is, therefore, an extreme form of the Type 2 response in which the handling-time exerts its effect not gradually but suddenly.

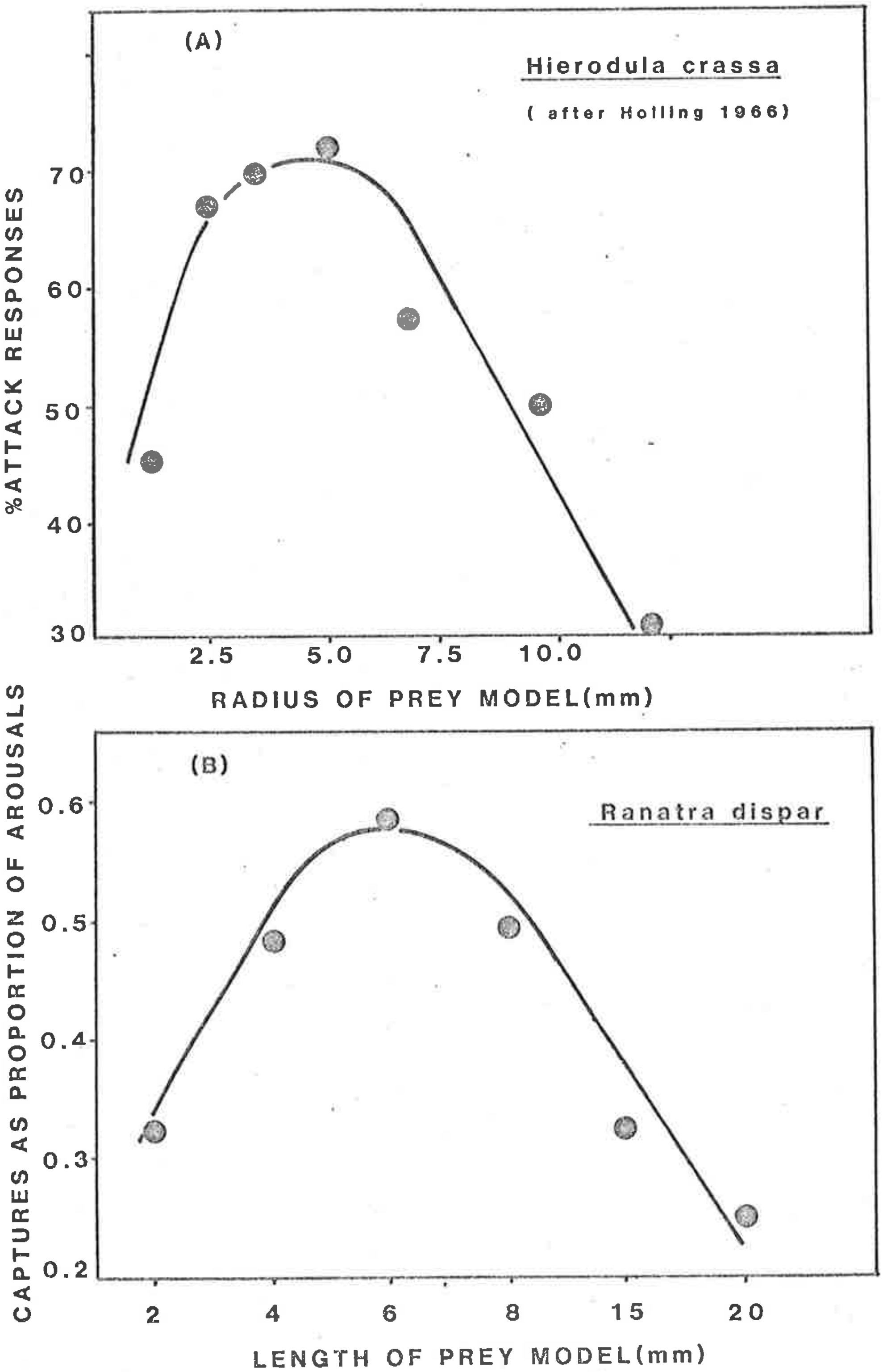
The present study shows that the larger Ranatra predators, when feeding on the small prey presented in densities resembling the natural situation, can process the prey at a rate which is not, as yet, restricted by 'handling time' constraints. It would be expected that, provided with a greater although unnatural density, saturation of the linear response would occur and a plateau would be reached. However, it is important to note that when using prey densities based on natural situations the same predator can exhibit different functional responses depending on the prey size. In the natural environment the predator may never encounter prey densities that are required to produce the plateau region of the curve.

As mentioned previously, very few data comparable to those in Fig. 4:6 and 4:7 have been published. The most complete are those of McArdle's and Lawton's (1979) attack-rate and handling-time surfaces for each instar of Notonecta glauca attacking four size classes of Daphnia magna as prey. For R.dispar the handling time surface is very similar to that reported by Thompson (1975). The attack rate surface however, is similar to that of Notonecta described by McArdle and Lawton (1979) except rather than the maxima being in opposite corners, the maxima are found about mid-way along the prey size axis for the larger predators (see Fig. 4:7). Slices through partial surfaces in the prey-size or predator-size planes for other species tend to suggest similar relationships (Hassell et al. 1976; Hassell 1978). In general, these results are to be expected. The larger the predator and the smaller the prey, the more the predator should be able to attack and eat, resulting in high attack-rates and short handling-times for large predators feeding on small prey. The reverse will also be true, with long handling times and low attack rates for small predators attacking and eating large prey. However, there must be a limit to this process, because all predators ignore prey that is very small or very large relative to their own size (Griffiths 1975; Salt 1967; Wilson 1975).

The effect of prey size on the proportion of encounters that initiated attack by adult female mantids (Holling 1964) and R.dispar (this work Chapter 3) are shown in Fig. 4:8 A & B. Obviously the attack-rate is determined not only by this proportion but also by the arousal distance of the predator to the prey and the encounter-rate between predator and prey (Holling 1965). Typically, the subcomponents (see Holling 1963; and later this chapter) contribute to the attack rate in different ways. Large prey may initiate a small number of attacks, few of which are successful (reducing a), but move about quickly, thus increasing the number of encounters (see Gerritsen 1980; Gerritsen and Strickler 1977; Vita et.al 1982), and being easy to observe (both of which increase a). McArdle and Lawton (1979) put forward the plausible assumption that although it could not be expected that changes in any one of the subcomponents would predict exactly what happens to the attack-rate, we may reasonably expect a values to first increase, plateau and then decrease with decreasing prey size, following the general pattern observed in Fig. 4:8 A & B. Furthermore, the turnover point might be expected to be at a small 'optimum' prey size in earlier (smaller) instars of the predator. Pertinent data supporting these inferences are provided, amongst others, by Dixon (1959), Dixon

Fig. 4:8 The effect of prey size on either (A) the percentage of encounters that initiated attack by female mantids (*Hierodula crassa*) or (B) the proportion of arousals resulting in a capture by female *R.dispar*.

(A) after Holling 1966


(A)
Hierodula crassa
(after Holling 1966)
%ATTACK RESPONSES
70
60
50
40
30
2.5
5.0
7.5
10.0
RADIUS OF PREY MODEL(mm)
(B)
Ranatra dispar
CAPTURES AS PROPORTION OF AROUSALS
0.6
0.5
0.4
0.3
0.2
2
4
6
8
15
20
LENGTH OF PREY MODEL(mm)

and Russel (1972), Glen (1975) and Wratten (1973). McArdle's and Lawton's own work (1979) with the Notonecta attack-rate surface also supported this hypothesis. A somewhat similar pattern is observed in R.dispar (see Fig. 4:7). For instars I to III and prey sizes 1 to 5 the maximum attack rate increases almost monotonically with increasing predator size and decreasing prey size. If there is an 'optimum' prey size beyond which the attack-rate starts to decline again it lies below (i.e. 'to the right of' in Fig. 4:7) Anisops prey-size 1. The plateau appears to be reached in Instar III however, and the decline in attack-rate for prey size 1 is very evident for instar IV. The shape of the surfaces for instar V and both adults is very much as predicted by McArdle and Lawton's (1979) hypothesis and also from the prediction of Fig. 3:22 in Chapter 3. Obviously the actual capturing pattern for different sized prey that is observed using live prey will not depend only on prey-length as Fig. 3:22. implies. Rather, a number of different characteristics of the prey itself will significantly influence the capture success.

The lower attack-rate observed for both adult sexes compared with instar V was also reported by McArdle and Lawton (1979) for Notonecta glauca. They suggested that food requirements of the last instar, which grow rapidly, are much higher than those of non-reproductive adults. Ellis and Borden (1970) also found that adult Notonecta undulata feeding on Aedes larvae ate considerably less on average than did instar V. As far as possible only non-reproductive Ranatra adults were used in the present experiments, so these data may support McArdle's and Lawton's hypothesis. However until comparative experiments are carried out using both non-reproductive and reproductive adults no conclusive statements can be made.

Attack rates and handling time surfaces are also useful to predict the relative proportions of several sizes of prey that each predator instar will take from a mixture of different sizes. Without exploitation, the number of prey of size class 1 eaten will be :

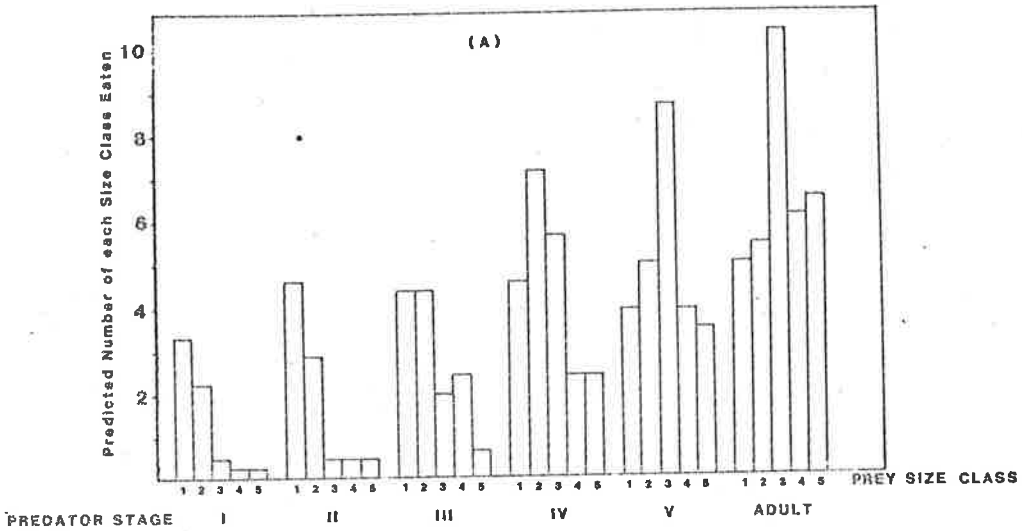
$$N_e = a_1N_1T_t/(1 + {}_i\Sigma_1 a_iT_{h_i}N_i) \qquad \ldots\ 4.14$$

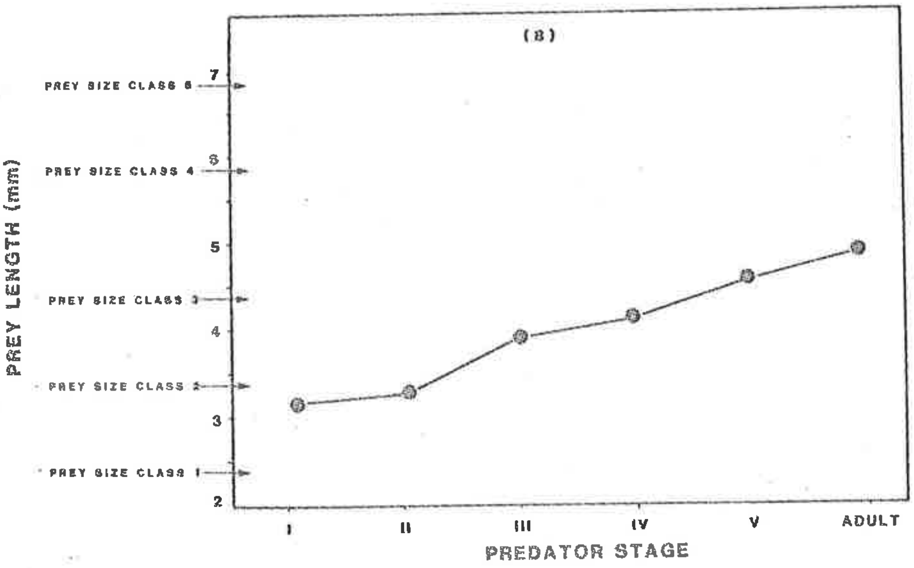
where there are n size classes, and the N_i is the number of prey available in the ith size class. *a*, $\underline{T_h}$ and T_t as defined previously (McArdle and Lawton 1979).
(The equation can be easily integrated to allow for exploitation, as shown by Lawton *et al*. 1974).
If *R.dispar* are given equal numbers of each of the five size classes of *A.deanei*, equation 4.14 predicts the number of each size class eaten by each predator stage will be as shown in Fig. 4:9 (A). The mean length of prey captured and eaten by each *R.dispar* stage can be calculated from the numbers eaten and is shown in Fig. 4:9 (B). Although the mean length of prey taken increases with predator size, the larger predators will take the smaller prey. The pattern of predicted sizes taken is similar to the results of McArdle and Lawton (1979) for *Notonecta* predator. In addition, other workers have presented results from real (as opposed to predicted) data on prey-size selection by a variety of different predators (see for example Adams 1980; Devonport and Winterbourn 1976; Malmquist and Sjostrom 1980; Pearson and Steinberger 1980; Sheldon 1969, 1980; Thompson 1978b; D.Wilson 1975; Winterbourn

Fig. 4:9 (A) The predicted number of each prey size class captured when equal numbers (n = 10) of each size class are presented at the same time to each predator instar and adult of *R.dispar*.

(B) The predicted mean length of prey captured by each predator instar or adult.

(See text for additional details and predictive equation).


(A)
Predicted Number of each Size Class Eaten
10
8
6
4
2
1 2 3 4 5
PREY SIZE CLASS
PREDATOR STAGE
I
II
III
IV
V
ADULT


(B)
PREY LENGTH (mm)
7
6
5
4
3
2
PREY SIZE CLASS 5
PREY SIZE CLASS 4
PREY SIZE CLASS 3
PREY SIZE CLASS 2
PREY SIZE CLASS 1
I
II
III
IV
V
ADULT
PREDATOR STAGE

1974 and additional references in Peckarsky 1982). Large predators have much broader niches in terms of prey size than smaller predators of the same species (Holling *et al*. 1976). This causes, as Wilson (1975) has suggested, an asymmetry in the competitive interactions of different sized predators. As McArdle and Lawton (1979) have pointed out, large predators eat things which are unavailable to small predators (large prey) but the reverse is much less true. If 'simple' attack-rate surfaces are found, as by Thompson (1978b) the effect will be particularly obvious. Even a more complex surface, for example that found by McArdle and Lawton (1979) for *Notonecta*, and *R.dispar* as found in this study provides only a partial relief from competition for the smallest predator instars, because the large predators still feed on the smallest prey. The same will probably be true for small instars of *R.dispar*. Size differences between successive instars may therefore provide only a poor means of reducing exploitation competition (Horn and May 1977).

How do the small instars of predators avoid intra-specific competition with larger individuals, apart from by simply being smaller? Two common features of the life-history patterns of predatory insects have been reported for Notonectidae. Successive instars of *Notonecta glauca* are staggered in time, so that large and small individuals very rarely occur together (reported in McArdle and Lawton 1979, p.273), whilst small instars of *N.hoffmani* may be spatially (but not temporally) separated from the adults (Murdoch and Sih 1978; Sih 1980). Instars of *R.dispar* are not staggered in time, all developmental stages being present in the same locality for most of the summer months (December to February, in Australia). However, examination of the spatial distribution of both R.dispar and A.deanei instars in the study area shows a very characteristic pattern, with the smallest instars concentrated in the shallower water around the perimeter of the pond and the larger instars found in the deeper water. These field results offer supportive evidences to Murdoch's and Sih's (1978) laboratory results concerning spatial distribution of Notonectidae, but perhaps more importantly provide additional evidence for reducing the intra-specific competition in insect predators by the utilization of different areas of the habitat. Interestingly enough, I have noticed that, not only do first and second instar prey (i.e. Size Class 1) provide a significant component of the diet of first instar predators but the shallow water areas (where both small instars of predator and prey are found) have, during the summer, dense aggregations of various macrozooplankton, predominantly ostracods. These provide an additional food source for both the prey and predator individuals. This spatial distribution of instars (for both prey and predator species) has the added important selective advantage (to the small insects) that it not only reduces the interference competition but also cannibalism which has been reported in Notonectidae (Fox 1975a,b,c; Murdoch and Sih 1978) and Ranatra fusca (Radinovsky 1964) and R.dispar (see Chapter 2).

These results demonstrate the multi-faceted selective forces that can operate in causing the observed spatial distribution of different developmental stages of predators. It is to be expected that selection will be operating to reduce the intra-specific competition in both the predator and prey species (the prey species used, Anisops deanei, is itself a predatory insect) in addition to it maximizing the probability of the various predator instars encountering the 'optimum' prey size that it can capture and eat. This highlights the care that must be taken in our 'identification' of proposed selective forces which result in the observed situation.

Obviously, as McArdle and Lawton (1979) point out, equation 4.14 is a simplification. In a natural mixture of prey of different sizes, the predator may not hunt or capture randomly (which is implied). Instead, the predator may 'select' profitable and discard or ignore unprofitable prey, using a far more complex mechanism than can be predicted purely from each functional response in isolation (Krebs 1977). The results from Chapters 3 and 5 suggest that this is undoubtedly true for R.dispar. In addition Blois and Cloarec (1983) have shown that R.linearis exhibits a density-dependent prey selection, with first instar nymphs showing a preference for small Daphnia while in larger predator nymphs the preference for big Daphnia increased. The selection was evident first when the relative densities for the preferred size-class were low, then when absolute densities were high, with the choice generally being made before striking.

Further discussion on prey-size selection falls outside the bounds of this present study, due in part to the lack of a solid-data base of selection in R.dispar when offered various prey size classes simultaneously. Time did not permit the completion of planned experiments, although initial results appear to support the predicted ones to a certain degree. Obviously further experimentation will shed light on the 'selectivity' of prey by a sit-and-wait predator.

This chapter sets out to examine the effect that prey density has on the numbers of prey eaten. Clearly, as the results show, progressively more prey are eaten as density increases until finally reaching a maximum. This being so, the questions that automatically come to mind are concerned with identifying particular attributes of both predator and prey that are involved in making this possible.

As discussed earlier, the two parameters widely used to describe the functional response are a, the attack-rate, and T_h, the handling-time. The overall values of a and T_h are a composite picture of the individual sub-components into which they can be divided (Holling 1963, 1965, 1966). Holling considers a to be a function of:

1. The reactive distance of the predator for prey, i.e. the maximum distance at which a predator will react by attacking prey,

2. the speed of movement of predator and prey, and

3. capture success, i.e. the proportion of prey, coming close enough to be attacked, that are successfully captured.

Handling time, T_h, was split into :

4. time spent pursuing and subduing each prey item,

5. time spent exploring and eating each prey, and

6. time spent in a 'digestive pause' after prey had been eaten during which the predator does not attack further prey.

Obviously a wide range of different variables will impinge on these factors, causing significant variation in both a and T_h. Nevertheless, using these sub-components, one can predict likely changes in T_h with prey and predator size more easily than similar predictions for a, because all the sub-components of T_h vary in the same direction (Thompson 1975); this is untrue for a. Thus, whereas prey that are relatively large will take longer to subdue, eat and digest (all causing an increase in T_h) (see Dixon 1959), these same prey may be seen or recognized further away (giving a rise to an increase in a), move faster (again increasing a) (Glen 1975), but escape more easily (leading to a decrease in a) (see also Wratten 1973; Brown 1974).

Chapter 3 has examined factors involved in the reactive distance and capture success of R.dispar. The following chapter (5) examines two features of R.dispar prey-capturing and feeding behaviour that have been observed and, it is believed, have a significant effect on the number of prey eaten. As mentioned above, particular features of the prey's behaviour, in addition to the predator's, are involved in determining the outcome of the interaction. Therefore Chapter 6 sets out to examine and identify some attributes of the prey's behaviour that play a significant part in the prey's encounter rate with the predator.

CHAPTER 5

THE EFFECT OF PREY DENSITY ON THE FEEDING AND PREY CAPTURING BEHAVIOUR

5:1 INTRODUCTION:

The way in which a sucking bug like R.dispar feeds on a single prey can be likened to the way in which a predator utilizes a patch of resource. As food is removed, so the quality of the patch decreases as the amount of food left in the prey (patch) and thus its ease of extraction (harvesting) declines.

Recently, two classes of models have been developed to examine the amount of food extracted from the prey (patch), the time spent in feeding and the effect of prey density.

MODEL 1 : OPTIMAL FORAGING (FEEDING)

Optimal foraging theory predicts that natural selection will favour those behavioural processes that maximize the net rate of food intake (Pyke, Pulliam and Charnov 1977). One important feature of this theory that has received a great deal of attention is the allocation of time to patches, i.e. how long a foraging predator should spend in a patch of resource of certain profitability (Krebs 1978, 1979; Pyke, *et al.* 1977; Schoener 1971) and what are the controlling factors. Two hypotheses have been suggested with respect to these factors. One suggests that the predator can monitor the relative resource qualities of patches in the environment and the subsequent selection of, and time spent in a patch is based on this information (e.g. Charnov 1976a; Krebs 1979; Krebs, Ryan and Charnov 1974). The other, which has been the subject of various models, predicts that the time spent in patches is dependent on some innate responses the predator makes to each patch on its own, and does not require the predator to have overall information about the environmental profitability (e.g. Hassell and May 1974; Waage 1979).

Recently, Cook and Cockrell (1978) extended optimal foraging theory to consider the amount of food extracted from a prey and the time spent in the extraction. They proposed that if some parts of a prey were easier (or more nutritious) to consume than others a predator could maximize the net rate of energy intake at high prey densities by selectively feeding on these parts. The mechanism suggested by Cook and Cockrell (1978) involves the predator's ability to 'measure' the time between prey captures, i.e. the intercatch-interval, the handling-time (feeding-time) for each prey being determined by this value, such that each prey should be discarded when the ingestion rate reaches the average rate of the energy harvest (i.e. similar to the marginal value theory of Charnov, 1976a). Since then this hypothesis has been further used to explain the variance in the allocation of time per patch and the partial consumption of prey in a number of different organisms (Giller 1980; Griffiths 1980a, b, 1982; Hodges 1981; Hodges and Wolf 1981; Kruse 1983; Sih 1980).

MODEL 2 : GUT-FILLING

The variability in feeding times and the partial consumption of prey can also be explained by a gut-filling model (Cook and Cockrell 1978; Gelperin 1971; Johnson, Akre and Crowley 1975). This model suggests that the predator continues feeding until particular regions of the gut are full. During the intercatch-interval food passes through the gut into a second region. The space in the fore-gut at the start of the next feeding determines how much food can be taken in and hence the feeding time.

The previous chapter showed the effect of prey density on the number of prey eaten. It is expected that mean intercatch-interval should fall as prey density increases. Both models predict that the mean handling-time (feeding time) should decrease with increase in prey density. The two models, however, will predict different relationships between individual intercatch-intervals and the subsequent individual feeding-times. No correlation between those two parameters is expected in the optimal foraging model, as the feeding-time for all prey items caught at each density is set at a value determined by the AVERAGE intercatch-interval. The gut-filling model, however, predicts a positive correlation, as the feeding-time on each prey is determined by the length of the intercatch-interval which determines the 'available space' in the gut.

The experiments reported in this chapter were designed to explore the relationships between feeding-time, ingestion-rate, prey-depletion and prey-density in the light of the above models; then to identify possible controlling mechanisms utilized and to compare these with other predators.

5:2 THE FEEDING DYNAMICS OF *R.dispar*

5:2.1 *Methods*

General - Adult female predators, *R.dispar* and adult prey, *A.deanei*, were used throughout the following experiments. (Time did not permit an analysis of other instars of the predator or sizes of the prey).

Before any feeding experiments predators were removed from the holding tanks, having been collected from the field during the preceding 48 hours, and fed a mixture of mosquito larvae, Notonectidae and various other aquatic invertebriates (Odonates, *Daphnia* spp. etc.) for 24 hours. They were then removed and deprived of food for between 48 and 54 hours, depending on the duration of the experiment. No predator was used for more than one set of experiments.

Adult prey were removed from holding tanks after being collected at the same location and time as the predators. During the holding period, prey individuals had access to a mixture of common food types (Mosquito larvae, *Daphnia* spp. smaller notonectid instars - normally II or III) at all times. By doing this it was assumed that irrespective of their past feeding history the prey animals would be at a comparable state as a food source at the beginning of the experiment.

Prey were removed from the tanks, gently blotted on absorbent tissue and weighed and measured as outlined in Chapter 2:2. Following the experiments, dead, partially digested prey were removed and weighed and measured by the same procedure. Prey carcasses were placed into individually marked glass vials and dried at 105°C for 48 hours and then reweighed. Because of the strong positive correlation between animal length and dry weight.(see Chapter 2:2) the amount of dry weight extracted could be calculated (± error) by subtraction.

Both predators and prey were randomly assigned to any of the treatments and all experiments were carried out in an insectary room of a constant temperature (22 ± 1.5°C water temp.) in light supplied by a bank of 3 'daylight' fluorescent tubes 1.5 metres above. A diffuser filter provided an even flooding of light of intensity 1200 lux at the water surface.

The term 'feeding time' and 'intercatch interval' are based on those of Cook and Cockrell (1978). 'Feeding time' is defined as the time from actual onset of feeding to termination on a single prey and has been adopted rather than the term 'handling time' of Cook and Cockrell (1978) to avoid confusion (see below). The 'intercatch interval' is defined as the time between successive captures, rather than the time from the termination of one feeding to the beginning of the next, because of the multiple prey capturing capability of R.dispar (see Section 5:3). In addition, when holding more than one prey, feeding can be interupted, thus enabling Ranatra to 'explore' the second prey. Normally the term 'handling time' includes these periods of exploration, and therefore to avoid confusion has not been used.

All times were measured with an electronic stopwatch. The terms 'ingestion rate' (weight of prey ingested/unit feeding time) in reference to predators artificially interrupted during their feeding activities, and 'marginal ingestion rate' (amount of prey ingested/unit feeding time) in reference to predators that were allowed to feed until they naturally discarded the prey have also been used as defined by Kruse (1983).

EXPERIMENT 1. To investigate the initial feeding behaviour (injection of toxins/digestive enzymes) and subsequent extraction of prey tissue, predators were allowed to feed on individual prey for fixed periods. Similar-sized prey an~~y~~imals ($\bar{x}$ = 13.37 mg., SD = 2.98 mg.) were selected and individually hand fed to adult *R.dispar* by carefully placing the notonectid in close proximity to the *Ranatra* with the aid of a pair of fine, soft forceps. Interruption of the meal (after 5, 15, 30, 60 and 105 minutes) was achieved by either grasping the prey carcass with forceps and removing it from the rostrum or gently grasping the predator and removing it from the water. This treatment always terminated feeding and the prey carcass could be removed. (Care was taken at all times in handling dead prey to prevent damage. This is particularly noticeable following long periods of feeding when the carcass has been exposed to the digestive enzymes and can literally 'fall apart'. During a few experiments this unfortunately happened and although the remains were collected and processed for other purposes, the results have not been included in the following analysis).

EXPERIMENT 2. The effect of initial prey-density on prey-depletion or utilization (percent of total available eaten) was also determined. Six densities (8, 12, 20, 24, 32, 40 prey/container) were tested. Notonectids were captured and the experiment terminated after the first 8 prey in every treatment had been consumed. Prey were removed, measured, weighed and dried as outlined previously. There were three replicates at each density.

EXPERIMENT 3. As prey-density increases, the intercatch-interval should decrease and both the optimal foraging and the gut-limiting hypotheses would predict a decrease in the feeding time per prey item. Therefore the effect of prey density was examined. Four prey densities (1, 10, 30, 60 prey/container) were tested. Predators treated with density 1 were hand fed as outlined in Experiment 1, while Ranatra treated with densities 10, 30 and 60, captured their prey naturally. As prey individuals were captured they were immediately replaced with a similar sized individual to maintain a constant density. As prey were discarded they were immediately removed, measured, weighed and transferred to the glass vial. Data was collected over an 8-prey catch sequence at each density.

5:2.2 Results and Discussion

Experiment 1. For an exterodigester like Ranatra, feeding may be able to be broken down into three stages. (1) Injection of venom/enzymes (2) digestive pause while enzymes act and (3) extraction of liquidified food (Griffith 1982). The results are consistent with this hypothesis when examining changes in wet weight of prey, Fig. 5:1. There is an initial weight increase when the 'cocktail' of venom and digestive enzymes is injected into the prey, (normally through an intersegmental membrane of one of the metathoracic legs - see Section 3:2) but within a few minutes the animal begins to extract food.

However, when examining changes in dry weight of the same animals, Fig. 5:2, prey body contents are apparently extracted from the onset of feeding. The ingestion rate decreases with time and supports the findings of Cook and Cockrell (1978), Giller (1980) and Kruse (1983). These results suggest that initially the prey contents are

Fig. 5:1 The change in wet weight of individual prey during feeding by adult *R.dispar*.

(+) Increase (-) Decrease

Value given is mean ± 95% Confidence Interval.

Curve is fitted by eye.

Figure in parenthesis indicates number of replicates.

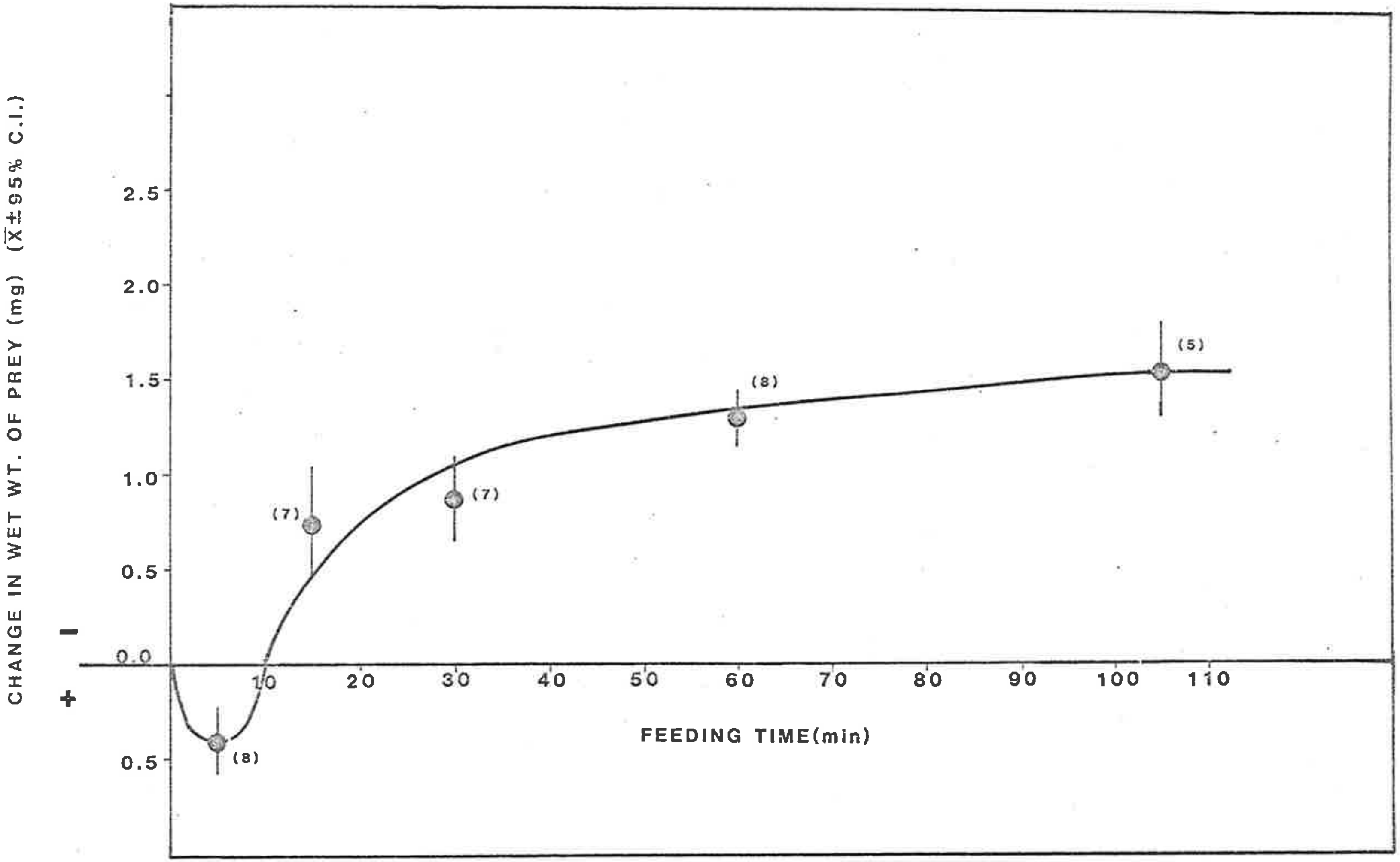
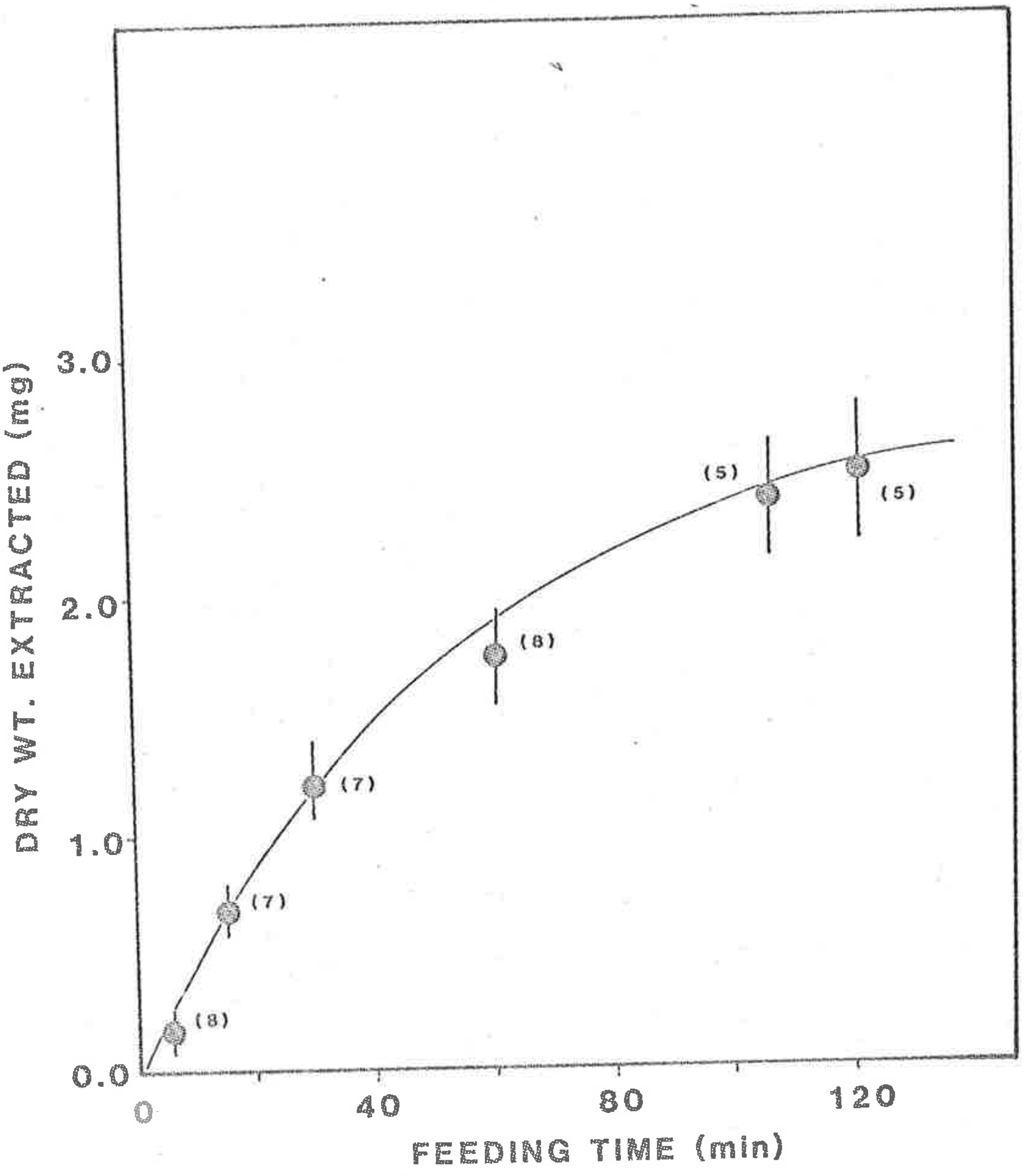

CHANGE IN WET WT. OF PREY (mg) ($\overline{X}$±95% C.I.)
2.5
2.0
1.5
1.0
0.5
−
0.0
+
0.5
10
20
30
40
50
60
70
80
90
100
110
FEEDING TIME(min)
(8)
(7)
(7)
(8)
(5)

Fig. 5:2 The cumulative dry weight of food extracted from individual prey with time spent feeding by *R.dispar*.

Value given is mean ± Standard Error.

Figure in parenthesis indicates number of replicates.


DRY WT. EXTRACTED (mg)
3.0
2.0
1.0
0.0
0
40
80
120
FEEDING TIME (min)
(8)
(7)
(7)
(8)
(5)
(5)

quickly ingested, but that the yield per unit feeding time decreases as the predator continues to feed. A one-way ANOVA suggested that the mean rates of extraction at different stages of feeding were not the same ($F_{5,26} = 6.72$, $P = 0.0004$) (Fig. 5:3). The SNK Multiple Range Test ($\alpha = 0.05$) revealed that extraction rate did significantly increase during the first 15 minutes before decreasing, although even after 30 minutes feeding the rate of extraction was still marginally, although not significantly, higher than the initial extraction rate. The rate of extraction then decreased almost linearly as the feeding session continued. This phenomenon is quite different from what has been previously reported for sucking insects and the significance of it will be discussed shortly.

Fig. 5:4 shows a comparison of the amounts extracted as measured by both wet weight and dry weight determination. Initially an impossible situation seems to exist, with the dry weight curve exhibiting higher values at the different interrupt times. This suggested that external water may have been passing into the prey as the feeding session continued, especially as R.dispar changes the location of the feeding site in the prey's body (see Section 3:2) on numerous occasions. This phenomenon was later confirmed as outlined in Section 5:2.

Cook and Cockrell (1978) found that in the back swimmer, Notonecta glauca, feeding on mosquito larvae, there appeared to be immediate extraction of food from the prey with no evidence of a digestive stage. In contrast to this, Griffiths (1982) measured changes in wet weight of prey, following capture by ant-lion larvae, and argued

Fig. 5:3 The change in mean rate of dry weight extracted from a single prey with time spent feeding by *R.dispar*.

Value given is mean ± Standard Error.

Means with same letter are not significantly different (SNK Multiple Range Test, α = 0.05).

Figures in parenthesis indicate number of replicates.

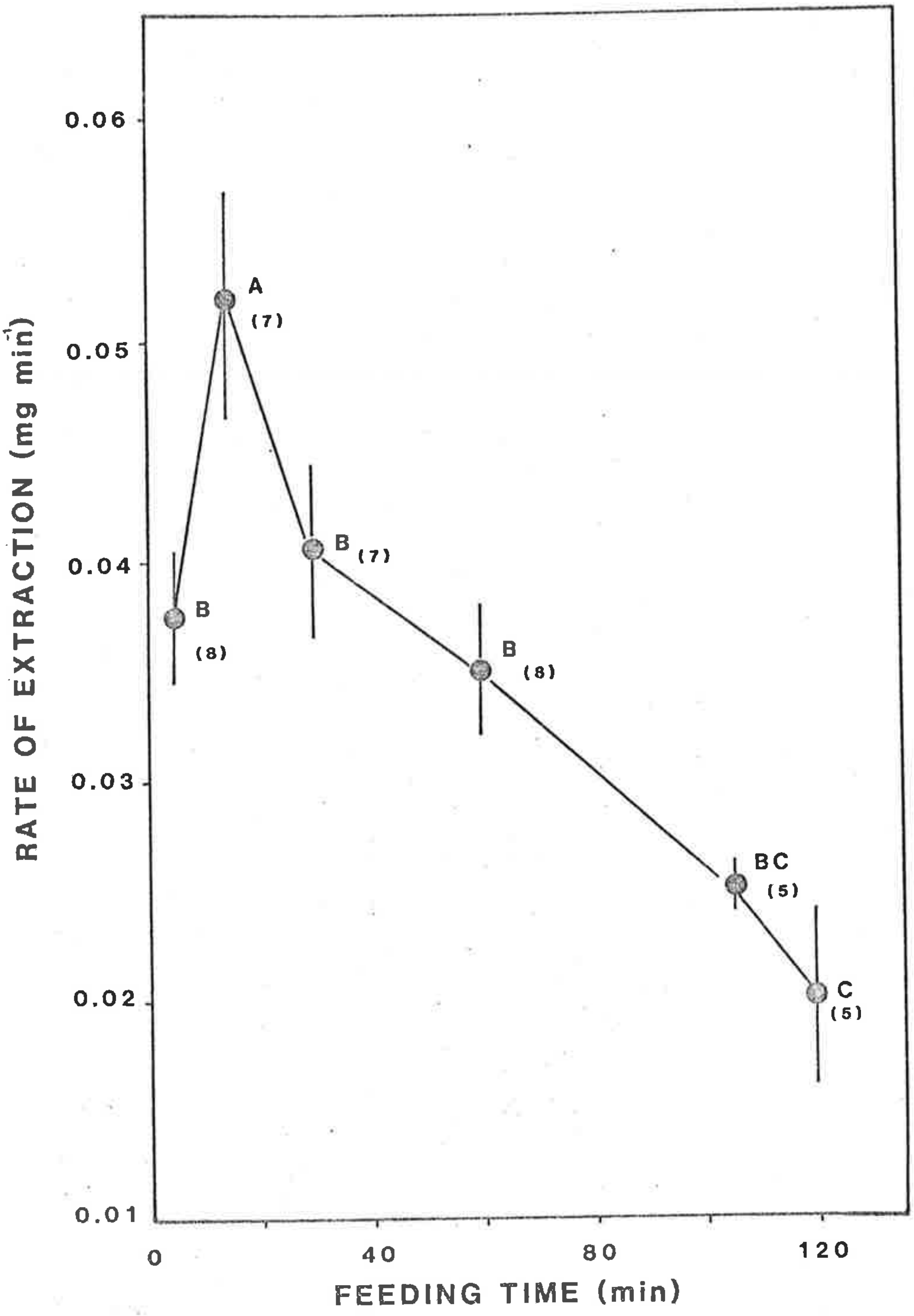

RATE OF EXTRACTION (mg min^{-1})
0.06
0.05
0.04
0.03
0.02
0.01
0
40
80
120
FEEDING TIME (min)
A
(7)
B
(8)
B (7)
B
(8)
BC
(5)
C
(5)

FIG. 5:4 A comparison of the weight change in individual prey during feeding by R.dispar as measured by both wet and dry weight.

Values given are mean ± 95% Confidence Interval.

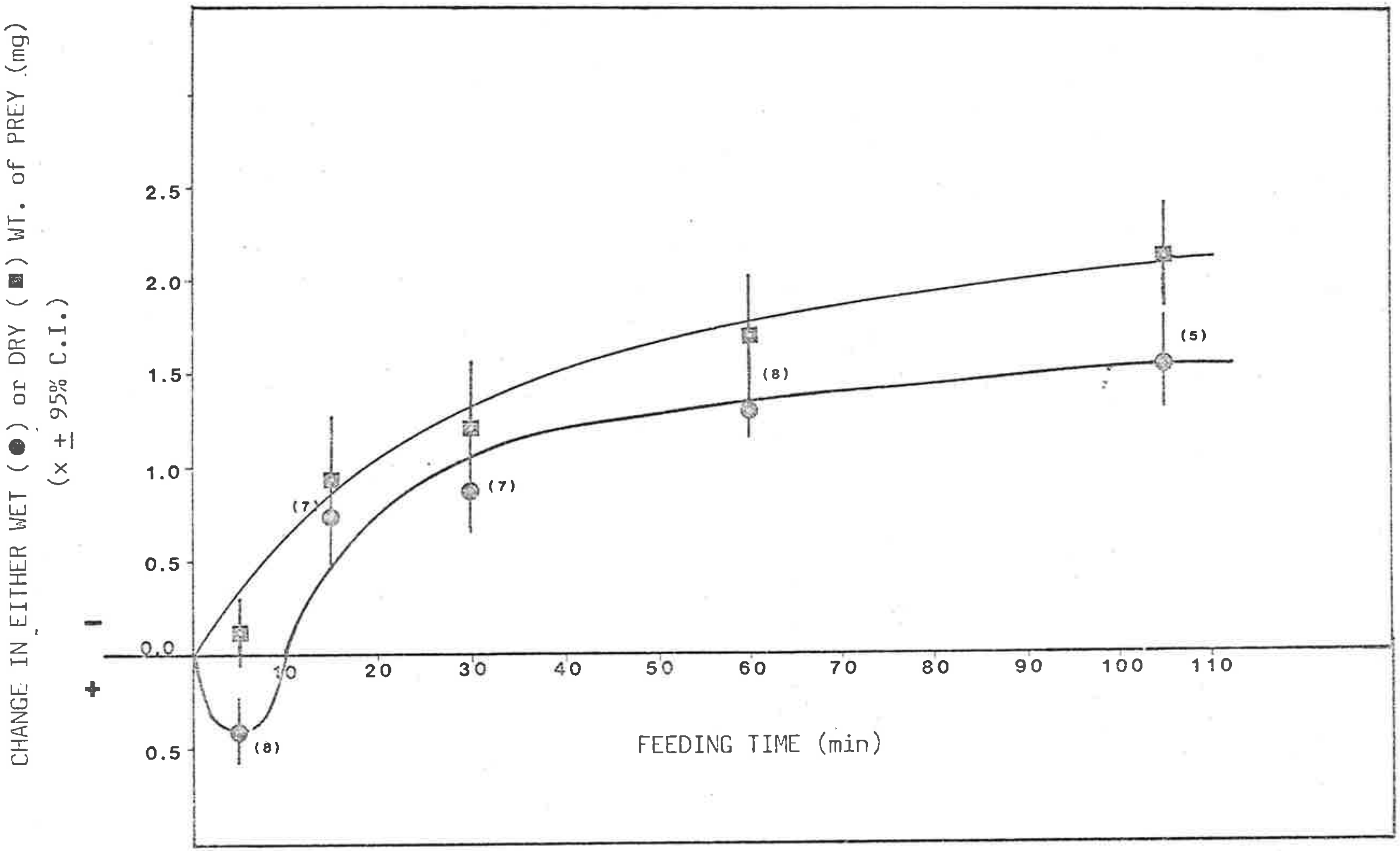
Figures in parenthesis indicate number of replicates.

Both curves are fitted by eye.

(●) Change in Wet Weight

(■) Change in Dry Weight

(See also Figs. 5:1 and 5:2 and text for additional details).


CHANGE IN EITHER WET (●) or DRY (■) WT. of PREY (mg)
(x ± 95% C.I.)
2.5
2.0
1.5
1.0
0.5
−
0.0
+
0.5
10
20
30
40
50
60
70
80
90
100
110
FEEDING TIME (min)
(7)
(7)
(8)
(8)
(5)

that the observed increase in prey weight was due to the injection of venom and enzymes. In addition, he pointed out that Cook and Cockrell's (1978) conclusion of immediate extraction of prey contents by N.glauca was probably partly due to their use of dry weights which would make enzyme injection difficult to detect; although he did conceed that the two animals may use different extraction techniques.

The results from R.dispar, using both wet and dry extraction weights, show that the two patterns observed in separate animals (wet weight in ant-lion, Griffiths 1982 and dry weight in Notonecta, Cook and Cockrell 1978) can occur in the same animal. What is believed to be happening in R.dispar is that in addition to pumping enzymes/toxins into the prey, samples of the prey tissue, probably haemolymph, are withdrawn at the same time. Because of the design of the experiment, with the first interruption not happening until 5 minutes after the onset of feeding, the injection/extraction dynamics over the first few minutes is unknown. It is quite possible that prey contents are extracted within the first few seconds (see references in Pollard 1973) and continue in a cyclic fashion, the changes in prey weight being either masked by the injection of saliva or well within the bounds of the error factor associated with weighing (see Chapter 2). However, the observed extraction of dry material may indicate a modified probing behaviour response, which is common in some other sucking insects, (Hennig 1968; McLean and Kinsey 1968; Zettler 1967) that can be likened to a pre-pouring wine taste, to ascertain the type and quality of the prey. In addition, it has been shown (see references in Miles 1972; Pollard 1973) that for many sucking organisms the release of quantities of enzymes is stimulated by the presence of food. The fact that R.dispar is submerged under the water may require this predator first to sample the potential food source, not only to allow identification via appropriate chemoreceptors in the mouth parts but also to cause adequate salivation. This hypothesis is speculative, although examination of Fig. 5:4 does show, in addition to an increase in wet weight of prey at the beginning of the meal, that prey contents (as measured by dry weight differences) are being extracted from the beginning of the meal.

EXPERIMENT 2. There was a negative relationship between increasing prey density and prey depletion (Fig. 5:5). Following an arcsine data transformation, a one-way ANOVA showed that the mean percentages eaten were significantly different ($F = 7.745$, df 5,12, $P<0.05$) among the six densities. Mean comparison tests (SNK Multiple Range Test, $\alpha = 0.05$) revealed that R.dispar feeding on prey at the two higher densities were significantly more 'wasteful' than those fed prey at the lower densities, whereas the remaining mean percentages eaten at the lower densities were not significantly distinguishable as Fig. 5:5 shows.

EXPERIMENT 3. It was suspected that the results from Experiment 2 related to differences in feeding-time per prey among the six densities; for this reason, the effect of density on feeding time was explored.

Fig. 5:6 shows the relationships between mean feeding time, mean intercatch interval and prey density, where mean intercatch interval and feeding time per prey both decreased as prey density increased. These findings support those of Cook and Cockrell (1978) and Giller (1980). In addition, Fig. 5:7 shows the subsequent expected relationship between the mean dry weight extracted per prey, the feeding time and the

Fig. 5:5 The relationship between initial prey density and prey depletion as measured by percent consumed. Value given is mean ± Standard Deviation. Figure in parenthesis is number of replicates. Means with same letter are not significantly different (SNK, Multiple Range Test, $\alpha = 0.05$). The percent consumed was calculated from the first 8 prey eaten at each density.

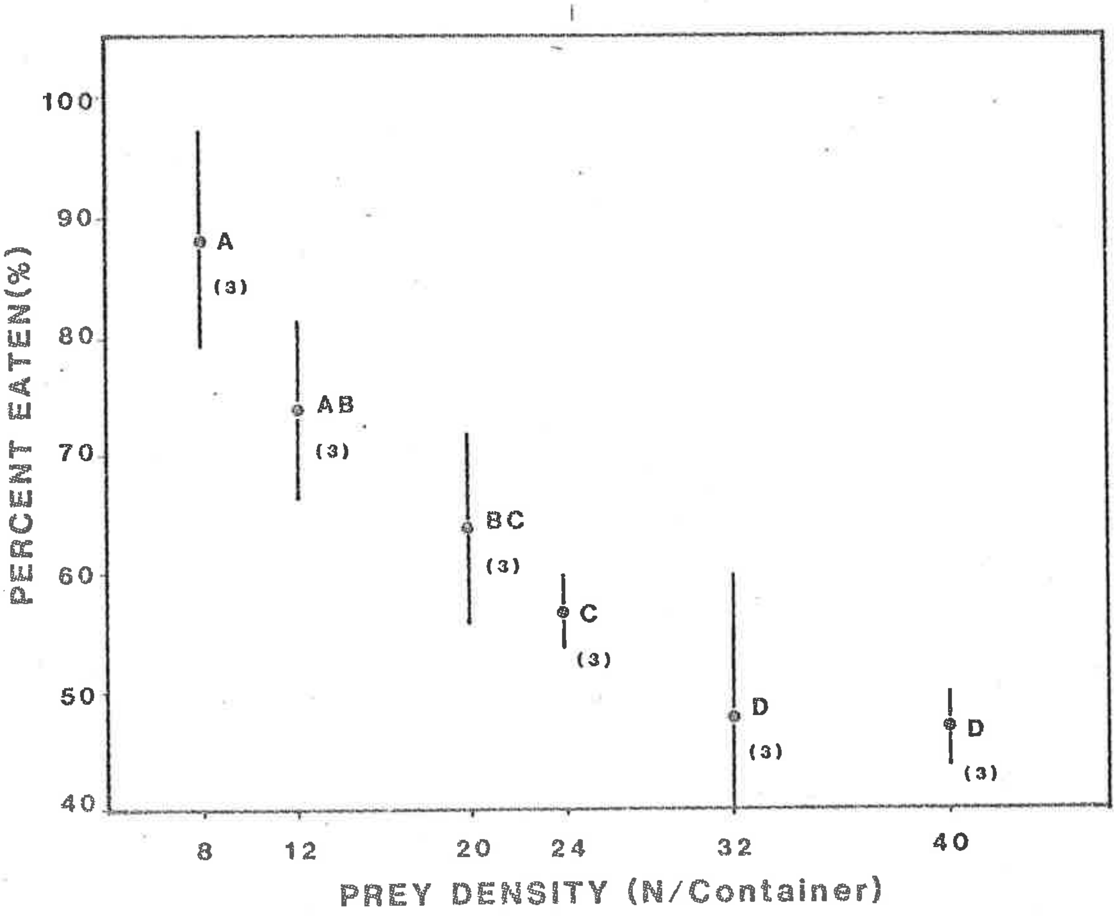

100
90
80
70
60
50
40
PERCENT EATEN(%)
A
(3)
AB
(3)
BC
(3)
C
(3)
D
(3)
D
(3)
8
12
20
24
32
40
PREY DENSITY (N/Container)

Fig. 5:6 The effect of prey density on the mean feeding time (○) and mean intercatch interval (●). Value given is mean ± 95% Confidence Interval. (For clarity only the upper half of the confidence interval is given for the feeding time mean, and lower half of the intercatch interval mean).

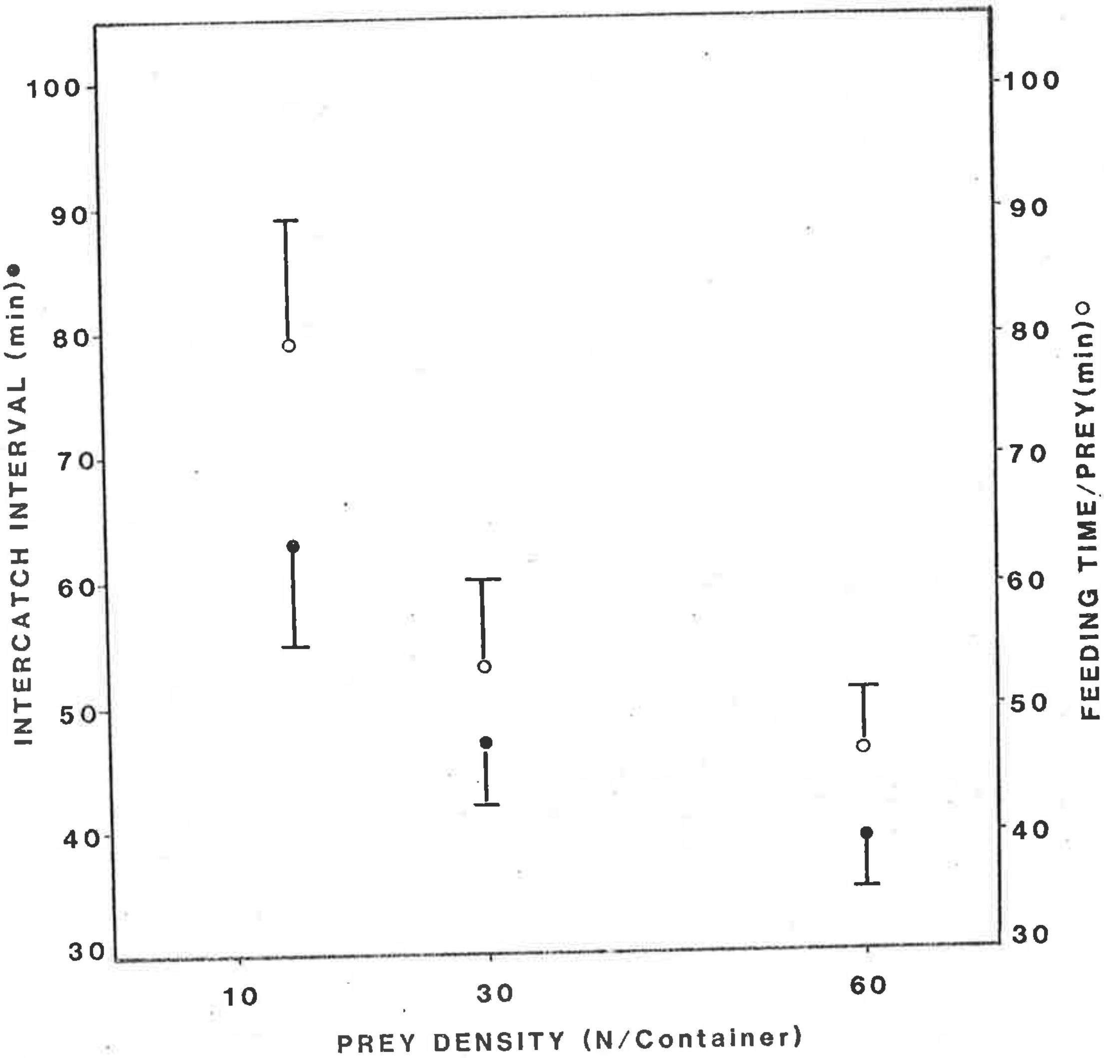
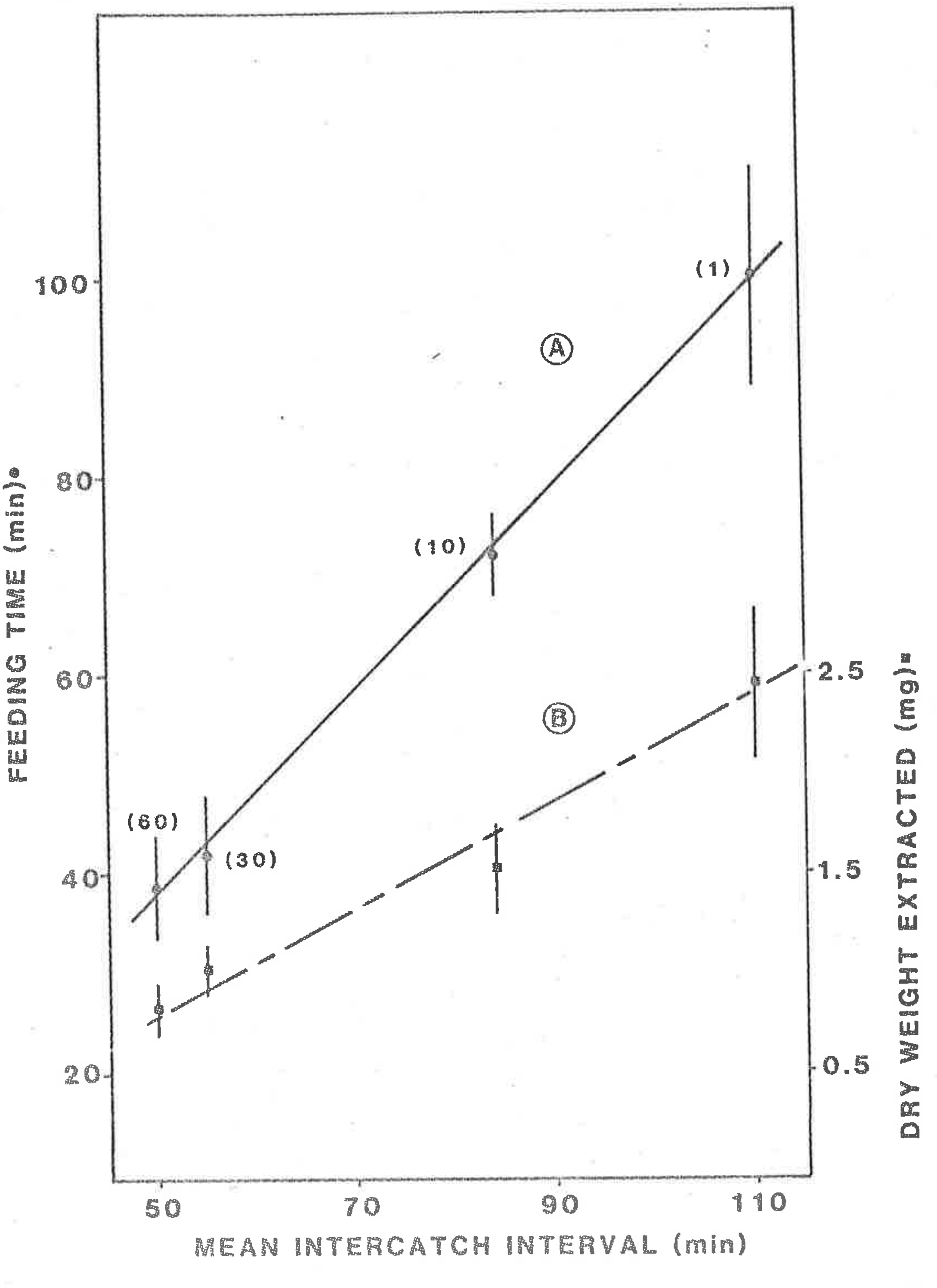

INTERCATCH INTERVAL (min)●
100
90
80
70
60
50
40
30
FEEDING TIME/PREY(min)○
100
90
80
70
60
50
40
30
10
30
60
PREY DENSITY (N/Container)

Fig. 5:7 The effect of Mean intercatch interval on (A) the time spent feeding (● mins) and (B) the dry weight of prey extracted from each prey (■ mg). Values given are mean ± Standard Error. Figure in parenthesis indicates prey density (number/container). Both slopes are significantly different from zero. (For A; $t = 30.6$, $p<0.01$; for B; $t = 11.33$, $p<0.01$).


(1)
Ⓐ
(10)
Ⓑ
(60)
(30)
100
80
60
40
20
FEEDING TIME (min)*
2.5
1.5
0.5
DRY WEIGHT EXTRACTED (mg)*
50
70
90
110
MEAN INTERCATCH INTERVAL (min)

intercatch interval. As the prey density decreased, from 60 to 1 prey per container, so the resultant intercatch interval and feeding time increased, and in conjunction with this the average dry weight extracted per prey also increased.

Both the 'optimal foraging' and the 'gut-filling' model predict these quantitative trends, however. In order to distinguish between them, the individual feeding times are plotted against their corresponding intercatch interval. When the density treatments are broken down into pairs of observations in this way, as suggested by Cook and Cockrell (1978), there is no correlation between intercatch interval and feeding time as found by the Spearman Rank Correlation Coefficient (r_S) Test, as shown in Table 5:1.

TABLE 5:1. Correlation between individual intercatch interval and individual feeding time as assessed by Spearman Rank Correlation Coefficient Test.

Density	r_s	p	
10	0.0175	.47	)
30	-0.1077	.28	) Not Significant
60	0.1464	.21	)

When examining the feeding time of each capture through the capture sequence it was found that the mean feeding time per prey decreased throughout the capture sequence at all prey densities tested.

Unlike that reported by Giller (1980) analysis of variance indicated the prey density did significantly affect the values for the mean feeding times. Fig. 5:8 shows the mean feeding time decay curve for the various prey densities.

The relationship between mean feeding time and prey density (Fig. 5:6) can be predicted by a combination of the decline in mean handling time through the catch sequence (Fig. 5:8A) and the number of prey killed and eaten at each density (Fig. 5:8B) as demonstrated by Giller (1980). The form of the relationship is very characteristic of the functional response curve as discussed in Chapter 4. At low prey densities, only the first few prey in sequence were caught, resulting in a high mean feeding time for that density. As the density increased, where larger numbers of prey were caught, correspondingly lower mean feeding times resulted. Similar declines in feeding times through a sequence of prey captures have been reported by Ellis and Borden (1970), Fox and Murdoch (1978) and Giller (1980) for notonectids.

Fig. 5:9 shows the overall effect of the extraction rate and duration of feeding on one prey item at different prey densities. At the higher prey densities, although spending less than half the time on a prey item, compared with the low density, the predator is still able to obtain almost 60% of the available prey contents before discarding the prey.

DISCUSSION

The results presented above are very much in support of the optimal foraging model. Overall, the ingestion rate of R.dispar adults

Fig. 5:8A The decay in mean feeding time ± 95% Confidence Interval through an 8 prey catch sequence.

(●) Prey density of 1 per container.

(○) Prey density of 30 per container.

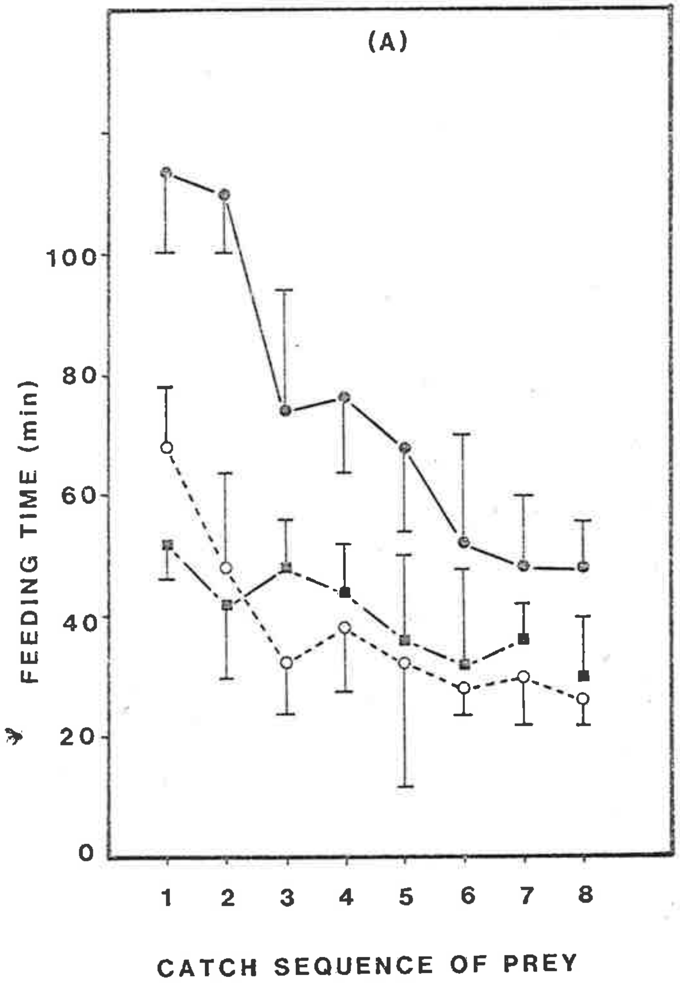
(■) Prey density of 60 per container.

For clarity only the top or bottom half of the confidence interval has been given for each mean.

(The curve for the 10 prey per container density followed the same trend but has been left out of the figure because of the same sample size with the associated large variance that overcomplicated the figure).

Fig. 5:8B The relationship between the number of prey eaten during the first 5 hours of the experiment and prey density.

Value given is mean ± 95% Confidence Interval.


(A)
FEEDING TIME (min)
100
80
60
40
20
0
1
2
3
4
5
6
7
8
CATCH SEQUENCE OF PREY

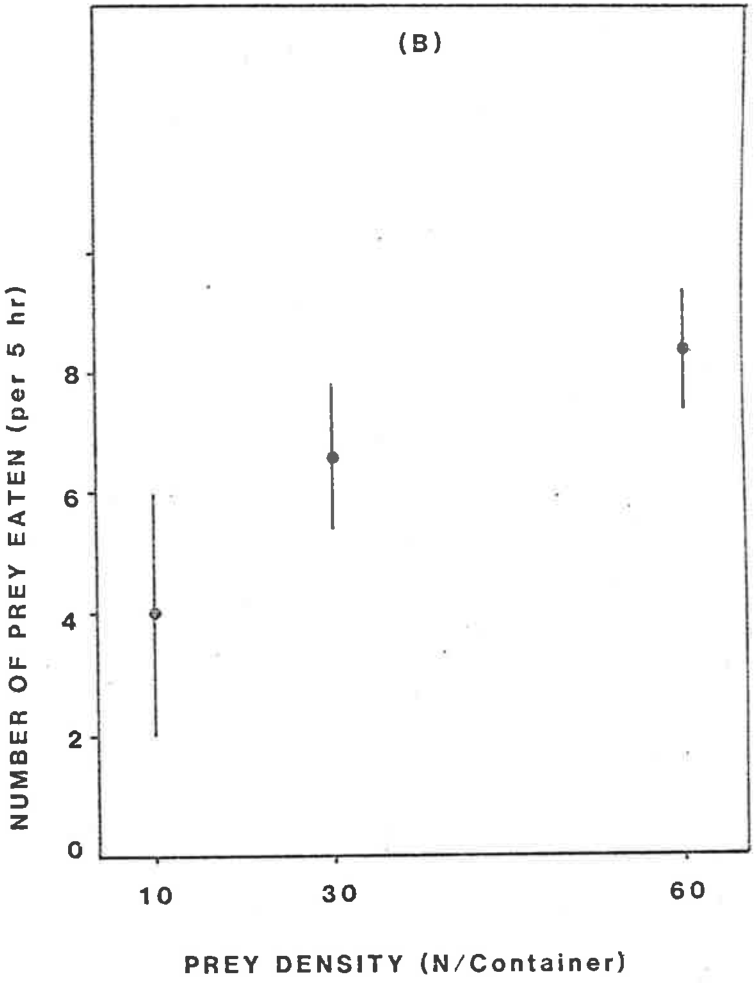
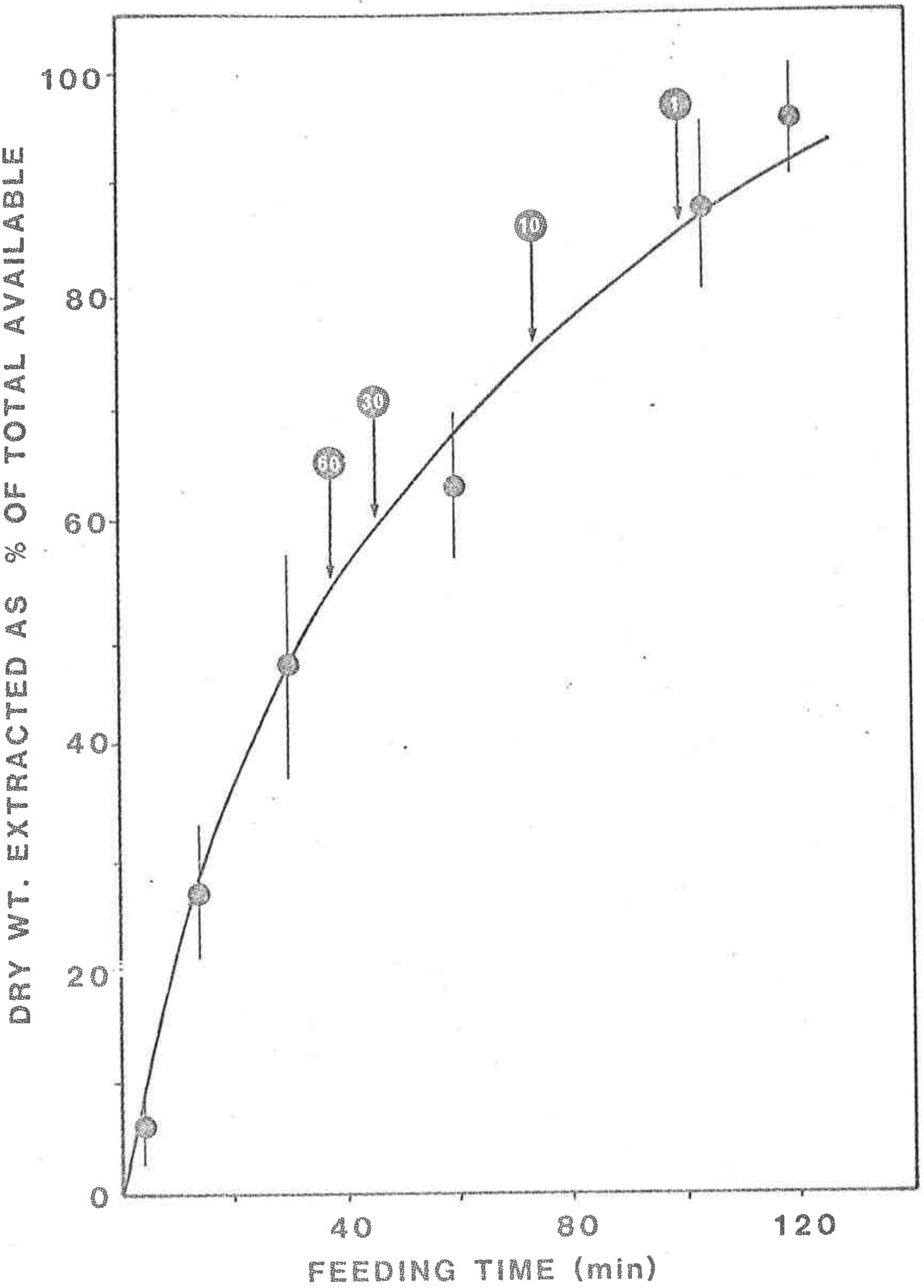

(B)
NUMBER OF PREY EATEN (per 5 hr)
8
6
4
2
0
10
30
60
PREY DENSITY (N/Container)

Fig. 5:9 The change is mean (± Standard Error) amount of dry weight extracted from a single prey with feeding time of *R.dispar*. Weight extracted is expressed as a percent of total dry weight of prey available. The arrows indicate the mean feeding time per prey at four different prey densities.

Prey density shown in parenthesis.


DRY WT. EXTRACTED AS % OF TOTAL AVAILABLE
0
20
40
60
80
100
40
80
120
FEEDING TIME (min)
60
30
10
1

feeding on an individual prey item decreases as the prey is consumed (although to begin with there is an increase as Fig. 5:3 shows). This decrease is in agreement with those reports for the other heteropteran predator *Notonecta* by Cook and Cockrell (1978) and Giller (1980) and for the coleopteran larvae, *Dytiscus fasciventris* (Kruse 1983). Because the ingestion rate decreases with time spent in a patch, optimal foraging theory predicts that as the probability of prey capture increases (increasing prey density in this case) the feeding time on individual prey items will decrease and the ultimate result would be an overall increase in the rate of food intake. Predators fed individual prey items had consistently longer feeding times (and therefore, lower marginal ingestion rates) per prey item than did predators which captured prey items naturally from constant densities of 30 and 60 per container (see Fig. 5:8). These results support those of Kruse (1983) and are in agreement with one of the predictions of optimal foraging theory (Charnov 1976a; Parker and Smith 1976), that is, the richer the habitat, the shorter the handling or feeding time per patch. Unlike Kruse (1983) however, the results shown in Fig. 5:7 and Table 5:1 suggest that the mean intercatch interval may very well be the mechanism responsible for this optimization for *R.dispar*. It suggests that the predator is reacting to the average profitability of the environment rather than the specific level of food in the gut which has resulted from the length of the intercatch interval. The optimal feeding model therefore gains support over the gut limitation hypothesis. This does not necessarily mean that the gut is never limiting and that hunger is not affecting the feeding-time; rather gut capacity defines the limits within which the optimal feeding strategy can occur (Cook and Cockrell 1978).

Because the ingestion rate at first increases and then decreases (Fig. 5:3) with time spent feeding on an individual prey item, the amount of food taken per unit feeding time is increased when each prey item is not fully exploited. One way that the predator could assess the prey density is for it to monitor the prey that are swimming in the close vicinity. This has recently been suggested by Kruse (1983). The results tend to suggest that at the lower prey densities *R.dispar* is able to differentiate between encounter rates but at higher densities it is unable to do so. This may of course be due in part to the experimental constraints imposed on the predators. When they were hand-fed individual prey (Density 1) no other prey were present and the optimal strategy would be to exploit the prey individual more completely.

The influence and assessment of encounter rates with prey by *R.dispar* is explored more fully in the next two chapters.

5:3 EXPERIMENT TO DEMONSTRATE THE PASSAGE OF WATER INTO THE PREY DURING FEEDING BY R.Dispar

5:3.1 Introduction

As mentioned in Section 5:2 Experiment 1, examination of both the wet weight and dry weights extracted from a single prey showed an apparently contradictory state to exist with higher values for dry weight being found. This suggested that as the feeding period continued on a single prey, water from the external environment was passing into the prey and artificially inflating the wet weight. This of course would lead to low estimates of the amount of wet weight extracted from the prey.

In addition, other observations tended to support such a hypothesis :

(i) Normally notonectids are buoyant and must swim against this natural buoyancy.

(ii) Notonectids killed artificially in boiling water always float.

(iii) Notonectids that have been fed on for long periods by R.dispar tend to sink when released.

(iv) The carcass shows no shrinkage or distortion following long feeding periods, quite the opposite in fact, with the abdomen normally showing signs of distension.

To test this hypothesis of external water moving into the carcass, possibly through previous feeding sites, the following experiment using a fluorescent dye, Acridine Orange, was carried out.

5:3.2 EXPERIMENT 1

5:3.2.1 Methods

A. Pilot Experiment : In order to ensure that the fluorescent dye would not naturally pass into and be taken up by tissues, a number of animals were tested as controls. From a 1% stock solution of Acridine Orange 1g/100 ml, three dilutions (0.1, 0.2 and 0.5%) were made up. One adult A.deanei was placed into 10 ml of each dilution and left for 6 hours. Following this the animal was removed, carefully blotted on absorbent tissue, taken through a series of ten washes of distilled water, killed in boiling water and immediately dissected and examined under U/V light. Five replicates of each treatment were used. Concurrently 6 adult R.dispar were placed in separate 1 litre beakers filled with either a 0.1 or 0.5% solution of Acridine Orange. Into each beaker one adult A.deanei was placed, and observed continuously for any noticeable variation of the normal swimming behaviour of A.deanei or the capturing behaviour of R.dispar. Following capture the predators were allowed to feed until they naturally discarded their prey, upon which the carcass was immediately carefully removed with a pipette, blotted on absorbent tissue, washed as before and immediately dissected and examined under U/V light. There were three replicates for each dilution used.

5:3.2.2 Results

(1) Control Prey Animals - following examination under U/V light no obvious fluorescence was observed in the internal tissues or haemolymph for any of the dilution treatments. There was fluorescence, however, in parts of the exoskeleton, especially on the legs and around the posterior tip of the abdomen. The animals treated with the higher concentrations of dye showed more intense fluorescence.

Prey animals that had been fed on, all showed signs of internal fluorescence, especially those prey that had been caught in the 0.5% solution. Again, there was fluorescence in the main body cuticle and legs. There were no obvious changes in either predatory behaviour of R.dispar or swimming behaviour of A.deanii. The mean (± SD) durations of feeding were 117 ± 21 min. and 106 ± 31 min. for the 0.1% and 0.5% dilutions respectively. A t-test showed that they were not significantly different ($t = 1.96$, df 5, $p > 0.05$).

It was concluded that although not permitting a quantitative assessment to be carried out, the technique allowed a gross identification of water movement.

5:3.3 EXPERIMENT 2

5:3.3.1 Methods

The design of the experiment was the same as that outlined in Section 5:2.1 except that predators were held in 1 litre plastic beakers filled with a 0.5% solution of Acridine Orange. Single prey were introduced and, following capture, the predators were allowed to feed for a pre-determined period before interruption. The location of all feeding sites was noted and the duration of each feeding period was recorded using an electronic stopwatch. Following the removal of prey, the carcass was treated as before. The interruption times were 5, 10, 20, 30, 60 and >100 minutes and there were 3 replicates for each time.

5:3.3.2 Results

Fluorescence was observed in all prey animals that had been fed on for longer than 20 minutes. Only one of the replicates interrupted after 10 minutes showed very slight fluorescence. Table 5:2 summarises all the results which suggest that as the meal continues, in conjunction with the change of feeding sites, external water passes into the prey's body.

5:3.4 Discussion

The results are consistent with the hypothesis that during feeding on a prey item by R.dispar water from the external environment

TABLE 5:2

FEEDING INTERRUPTION TIME (mins)

	5			10			20			30			60			>100		
Replicate	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Fluorescence Present	-	-	-	-	-	+	+	++	+	++	++	+	+	++	+++	+++	+++	++
No. of feeding site locations	1	1	1	1	1	3	2	3	2	2	3	2	1	4	5	9	11	7
Location of 1st Site[1]	RL	RL	RL	RL	RL	RL	RL	RL	RL	RL	RL	RL	Ab	RL	RL	RL	RL	RL
Duration (mins.)	3	4	4	3	3	2	4	5	6	6	3	4	60	4	3	4	2	3

1. RL = (Rear) Metathoracic Leg. Ab = Abdomen.

The effect of meal length on (i) the number of feeding site changes on prey body and the subsequent presence or absence of Acridine Orange Dye in prey body. The fluorescence rating was a subjective classification by on the spot comparison between prey contents.
(-) indicates no fluorescence present.

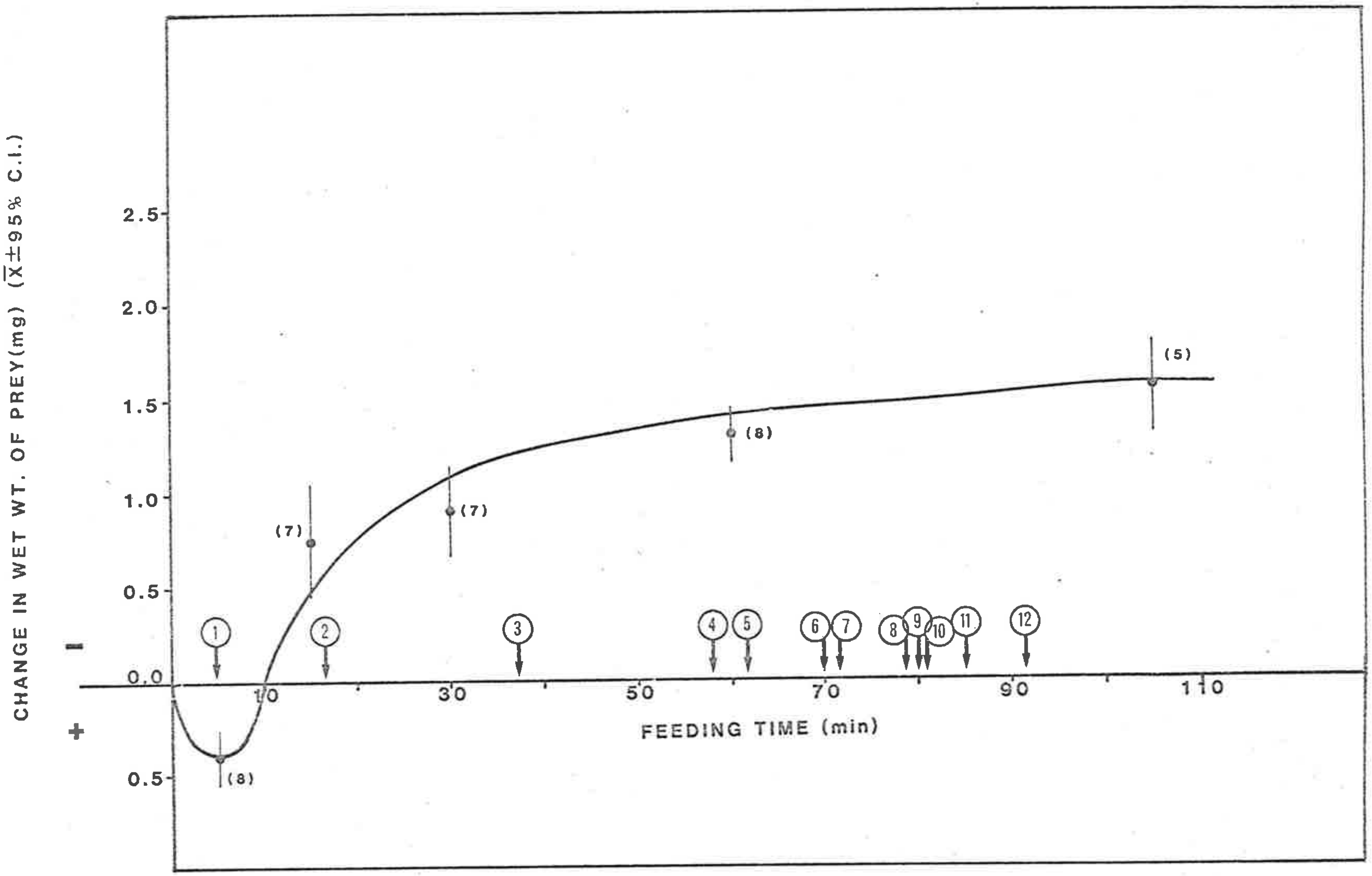
can pass into the prey's body. However, it appears that this is very dependent on the number of feeding site changes during the meal that the predator makes. As previously demonstrated in other studies in this work, there is a strong correlation between duration of meal and the number of feeding site changes. Previous data collected on 60 different individuals were re-analysed to provide the number of feeding site changes and the duration at each site, (these observations were made while conducting other feeding experiments when a prey item was fed on until naturally discarded). Fig. 5:10 shows the wet weight extraction curve (reported earlier Fig. 5:1) with the mean site change indicated on the feeding time axis. As the duration of the meal increases the rate of site changes increases, this being particularly noticeable after about 60 minutes of feeding. It would appear that during feeding water may be passing into the prey carcass either through the feeding sites or damaged intersegmental membranes that result from puncturing or tearing by the stylets or by the combined effect of manipulation and the digestive enzymes present in the prey. This in turn would cause the discrepancy between the observed extraction weights in the wet and dry calculations.

The fact that water could be passing into the prey's body during feeding also introduces some interesting physiological and behavioural factors. The obvious diluting effect following long periods of feeding could be used to provide a stimulus to cease feeding and discard the prey. Obviously, due to the design of the experiment, which was purposely left simple, no quantitative measurements could be taken and used to calculate rates of flow. In all likelihood, the use of such a crude method of measuring such small quantities of water flow would be

Fig. 5:10 The change in wet weight of individual prey during feeding by *R.dispar* along with the number of feeding site changes during the feeding period. Value given is mean ± 95% Confidence Interval; figure in parenthesis indicates number of replicates.

The mean duration from commencement of feeding at each site was calculated from additional experiments. (See text for additional experiments).

Feeding Site Number	$\bar{x}$ Duration (min) (from commencement of feeding)	Range	n
1	4.2	2 to 6.4	60
2	16.8	8 to 31	51
3	36.9	17 to 42	44
4	58.2	31 to 71	44
5	62.0	38 to 90	40
6	70.0	61 to 111	28
7	72.6	63 to 105	17
8	77.5	70 to 92	17
9	80.0	70 to 95	16
10	81.2	74 to 101	15
11	85.0	75 to 107	10
12	91.8	80 to 107	4


CHANGE IN WET WT. OF PREY(mg) ($\bar{X}$±95% C.I.)
2.5
2.0
1.5
1.0
0.5
0.0
0.5
−
+
10
30
50
70
90
110
FEEDING TIME (min)
(8)
(7)
(7)
(8)
(5)
①
②
③
④
⑤
⑥
⑦
⑧
⑨
⑩
⑪
⑫

quite unsuitable, and would probably require radioactive labels and a far more controlled experiment.

However the fact remains that the evidence is very much in agreement with the idea that as R.dispar feeds on the more complex prey (in overall shape and structure) the opportunity exists, over time, for water to pass into the prey. The rate of flow of water may in turn be used indirectly as a physiological stimulus on the current quality of the prey, a topic very much in discussion at the present time. Gibb (1962), Krebs (1973) and Charnov (1976a) have each formulated different hypotheses concerning the mechanisms that govern the allocation of time to patches. Both Gibbs (1962) and Krebs (1973) predict that the marginal rate of food intake (the rate of intake at the time predators opt to depart from patches) will increase with patch quality. They differ however in that Gibb (1962) proposes that the amount consumed per patch remains a constant, regardless of patch quality, whereas Krebs (1973) suggests that the time spent per patch remains constant. In contrast, Charnov (1976a) predicts that both the time spent and the amount consumed per patch are positively correlated with patch quality. Consequently, the rate of food intake at the time a predator leaves a patch is suggested to remain a constant over patch quality, i.e. all patches should be reduced to the same marginal rate. Charnov's hypothesis has recently been supported by Hodges (1981) and Kruse (1983).

While the present work does not attempt to offer evidence for any of the above hypotheses (different patch or prey qualities were not offered, e.g. small and large prey) it is felt that it provides some evidence of a possible physiological mechanism by which R.dispar can assess the state of the patch and, depending on other associated variables react to the stimulus in the optimal way.

5:4 MULTIPLE PREY CAPTURE AND HANDLING OF R.dispar

5:4.1 Introduction

Three distinct but interrelated forms of prey capture have been observed in Ranatra dispar (Figs. 5:11, 5:12, 5:13).

TYPE 1 - A single prey is caught and once feeding has commenced, no further attempt is made to catch another. Only after discarding the old carcass is a new prey caught.

TYPE 2 - 2 prey are caught, the second while the predator is feeding on the first. The second prey may be caught by either one or both raptorial legs, the first prey remaining 'speared' on the stylets during feeding (see Chapter 3). If both legs are used the prey can remain held by both or transferred to one leaving the second leg free. On cessation of feeding on the first prey, the carcass is discarded and the second prey brought to the rostrum for exploration and feeding. Once the stylets are in position another prey can be caught.

TYPE 3 - 3 prey are caught, both the second and the third whilst the predator is feeding on the first. The third prey is caught by the second free raptorial leg mentioned in Type 2. As in Type 2, as each prey is utilized and discarded subsequent exploratory/feeding movements take place with either of the prey held. (In some cases predators have been seen to switch between the two during both exploratory and/or

Fig. 5:11 Diagramatic representation of Type I prey capturing behaviour of *R.dispar*.

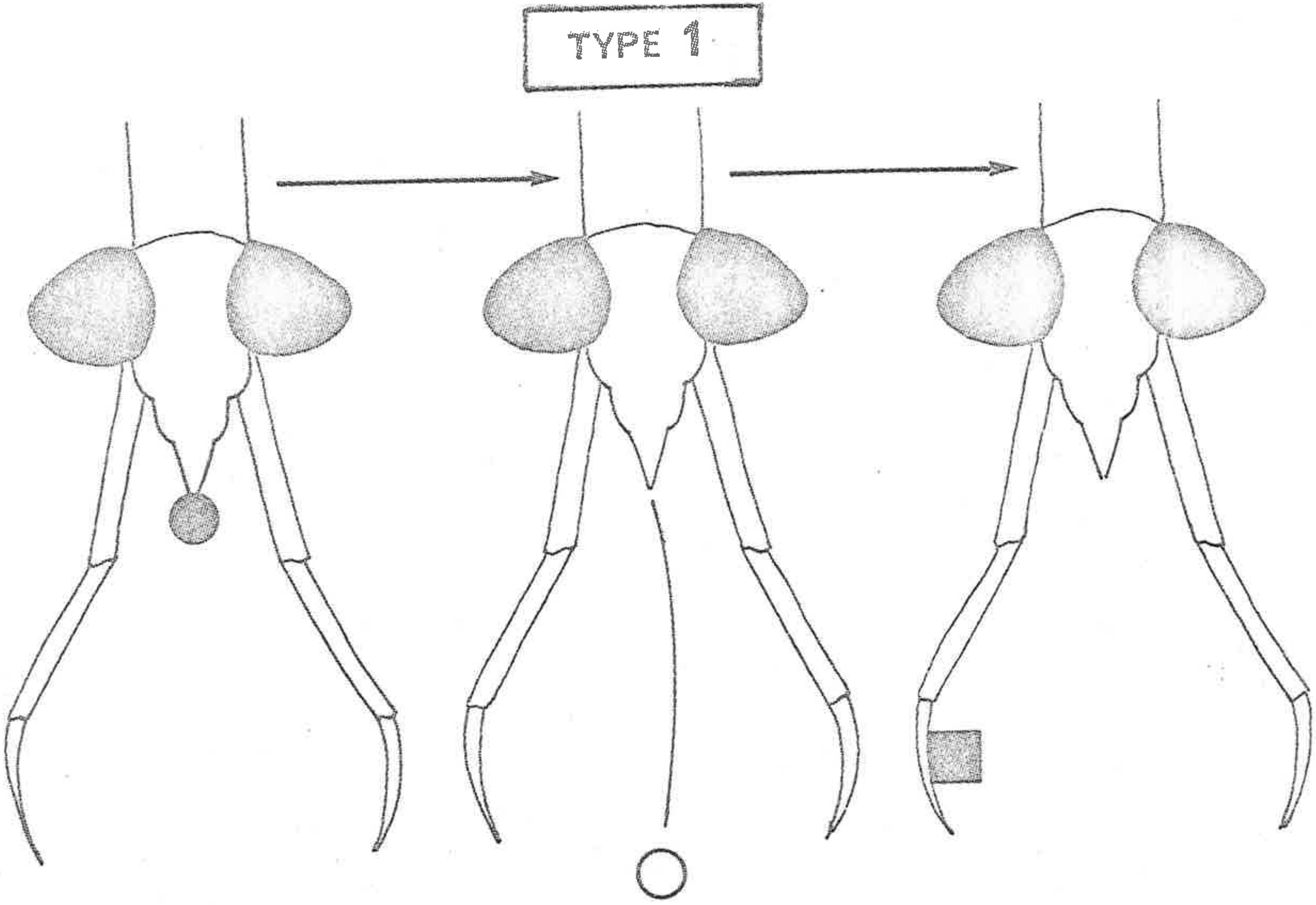

TYPE 1

Fig. 5:12 Diagramatic representation of Type 2 prey capturing behaviour.

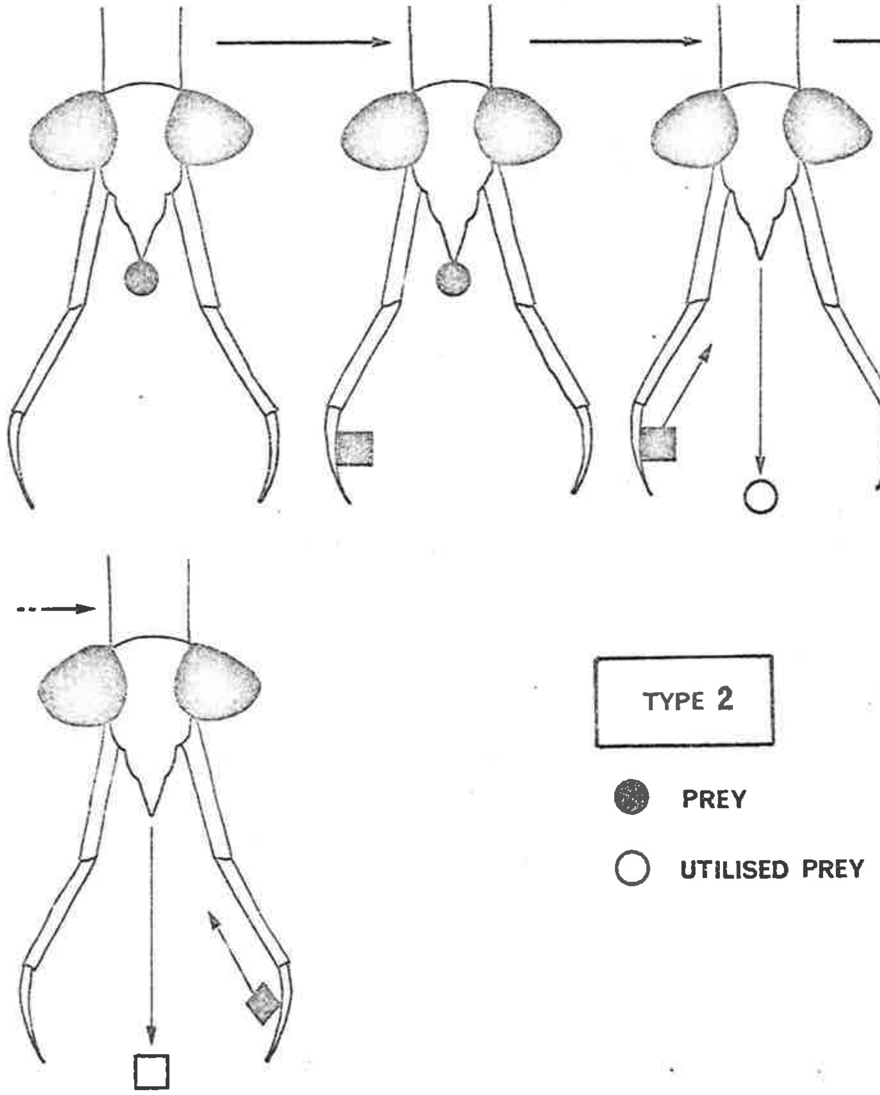
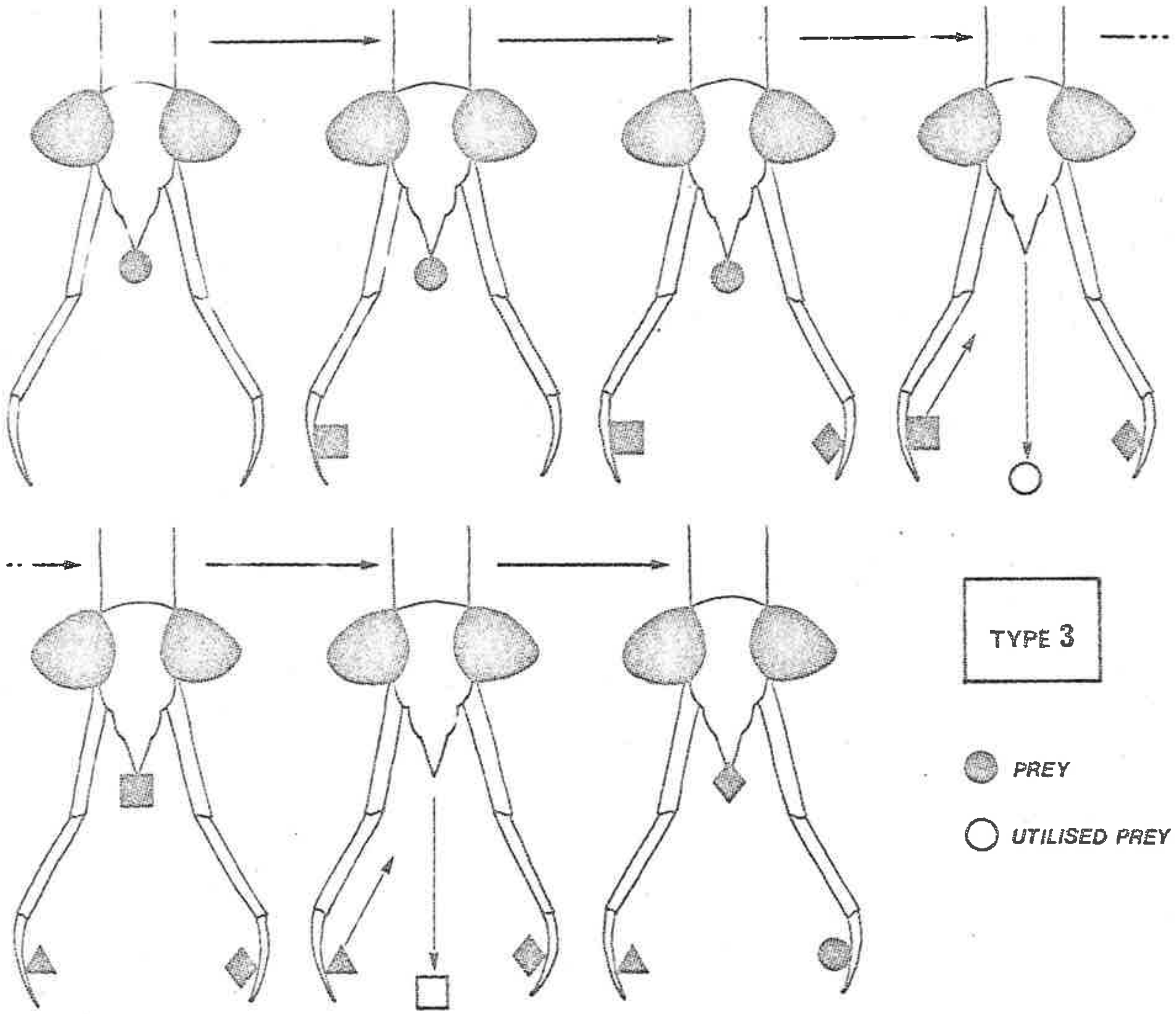

TYPE 2
● PREY
○ UTILISED PREY

Fig. 5:13 Diagramatic representation of Type 3 prey capturing behaviour.


TYPE 3
PREY
UTILISED PREY

feeding stages although the incidence is rare, < 5% in over 150 separate observations). A new prey can then be caught with the second raptorial leg.

The incidence of such behaviours was believed to be more likely at high prey densities (in association with the related increase in encounter rate). Obviously more than one prey must be encountered during a feeding period for the behaviour to be exhibited. However, it was considered to be of importance in investigating this phenomenon to see if these behaviours were purely random in any one feeding period or if they followed a sequential pattern and if so was the behaviour correlated with any identifiable variable. Food deprivation has previously been shown to significantly affect capture and feeding behaviour therefore the following experiment was carried out.

5:4.2 Materials and Methods

As the behaviours had been observed in a number of different instars of R.dispar, 3 different developmental stages were chosen for investigation.

Predators : Instars IV and V and adult females were selected from individuals that had moulted at least 36 hours (normally 48 hours) before being used in the experiments. They had access to an excess of natural prey of various sizes for 2 to 3 days and then were removed from the food tanks and fasted for either 0, 12, 24 or 48 hours.

PLATE 5

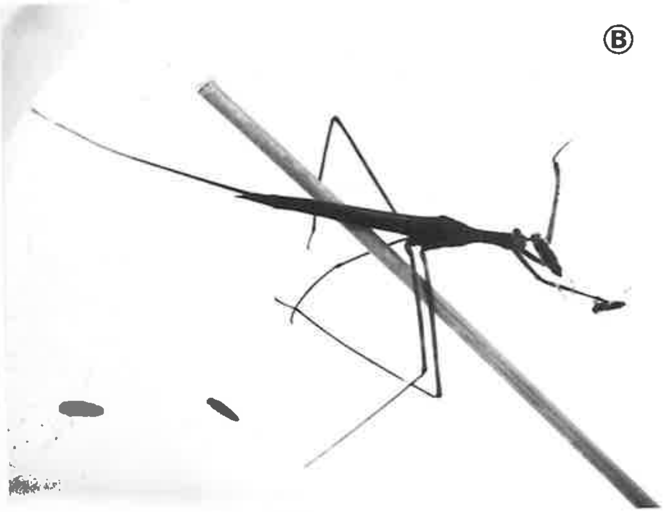
Multi-prey capturing behaviour of adult female R.dispar.

A. Type 1

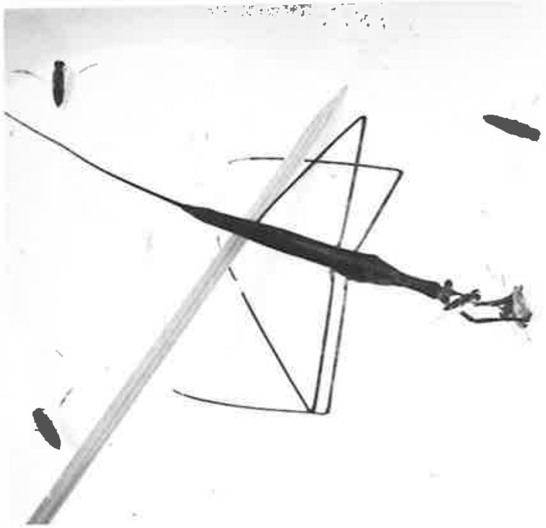
B. Type 2

C. Type 3

Ⓐ



Ⓑ



Ⓒ

Prey : Adult Anisops deanei were used in all experiments. They were chosen to be of comparable size ($\bar{x}$ = 6.8 mm, Std. Dev = 0.4, Range 5.7 to 7.9).

Following fasting the individual predator was introduced into a 1 litre translucent plastic beaker filled with 800 ml of filtered, dechlorinated tap water. A wooden satay stick (2mm diameter x 200mm), weighted at one end, provided a support/foraging site. The predator was allowed 30 minutes to settle, but normally took up the characteristic prey capture posture (see Section 3:2) after a few minutes.

Prey were added carefully along with water to make up the quantity in the beaker to 1000 ml. Two densities were used, and either 12 or 20 prey were introduced, which iniated the beginning of the experiment. As each prey was captured a new individual of similar size was added, maintaining the density. Observations were carried out in either of two ways :

(i) By a narrative recorded onto a continuously running tape recorded, with times being taken by an electronic stopwatch; or

(ii) By time-lapse movie photography. The camera was positioned vertically above 4 containers that could be monitored simultaneously. One frame was taken every ten seconds. Prey were not replaced as they were caught in these experiments. Replaying the film frame by frame permitted analysis to be carried out to the nearest 10 seconds, a negligible factor considering previous observations.

The availability of subjects restricted the number of replicates, the number observed is shown in Table 5:3. The duration of each experiment was normally nine hours (540 minutes).

TABLE 5:3. Number of Replicates for each developmental stage and fast treatment.

	0h		12h		24h		48 Fast Time	
Prey Density	12	20	12	20	12	20	12	20
Pred. Instars								
IV	2	3	4	2	2	3	3	4
V	6	6	8	8	10	10	12	12
Adult ♀	3	2	3	4	3	3	3	3

5:4.3 Results

The same basic pattern of behaviours was exhibited by the 3 predator stages and, in addition, the two densities showed no significant effect between them. As a result of this and the low number of replicates in both the Instar IV and Adult treatments; only the results from the V Instar are presented.

Table 5:4 summarises the effect that food deprivation has on whether the predator captures more than one prey at the same time.

TABLE 5:4 The effect of fasting on the likelihood of the predator exhibiting multi-prey capture. The number in parenthesis indicates the number of replicates observed.

FAST TIME (h)	Type 1	Type 2	Type 3
0 (6)	Yes (6)	No	No
12 (8)	Yes (6)	Yes (2)	No
24 (10)	Yes (10)	Yes (8)	Yes (2)
48 (12)	Yes (12)	Yes (6)	Yes (6)

Clearly the hunger level of the predator has a significant effect on whether the predator, given the opportunity, will capture more than one prey. Figs. 5:14 to 5:17 show the mean sequence of behaviours for the four levels of fasting tested. They show that the probability of attempting to capture more than one prey is not only influenced by the food deprivation time but also on the rate of encounter with the prey. Once feeding has commenced there appears to be a critical period during which, if an encounter takes place, the predator will attempt to capture

Fig. 5:14 The prey capturing behaviour exhibited by satiated V instar *R.dispar*.

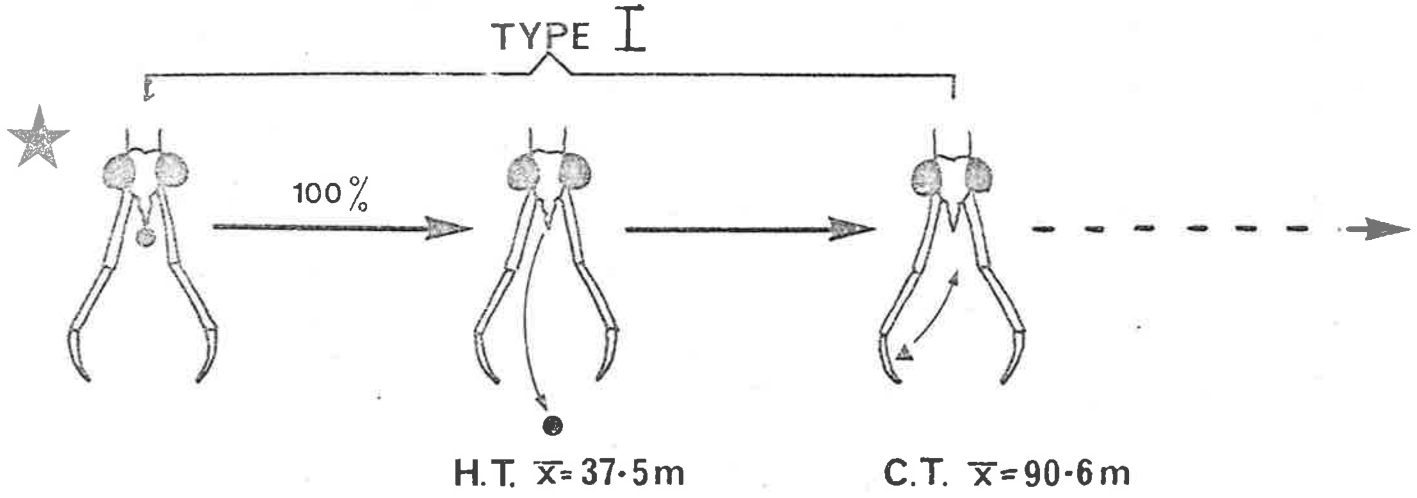
(★) signifies beginning of feeding.

HT = Time in minutes spent handling prey.

CT = Time in minutes from beginning of feeding to capturing next prey.

N = Number of replicates.

(For Figs. 5:14 to 5:17 see text for additional details).



Satiated

N=6

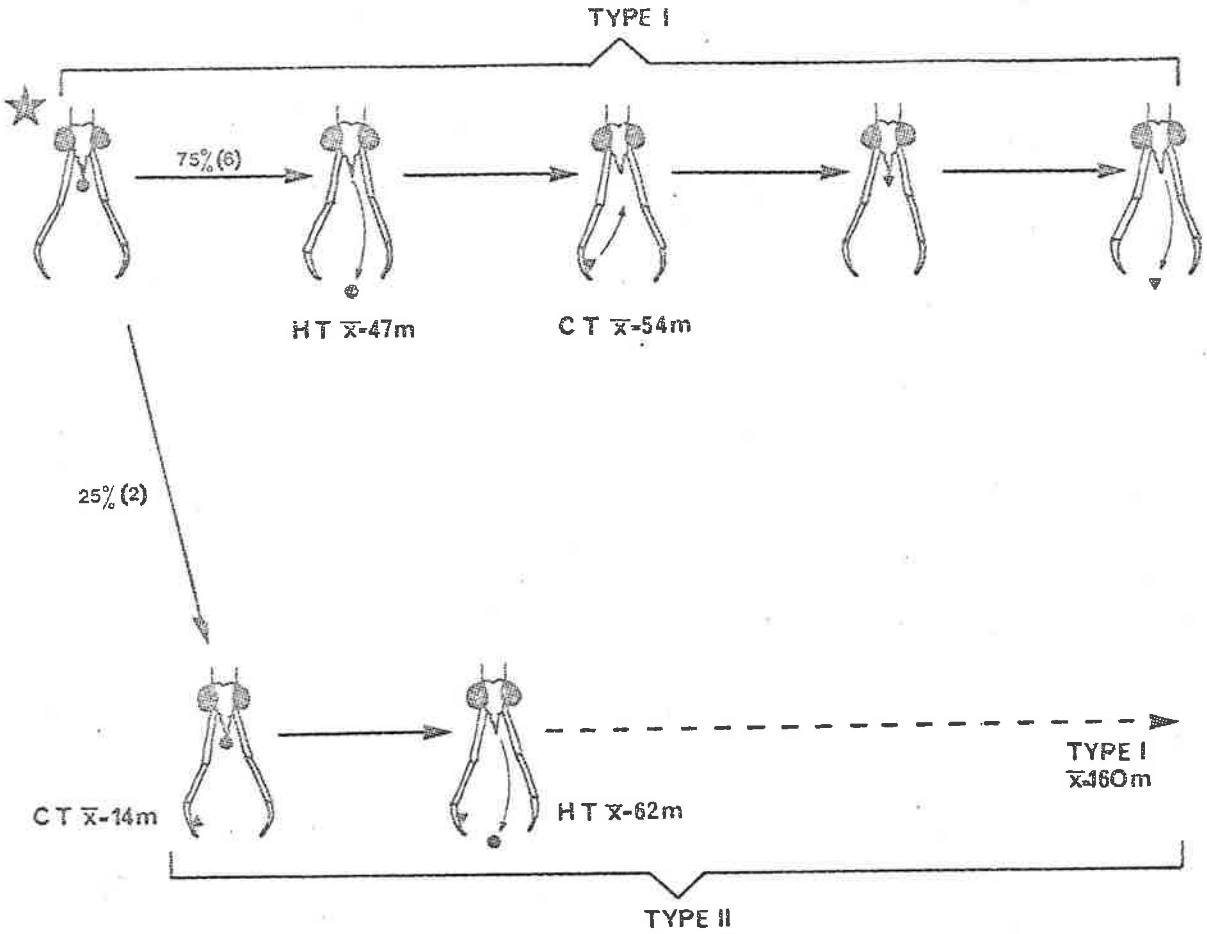
12–2100 h

HT Handling Time

CT Time to Capture

Fig. 5:15 The effect of a 12 hour fast on the number of V instar *R.dispar* exhibiting either Type 1 or Type 2 prey capturing behaviour.

Abbreviations same as Fig. 5:14


TYPE I
75% (6)
H T x̄-47m
C T x̄-54m
25% (2)
C T x̄-14m
H T x̄-62m
TYPE I
x̄-160m
TYPE II

12 h fast
N=8

Fig. 5:16 The effect of a 24 hour fast on the number of V instar *R.dispar* exhibiting either Type 1, Type 2 or Type 3 prey capturing behaviour. Abbreviations same as Fig. 5:14.

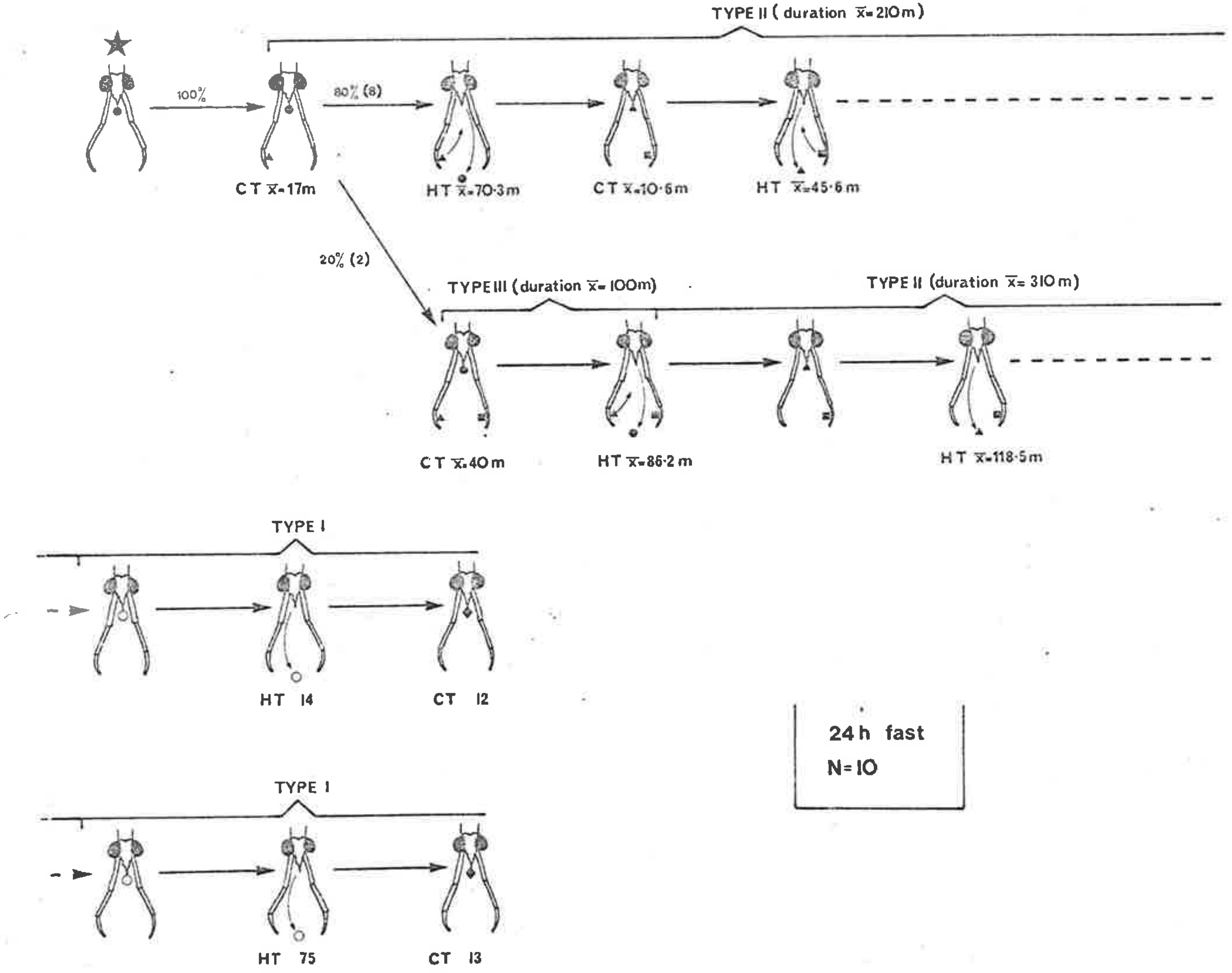
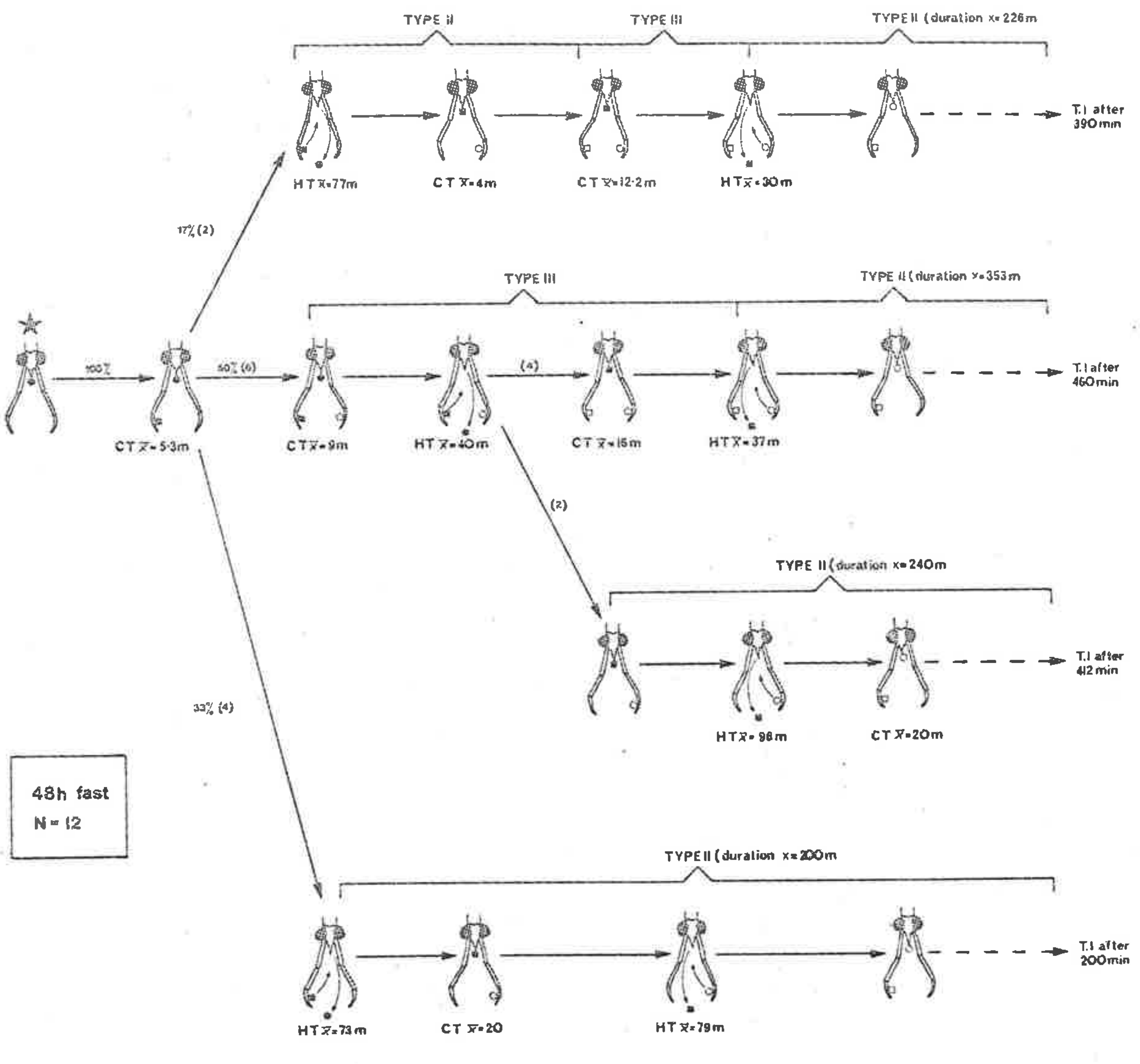

TYPE II (duration x̄= 210 m)
100%
80% (8)
CT x̄= 17m
HT x̄= 70·3m
CT x̄= 10·6m
HT x̄= 45·6m
20% (2)
TYPE III (duration x̄= 100m)
TYPE II (duration x̄= 310 m)
CT x̄= 40m
HT x̄= 86·2 m
HT x̄= 118·5m
TYPE I
HT 14
CT 12
TYPE I
HT 75
CT 13
24 h fast
N= 10

Fig. 5:17 The effect of 48 hour fast on the number of V instar *R.dispar* exhibiting either Type 1, Type 2 or Type 3 prey capturing behaviour. Abbreviations same as Fig. 5:14.


TYPE II
TYPE III
TYPE II (duration x= 226m
T.I after 390 min
HT x̄=77m
CT x̄=4m
CT x̄=12·2m
HT x̄=30m
17% (2)
TYPE III
TYPE II (duration x=353m
100%
50% (6)
(4)
T.I after 460 min
CT x̄=5·3m
CT x̄=9m
HT x̄=40m
CT x̄=15m
HT x̄=37m
(2)
TYPE II (duration x=240m
T.I after 412 min
HT x̄=98m
CT x̄=20m
33% (4)
48h fast
N=12
TYPE II (duration x=200m
T.I after 200 min
HT x̄=73m
CT x̄=20
HT x̄=79m

the prey. Once past that period prey are ignored even if they come well within strike/capture range (see Chapter 3). This critical period is apparently longer the higher the motivational or hunger level, as evidenced between the 24 and 48 hour fasts in particular.

No statistical analysis was carried out due to the low number of replicates. Figs. 5:14 to 5:17 show that the multi-prey capturing follows a sequential pattern through the feeding period, the exhibited pattern dependent on the initial hunger level of the predator. The end of the experiment (about 9 hours) always saw the predators exhibiting a typical Type 1 behaviour, irrespective of prey encounter rate. Type 3 behaviour was always followed by a period of Type 2 which then merged into the Type 1.

Table 5:5 shows the allocation of time to each of the behaviour types during the entire 540 minute experiment, following the different fast periods. Clearly the predators spend a significantly greater time in Type 1 after no fast (predators satiated) and a 12 hour fast. Following a 24 hour fast the predators spent about equal time between Type 2 and 1, both of which were significantly longer than the Type 3 duration.

TABLE 5:5 The time spent in each of the 3 multi-prey capturing behaviours by V Instar R.dispar following four levels of food deprivation. The value shown is the mean ± Standard Error, the number in parenthesis indicate replicates**

	Mean time* spent in each behavioural type		
	Type 1	Type 2	Type 3
Fast Level			
Satiated	540 ± 0 (8)	0	0
12h Fast	380 ± 26.2 (8)	160 ± 23.3 (2)	0
24h Fast	230 ± 15.9 (10)	210 ± 46 (8)	100[1] ± 15 (2)
48h Fast	174 ± 22.4 (10)	216[1] ± 27.3 (5)	150 ± 38 (5)

* Total time of Experiment was 9 hours (540 minutes)

** Prey density was kept constant at 12 per container - see Methods Section, 5:4.2.

1 $p < 0.05$, t - test

After the 48 hour fast, predators spent significantly more time in Type 2 behaviour while about equal time was spent in Type 1 and Type 3. Obviously the probability of a predator exhibiting the different prey capturing techniques is very much affected by its current hunger level. In association with the mean time spent in each of the behaviours, Table 5:6 shows the mean time spent feeding on each prey whilst exhibiting the different behaviours.

TABLE 5:6 The mean time spent by the predator feeding on one individual prey while either holding one, two or three prey (i.e. Type 1, Type 2, Type 3 behaviours), following four levels of food deprivation. The values given are $\bar{x} \pm$ Std. Err. and in parenthesis the mean number of prey eaten per predator. [Number of replicates same as Table 5:5].

	Mean Time spent Feeding on each Prey		
	Type 1	Type 2	Type 3
Fast Time			
Satiated	55 ± 12.1 (1.5)	–	–
12h Fast	67 ± 19.8 (2)	81 ± 31.5 (1.2)	
24h Fast	68.3 ± 6.7 (2.1)	86 ± 14.6 (2.4)	47 ± 20 (2.0)
48h Fast	60 ± 11.9 (2.7)	81.7 ± 6.3 (2.6)	35.6 ± 7.1 (4.2)

During Type 3 behaviour the prey individual is processed much faster, being discarded before it has been totally utilized. As the feeding session continues, about the same time per prey is spent feeding in the Type 2 behaviour and Type 1.

5:4.4 Discussion

The ability of invertebrate predators to capture more than one prey at a time has been reported for a number of different groups. Cook and Cockrell (1972) showed that the reduction in feeding time by Notonecta glauca was probably due to an increased ability of the predator to handle small items, enabling it to catch a new item without first having to abandon the previous one. Similarly, both Hardman and Turnbull (1980) and Haynes and Sisojevic (1966) reported multiple prey catching in the wolf spider, Pardosa vancouveri and the crab spider, Philodromus rufus respectively, and related it to the increase in the number of prey caught at higher prey densities. Nakamura (1977) observed in a number of different species of wolf spider the ability to capture more than one prey. In such cases the spider was able to easily handle two to three flies (Drosophila melanogaster) at the same time, but rarely more than four. The number of flies a spider was able to hold at any given moment, seemed to depend on the body size of the spider. This is due to the spider having to store the prey under its abdomen. Spiders were observed to capture a fly, feed upon it, discard the remains, and then 'recapture' the dead fly a second or subsequent time. For each subsequent 'recapture' of a dead fly the spider repeated the process of feeding upon it and then discarding the remains. In the case of multiple prey capture, the spider discarded the flies either all at the same time or singly at intervals. The first prey to be caught was always the first to be discarded.

In Ranatra, the predator was often seen momentarily to explore a second prey that had been caught. On only one occasion was a predator seen to alternate feeding between two prey. Obviously, when holding 3 prey this would not be possible, as both legs are holding prey and the third is on the stylets. Also, in R.dispar once the prey is discarded it sinks to the bottom and is never 'recaptured'.

The effect of body size on multiple prey capturing was also discussed by Williams (1979) working with the aquatic spider, Dolomedes aquaticus. When feeding on small prey, adults were observed to gather more than one individual. (One adult D.aquaticus was observed to hold eight crane flies, Aphrophilia neozelandia, in its mouthparts and pedipalps). However, when capturing larger prey, for example a 3 cm long cockabully fish, Gobiomorphus, it required not only the mouthparts to seize the prey but also the legs to secure it. Williams (1979) suggested that this multi-prey capture behaviour increased the size of each meal, and therefore enabled the spider to feed less frequently. This was probably a direct consequence of prey being readily available for only a very short period while the spiders were active, the numbers of insects in flight decreasing very rapidly after twilight.

It is suggested that a somewhat similar pattern exists for R.dispar. Many of its prey move in discrete groups. Daphnia and other macro-zooplankton, which in addition to forming a large component of the diet of small instars, can also be eaten by older instars and adults, move in dense aggregations. Furthermore, the common prey of R.dispar in local habitats; A.deanei and other notonectid species, tadpoles and small fish all move in groups or schools through the water body (see Andorfer 1980; Braden 1982; Wassersug 1981); as well as surface dwelling species, for example water-striders, Gerris, (see Riley 1921; Spence 1980) and whirligig beetles, Gyrinus, (see Heinrich and Vogt

1980). Therefore, *R.dispar* individuals can be exposed, on occasions, to a group of potential prey almost simultaneously or over a very short period. This capability of multi-prey capture allows *R.dispar* to 'capitalize' on the situation and to capture additional prey.

The multi-prey capture has been observed in all instars of *R.dispar* but with the smaller individuals taking proportionately smaller prey. This supports the observations of Radinovsky (1964) on the early instars of *R.fusca*. In addition, adult and a number of smaller instars (I and II) of *R.dispar* have been observed holding more than one prey in the natural habitat. Therefore it appears that this prey-capturing behaviour is not an artifact of laboratory experimentation but represents a good example of how selection can act to improve the prey capturing capability of a sit-and-wait predator.

The design of the experiment did not permit the mechanism involved in controlling the multi-prey capture to be identified. In all likelihood the presence or absence of food in the alimentary canal acts as the governing stimulus controlling prey capture, with perhaps more than one region of the gut, with its appropriate stretch receptors, having an effect on the behaviour. Johnson, Arke and Crowley (1975) postulated that 'hunger' (space in the midgut) of damsel fly nymphs motivated attack and prey capture, but that fullness of the foregut could prevent eating. This led to what they called 'wasteful killing', where the predator did not consume all of a prey item. Whether such a mechanism is involved in the multi-prey capturing of *R.dispar* cannot be ruled out. The very evident hunger effect is certainly consistent with the possibility of a similar mechanism. However further work is required before more conclusive statements can be made.

5:5 DISCUSSION

This Chapter set out to examine related behaviours of the predator that could possibly be involved in the increase in the numbers of prey eaten at different prey densities as presented in Chapter 4. The first is the way individual prey are utilized, with the associated feeding time and extraction dynamics, at different prey densities. The second is the behavioural capability of R.dispar in capturing and processing more than one prey at a time, and the time budget associated with each prey. Both of these phenomena are, as is to be expected, interrelated to some degree.

Both the above have been shown to be density dependent with the feeding time per prey being shorter at high densities and more than one prey being caught where prey density is high enough, with the associated increase in prey encounter rate.

Cook and Cockrell (1978) modelled the possible relationship between the prey extraction curves and the functional response curves obtained, arguing that as prey density increases search costs (intercatch-interval) will decrease, so will optimal feeding time. The number of prey items which may be eaten in a given time will thus increase but at an ever-decreasing rate, producing a typical Type 2 functional response curve. The results obtained in Section 5:2 and in Chapter 4 are consistent with this hypothesis, particularly for functional response curves of the larger predator and medium sized prey.

In addition Section 5:2 also demonstrated the reduction in feeding time through the catch sequence. As mentioned previously this would have the effect of having high feeding times at low prey densities and progressively shorter feeding times at higher densities, as the predator moves through the catch sequence. In conjunction with the shorter feeding time more prey will be seen to be eaten at the higher densities.

CHAPTER 6

FACTORS AFFECTING THE ENCOUNTER RATE OF A.deanei WITH R.dispar:- THE EFFECT OF PREY DENSITY AND WATER TEMPERATURE ON SWIMMING AND AGGREGATING BEHAVIOUR

6:1 INTRODUCTION

The observed number of prey eaten at different densities is depend~~a~~ent on not only the predator's feeding behaviour but also the prey's behaviour (see Discussion Chapter 4). This is particularly true in examining the changes in the predator's attack rate $\underline{a}$. Furthermore, in a 'sit-and-wait'/mobile prey interaction' those particular behaviours of the prey for example, speed of movement, movement patterns, aggregation behaviour, will play a significant part in determining the frequency or rate of encounters with the predator.

It has already been shown in Chapters 3, 4 and 5 that a number of the sub-components of the handling time ($\underline{T_h}$) and attack rate ($\underline{a}$) change with length of time since last the predator ate (hunger effect) and that predator age (see also Griffiths 1969) and prey size (see also Thompson 1975) will have an effect on the number of prey eaten. Of particular importance, however, is the way in which these components vary with prey density.

Chapter 5 discussed changes in the predator's behaviour that will influence the numbers of prey captured as a result of changes in prey density, this Chapter examines the prey's behaviour in more detail, in particular prey density effects, in order to identify those particular features that will effect its movement and resultant encounter rate.

6:2 DESCRIPTION OF BASIC SWIMMING BEHAVIOUR OF *Anisops deanei* ADULTS.

6:2.1 Materials and Methods

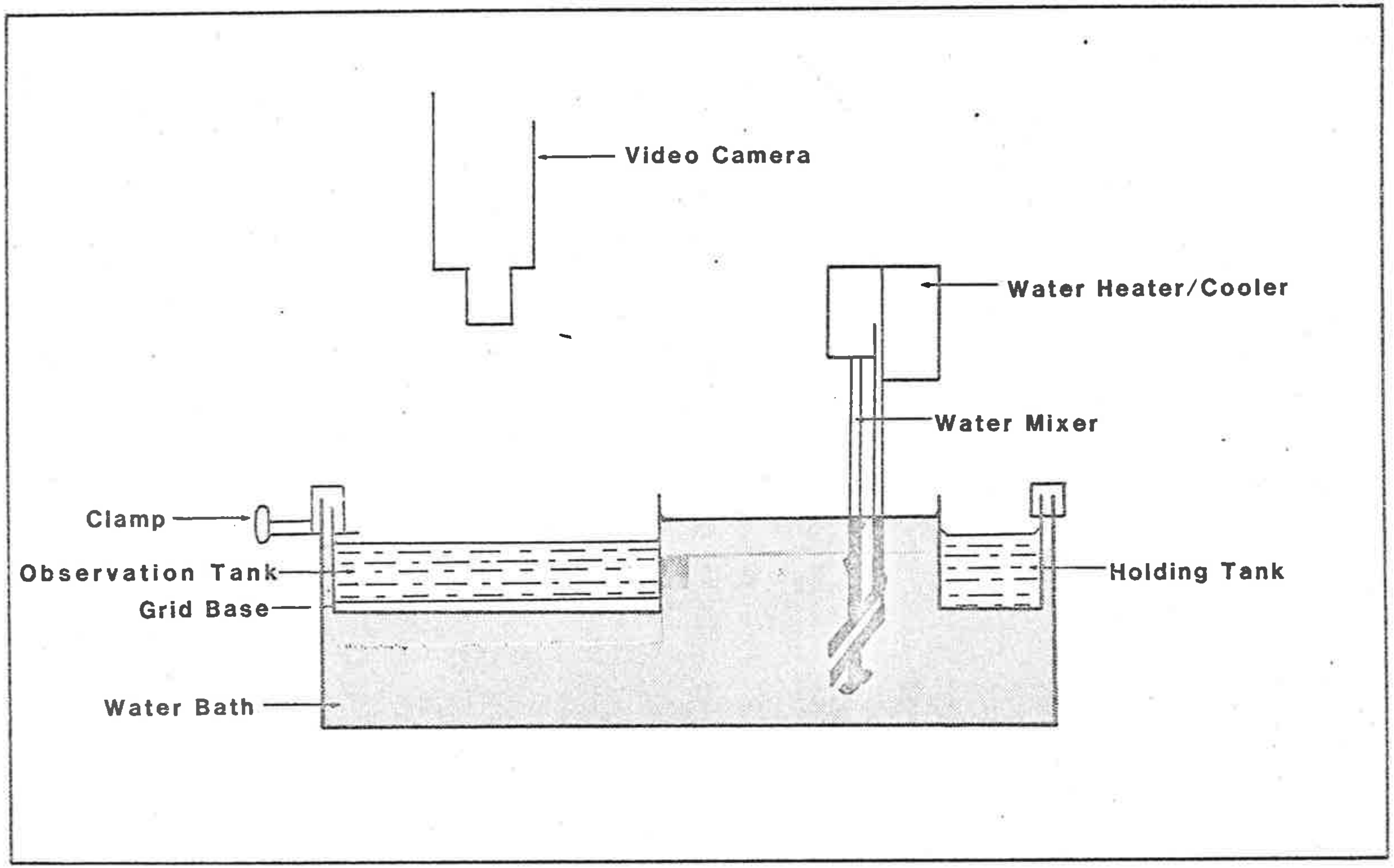
As shown in Fig. 6:1 a video camera was positioned vertically above an observation tank in which water was maintained at a constant temperature (22 ± 0.5^{o}) and depth (5 cm).

Fed *A.deanei* adults were placed in the holding tanks and held overnight. After about 18 hr. fast individual animals were transferred to the observation tank, allowed 15 minutes to settle and their 'swimming' movements observed continuously for 15 minutes via the video monitor. A total of 20 randomly selected adults were observed and recorded. Reanalysis of some video tapes and direct observations showed that there were at least 4 categories of swimming movement that could be recognized and measured (Types 1 to 4).

Having identified the 4 movement patterns, the remaining video tapes were scanned to isolate a suitable example of either one of the movement categories. Once located the length of tape was replayed frame by frame (1/24 sec. = 1 frame) while the position of the animal was recorded on a transparent acetate sheet fixed on the monitor screen. The distance travelled and time taken could then be calculated. Movements by the animals in the vertical plane (i.e. water column) could not be measured. However, where possible only animals moving horizontally were selected for measurement, but nevertheless an unknown error was unavoidable, although every attempt was made to keep this to a

Fig. 6:1 Diagramatic representation of the apparatus used in examining the swimming behaviour of A.deanei.

Not to scale.


Video Camera
Water Heater/Cooler
Water Mixer
Clamp
Observation Tank
Grid Base
Holding Tank
Water Bath

minimum, by using swallow water.

For each category a total of 15 complete movements were measured using 5 different animals.

6:2.2 Results : The four movement categories identified were :

A. TYPE 1 - Animal remains in same location but moves about its vertical axis either to left or right. This is accomplished by only moving one of the metathoracic 'rowing' legs.

B. TYPE 2 - A 'swimming' movement of a 'jerky' fashion. Each stroke resulted in the animal moving no more than 5 mm ($\bar{x}$ = 3.5, SE = 0.3 mm). The animal can remain stationary between each power stroke. The duration of the stroke lasts 0.11 ± 0.04 sec., which gives a theoretical speed of about 50 mm sec^{-1}.The observed speed however, was 10 ± 3.3 mm $sec.^{-1}$, the difference existing because of the pauses between power strokes. The angle that the metathoracic leg makes with the longitudinal body axis (in the horizontal plane) changes from a 45^o to $90-100^o$ during the stroke.

C. TYPE 3 - As in Type 2 but distance travelled at each stroke is between 5 and 10 mm ($\bar{x}$ = 8.5, ± SE= 0.7 mm). The duration of the stroke is about 0.25 sec. ($\bar{x}$ ± SE = 0.27 ± 0.06) while the metathoracic leg angle changes from 45^o at the beginning of the stroke to $> 100^o$ at the end. As in Type 2 there may be pauses between strokes. Estimated Speed = 25 ± 5.2 mm $sec.^{-1}$.

D. TYPE 4 - From a stationary position the animal moves with a rapid 'dart', stopping up to 30 mm away from starting position. The incidence of the animals exhibiting this behaviour is very low. Animals were observed to have completed the movement in consecutive frames (i.e. 0.04 sec. later). The average distance moved with this type of 'swimming' was 21 ± 5 mm, and therefore theoretically one can estimate a speed of about 50 cm $sec.^{-1}$. How accurate a figure this represents is unknown. Due to the low incidence however it has been disregarded from later observations and analysis. Having identified three clear categories of movement in *Anisops* the next step was to investigate the effect of both water temperature and density on the proportion of time spent in each category and the overall effect this has on encounter rate with the predator.

6:3 EFFECT OF WATER TEMPERATURE AND DENSITY ON THE MOVEMENT PATTERNS OF ADULT *Anisops deanei*.

6:3.1 Materials and Methods

The apparatus was arranged as outlined in Section 6:2. The desired temperature was selected and the apparatus and experimental animals were gradually acclimatized for between 16 to 18 hours before the experiment (this was also the animal's fast time).

Animals were carefully introduced into the experimental tank, left for 15 minutes and then their movement patterns were simultaneously observed (via the T.V. Monitor) and recorded on video tape for 5 minutes. Once observations were finished, the animals were removed and a fresh group of Anisops introduced.

Four prey densities (1, 4, 12 and 30 prey/container) and four experimental temperatures (15°, 20°, 25° and 28°C) were used. Each prey density was replicated a minimum of 5 times at each temperature and animals were used only once.

During a video tape analysis one animal was chosen at random and continuously observed for the 5 minutes, recording on an 8-channel multi-event recorder, the number of times each movewment category was seen, and its duration.

6:3.2 Results and Discussion

Because of the unequal and in some cases low sample sizes the time spent in each of the movement categories was combined to produce a total time spent moving per 5 minutes observation time.

A 2-way analysis of variance demonstrated that both Temperature and Density had a significant effect on the time spent moving, as shown in Fig. 6:2. The two overall trends shown in Fig. 6:2 are that animals move more at the higher temperature but less as density increases. It appears therefore that intraspecific interactions are significant in groups of A.deanei and this is expressed in a significant decrease in movement.

Observations made during the experiments support these findings, in that A.deanei individuals at the higher densities tended to form

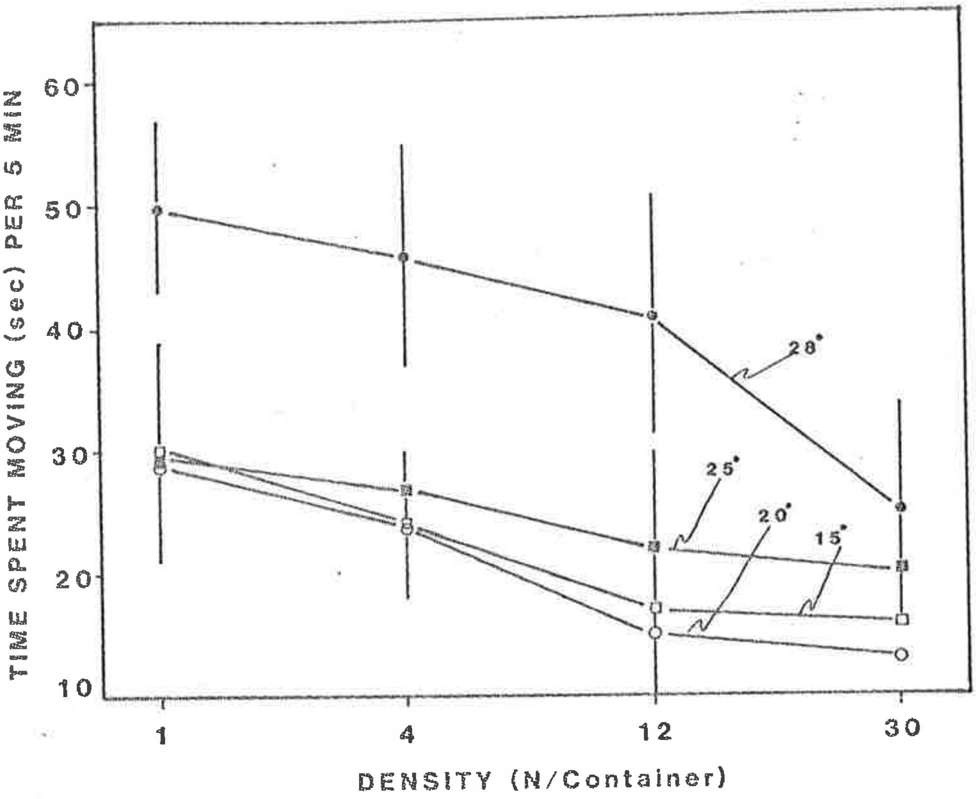
Fig. 6:2 The effect of water temperature and density on time spent moving per 5 min observation period. Means with some letter are not significantly different (SNK Multiple Range Test, $\alpha = 0.05$). Value given is mean ± 95% Confidence Interval.

(□) Water temp. 15°C.

(○) Water temp. 20°C.

(▨) Water temp. 25°C.

(◍) Water temp. 28°C.



SOURCE	DF	SS	MS	F-ratio	SIGNIF.
TEMP.	3	1046.43	348.81	22.93	p=0.0001
DENSITY	3	580.62	193.54	12.72	p=0.001
Error	9	136.88	15.21		
TOTAL	15	1763.94			

Comparison of Means	SNK-Multiple Range Test (α=0.05)			
TEMPS.	15^A	20^A	25^A	28^B
DENSITIES	1^C	4^C	12^D	30^E

aggregation, i.e. they formed a group or groups of individuals (depending on the density) that moved around the experimental tank in a fashion resembling a school of fish. In addition, as mentioned in Chapter 2, A.deanei form very dense aggregations in their natural habitat, moving around the pond or dam in groups of up to hundreds of individuals. Unfortunately time did not permit the collection of additional data on the structure and dynamics of these aggregations in order to more fully corroborate their probable significance. Examination of the literature suggests that this behaviour has evolved as an anti-predator defence mechanism (see for example Bertram 1978; Hamilton 1971; Pulliam 1976; Rubenstein 1978; Wilson 1975) as that found in bird flocks (see for example Bertram 1980; Elgar and Catterall 1981; Kenward 1978; Lazarus 1978, 1979; Powell 1974; Pulliam 1973; Siegfried and Underhill 1975; Vine 1971) or, perphaps more pertinent to A.deanei, fish schools (see for example Andorfer 1980; Aoki 1980; Brock and Riffenburgh 1960; Neill and Cullen 1974;). Whether this behaviour may confer an advantage to the group as a whole (see for example Vine 1971; Wyñe-Edwards 1962) or to the individual (see for example Dawkins 1976; Hamilton 1971) is still somewhat of an unanswered question. Although many well known biologists who subscribed, outspokenly or by implication, to the former have, at the same time, for example Fisher (1953) and Lorenz (1966), admitted that the nature of the group advantage remains obscure in many cases.

Anti-predator aggregation behaviour has been reported for a number of aquatic insects (see for example Brown and Orians 1970; Deshefy 1980; Heinrich and Vogt 1980; Hildrew and Townsend 1982; Miller 1966; Treherne and Foster 1980, 1981, 1982), and in particular in possible response to ambush or sit-and-wait predators (Taylor 1976;

see also Gerritsen 1980; Gerritsen and Strickler 1977; Williams 1966 for additional discussion). Miller (1966) used the term 'flock' for the aggregation of a related species Anisops pellucens, and reported a synchronized diving and ascending behaviour, where individuals of A.pellucens 'follow a leader' to the water surface for renewal of the airstore. Miller argued that on ascending, the leading bug is more likely to be caught by a waiting predator than are those which follow immediately after, and therefore selection would be expected to favour 'following', were it not for the fact that the renewal of airstores is essential and there must therefore be 'leaders'. In opposition to Miller's conclusion, using the 'hawks and doves' argument of Maynard-Smith and Parker (1976) and Dawkins (1976), natural selection would favour following in every case - the animal simply developing a larger air store and thus always being able to follow (see also Maynard-Smith and Price 1973; Kenward 1978).

Synchronized ascents represent a behaviour pattern that can only be developed in gregarious species and he cited a second species, A.debilis, that do not form aggregation, where this behaviour does not occur.

In the present work it has been observed that A.deanei certainly form very dense aggregations of mixed immature and mature individuals of both sexes that do not appear to be feeding aggregations. Whether synchronized diving behaviour in A.deanei occurs is unknown, no detailed observations were made.

Examining the aggregating behaviour of A.deanei in the light of an 'anti-ambush predation strategy' one can hypothesize the selective advantage on moving in a group, with the average rate of encounter with a stationary predator being reduced. However, until further work is done in this field of A.deanei group behaviour no conclusive statements can be made.

The effect of change of temperature, either high or low, on the activity level of aquatic insects is well known, as it is for most poikilotherms (see for example Cofrancesco and Howell 1982; and review by Ward and Stanford 1982). In the present study no significant effect of temperature was observed between 15° and 25°, but a rapid rise in activity level was found at 28°. This is probably due to this temperature approaching non-optimum limits for this aquatic insect, although during mid-summer (January/February) the water temperature in the upper strata reaches 27° to 28°C, some times higher. The following figures represent the temperatures at which there was a 50 per cent mortality after 24 hours exposure in some Ephemerid aquatic nymphs. Ecdyoneurus from stones at side of stream : 26.6°C; Caenis from slow weed-choked stream : 26.7°C; Cloeon from weedy pond 28.5 - 30.2°C (Whitney 1939). Comparable figures for A.deanei have not been located in the literature.

The effect of temperature on movement has also been used to investigate the prey capturing behaviour of predators. Holling (1963, 1965, 1966) showed that 'the speed of movement of predator and prey' was a significant component of the 'attack rate' of the predator (see also

Chapter 4 this study), while Thompson (1978a) demonstrated that Daphnia spp., the common prey species he used in predation experiments with Odonata predators, were more active at 16° than 8°C, and this had a significant effect on the overall predatory success.

Clearly, this present experiment demonstrated that both animal density and water temperature have significant effects on the activity level of A.deanei. However the question that needs to be asked is whether these variables have a corresponding effect on the encounter rate with a sit-and-wait predator like R.dispar. Accordingly, the following experiment was carried out to test the effect of both prey density and water temperature on the encounter rate with R.dispar.

6:4 THE EFFECT OF PREY DENSITY AND WATER TEMPERATURE ON THE SUBSEQUENT ENCOUNTER RATE WITH AN 'AMBUSH PREDATOR'

6:4.1 Method

Three large glass aquaria (50 x 35 x 20 cm deep) were filled with 20 litres of filtered, dechlorinated tap water, and positioned out of direct sunlight on a work bench. Working from the shape of the 'Arousal' and 'Strike' fields described in Chapter 3, approximate 3-D models of the combined shapes were constructed from fine fuse wire. One model was fixed to a piece of cocktail stick (2 mm diameter x 200 mm) that had previously been weighted with a cube of bees wax and a lead sinker. The cube of wax fitted into empty ice-cube blocks arranged in a grid pattern on the bottom of the tank, thus securing it. The model 'predator' was arranged on the vertical stick so that it was about 10 cm below the water surface and positioned, as far as possible, in the same angular location as found in a normal predator. Three models were made, 1 each being placed in the centre of the grid of each tank.

Prey animals, caught the previous day, were introduced into the tanks and left for 24 hours. The water temperature was continuously monitored every 15 minutes by a thermistor fitted to a calibrated Rustrak event recorder.

Observations were made continuously for one hour on each tank in turn, using a multi-channelled event recorder. Each time a prey animal swam into the 'Arousal' or closer into the 'Strike' fields it was scored as an appropriate encounter. All observations were conducted between 0900 h and 1500 h under the natural light and air temperature levels prevailing at the time. Four prey densities : 1, 4, 12 and 20 animals per tank (equivalent to 0.05, 0.2, 0.6 and 1.0 animals per litre) and three water temperatures, 15 ± 1.5°, 19.5 ± 1.5° and 25 ± 1.0°C, were observed. By observing the water temperature from the Rustrak recorder at different times of the observation period, the required water temperatures for the experiment could be identified. Through necessity this normally meant that observations for the 15°C treatment were conducted at the beginning of the session, (i.e. between 0900 and 1100 h), 20° mid-way through (i.e. between 1100 and 1300 h) and 25°C towards the end (i.e. between 1300 and 1500 h). There were no obvious signs of any changes in overall swimming behaviour as a result of 'diurnal rhythms' although admittedly they cannot be totally discounted. The positioning of the table and tanks was such that there was no appreciable change in the light intensity during the observation session.

Each treatment was replicated twice and no animal was used more than once. The duration of the complete experiment lasted over a 16 day period during May 1983.

6:4.2 Results and Discussion

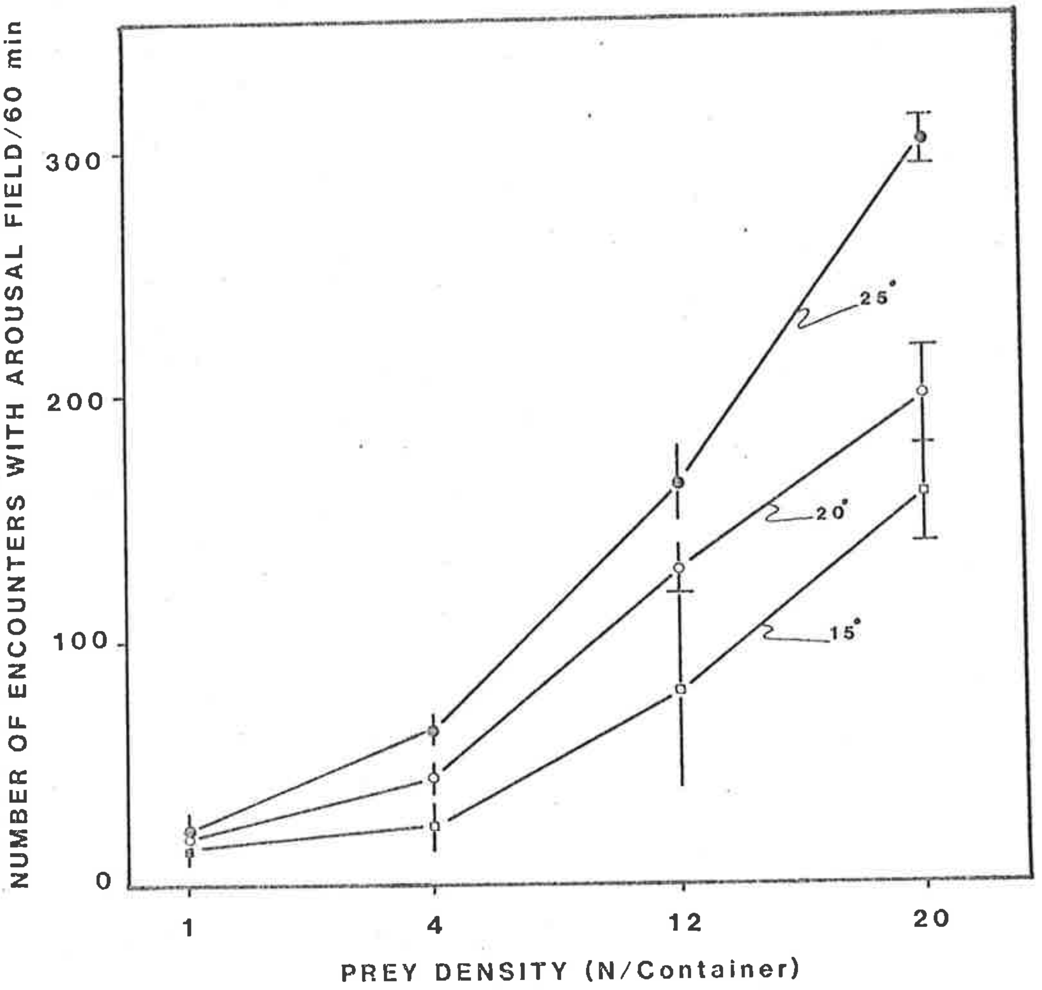
Both prey density and temperature have a significant effect on the rate at which prey encounter the model 'Arousal' field of R.dispar. Fig. 6:3 shows graphically the trends observed and also gives the results of the 2-way ANOVA analysis. Similarly, Fig. 6:4 shows the prey density and temperature effects on the increase in encounter rate of prey with the model 'Strike' field. In this case temperature apparently did not significantly influence the encounter rate, although examination of Fig. 6:4 shows the encounter rate at 15°C was much lower at the high density.

These results appear to contradict the findings of Section 6:3 in so far as it was suggested that at the higher density the rate of encounter would be lower. However, the significant effect of the lower level of activity and intraspecific grouping of prey, at the higher densities, can be seen clearly when one predicts the expected encounter rate for a group of prey based on one individual. If a uniform distribution of prey exists the encounter rate for 4 prey individuals should be four times that found for 1 individual. Likewise for densities of 12 and 20, all other things, for example swimming speed, behaviour, etc., being equal.

Table 6:1 compares the number of encounters per 60 minutes that

Fig. 6:3 The effect of density and water temperature on the number of encounters with a 'model' predator's arousal field in a 60 min observation period. Value given is mean ± Standard Error.

(□) Water temp. 15°C.
(○) Water temp. 20°C.
(◍) Water temp. 25°C.



SOURCE	DF	SS	MS	F-ratio	SIGNIF.
Density	3	76429	25476	25.12	p=0.0002
Temp.	2	9744	4872	4.8	p=0.05
Error	6	6083	1013		
Total	11	92258			

were observed compared with the expected number assuming a uniform distribution of prey individuals.

TABLE 6:1 The observed mean number of encounters per hour by prey with (A) the Arousal or (B) the Strike Fields of *R.dispar* model at 4 different prey densities and 3 different water temperatures compared with the expected number of encounters assuming a uniform distribution of prey individuals.

A. AROUSAL FIELD

		PREY DENSITY (N/container)			
		1	4	12	20
15°	Observed	15.5	23.5	78.5	162
	Expected	15.5	62	186	310
20°	Observed	21	44	129	202
	Expected	21	84	252	420
25°	Observed	19.5	66	166	306
	Expected	19.5	78	234	390

B. STRIKE FIELD

15°	Observed	3.5	4	18.5	30.5
	Expected	3.5	14	42	70
20°	Observed	4	6.5	47	67
	Expected	4	16	48	80
25°	Observed	4.5	13	45	85
	Expected	4.5	18	54	90

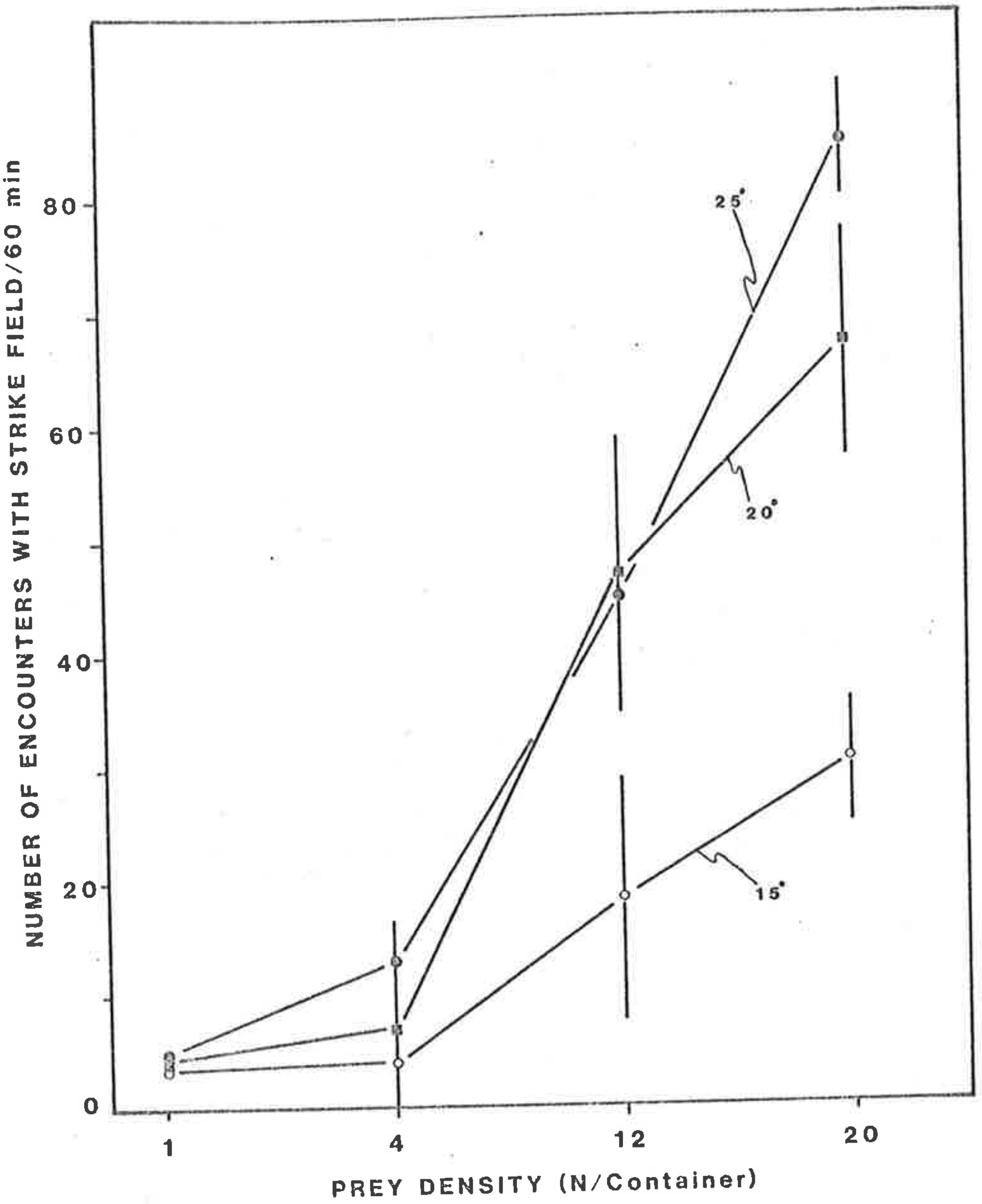
Fig. 6:4 The effect of density and water temperature on the number of encounters with a 'model' predator's strike field in a 60 min. observation period.

Value given is mean ± Standard Error.

(○) Water temp. 15°C.

(□) Water temp. 20°C.

(●) Water temp. 25°C.



SOURCE	DF	SS	MS	F-ratio	SIGNIF.
Density	3	6411	2137	13.18	p=0.005
Temp.	2	1119	559	3.4	p=0.1 (NS)
Error	6	972	162		
Total	11	8503			

The effect is quite obvious, being repeated over the three temperatures, showing the overall effect of density (and temperature) on reducing the encounter rate with the predator. It is suggested that the aggregation behaviour and density effect in reducing activity of A.deanei significantly reduces the encounter rate with the predator. The type of behaviour will, in turn, effect the incidence of prey capturing behaviour of R.dispar.

However, in considering the functional response (see Chapter 4) it is often assumed that the number of prey killed is proportional to the number of prey encountered by the predator. Although it is clear that the predation rate might not directly depend on the encounter rate (Hassell 1978; Murdoch and Oaten 1975), the encounter rate has only rarely been investigated separately in functional response experiments (see for example Everson 1980; Sabelis 1981). Furthermore, recently Kaiser (1983) has shown that the functional response curves and the encounter rates differ markedly in several aspects. He showed the assumption that the predation rate is proportional to the encounter rate is clearly not justified, at least not in the mite species that he tested. However, it seems obvious that for a sit-and-wait predator, like R.dispar, if there is no encounter between predator and prey, then can be no predation. Therefore although not attempting to relate the functional response of R.dispar solely to the encounter rate, it can be seen that indirectly, bearing in mind the other components of the predatory process discussed in Chapter 3, encounter rate will significantly affect the prey-capture of R.dispar.

In addition, it would be expected that the prey-encounter rate would not only influence the numbers captured and eaten by an ambush predator but significantly affect other components of the predatory behaviour. In particular, the choice and duration of stay at a foraging site, it may be hypothesized, may be very much affected by the extent and frequency of encountering prey.

The next chapter sets out to test this hypothesis by observing the effect of

(i) prey density on duration at and rate of movement between foraging sites; and

(ii) the effect of encounter rate with prey on foraging site selection.

CHAPTER 7

THE EFFECT OF PREY DENSITY ON AMBUSH SITE SELECTION BY *R.dispar*

7:1 INTRODUCTION

Surprisingly, one of the most obvious questions concerning selection of an optimal ambush site, by an ambush predator, has not received the attention it deserves (Curio 1976). Clearly one of the most important criteria for any sit-and-wait predator in evaluating an ambush site is the assessment of prey availability. This is in turn a basic assumption of current optimal foraging theories, in that an optimally foraging predator must be able to measure or assess prey availability and therefore determine an expected rate of food intake for a given environment or patch (Pyke, Pulliam and Charnov 1977; Krebs 1978; Krebs and Davis 1978; references in Kamil and Sargent 1981; Orians 1981). This assessment of expected food intake forms the basis for the predator's evaluation and subsequent decision making process concerning optimal patch choice, optimal feeding times and handling time, optimal choice of diet, choice of search tactics (Charnov 1976b; Pyke, Pulliam and Charnov 1977; Cook and Cockrell 1978; Krebs, Kacelnik and Taylor 1978; Sih 1980; Formanowicz 1982; Morse and Fritz 1982; Inove and Matsura 1983; Morse 1983). The expected rate of food intake is used to update and possibly 'fine tune', the appropriate behavioural responses continously, and therefore make adjustments in the resultant foraging strategy. How foragers assess prey availability and derive such expectations, however, remains an unanswered question (Krebs, Houston and Charnov 1981; Pulliam 1981; Orians 1981). A number of hypotheses have been put forward in attempting to explain a possible mechanism by which predators assess the availability or density of prey. Johnson, Akre and Crowley (1975) suggested that a predator could assess the availability of prey by how full its gut was frequently when surrounding prey density is low. Evidence for this hypothesis exists from Łommicki and Slobodkin (1966) working with *Hydra littoralis*. When the density of prey was reduced the *Hydra* floated free from the substrate and moved to another site. Additional work on various web building spiders (see for example Riechert 1974, 1976; Janetos 1982; Janetos and Cole 1981) have shown that when prey availability is low spiders move and reconstruct their webs at another location. In addition Morse and Fritz (1982) and Morse (1983) working with the crab spiders, *Misumena vatia* and *Xysticus emertoni*, reported that the spatial distribution of the spiders most closely resembled that predicted if spiders responded to the number of times insect prey visited an umbel rather than more direct measures, e.g. attack or capture frequency. They also showed that, for those spiders that moved, their probability of eventually occupying a high-quality stem markedly increased. However, the two species, although commonly found on the same plants, responded to very different densities of prey, resulting in *M.vatia* spending twice as long on milkweed plants compared with *X.emertoni*. More recently, Formanowicz, Bobka and Brodie (1982) reported their studies on an 'extreme' ambush predator, the water scavenger beetle, *Hydrochara obtusata* (Coleoptera : Hydrophilidae). Larvae of this species were found to move significantly less at high compared with low densities, although there was no significant difference in the number of prey captured at the four experimental densities. From their results they concluded that capture rate and satiation (gut fullness) could be ruled out as possible mechanisms of assessing prey density. Additional work by Formanowicz (1982a) on another beetle species, *Dytiscus verticalis*, suggested that this species utilized an encounter rate mechanism in assessing prey density.

The experiments reported in this chapter set out to investigate the effect of prey density on the duration of stay at and subsequent number of changes between ambush or foraging sites. In particular I proposed to test the hypothesis that R.dispar would change the position of their ambush site more often and stay for shorter periods of time when the prey density was low, and will decrease the frequency of changing and therefore remain at a site for longer when prey density is higher. Secondly, experiments were undertaken to try to identify factors involved in the mechanism used by R.dispar in assessing prey density or availability in addition to the 'mean intercatch interval' reported in Chapter 5.

7:2 THE EFFECT OF PREY DENSITY ON MOVEMENTS BETWEEN AND AROUND AN AMBUSH SITE BY R.dispar

7:2.1 Material and Methods

Fifth instar R.dispar were collected and maintained as outlined in Chapter 2 during January to March 1981. After moulting, males and females were separated but maintained as before. The animals were used 5 to 8 days after the moult, thus standardizing (as closely as the experimental conditions and availability of animals allowed) post-moult behaviour. Each animal was used once only.

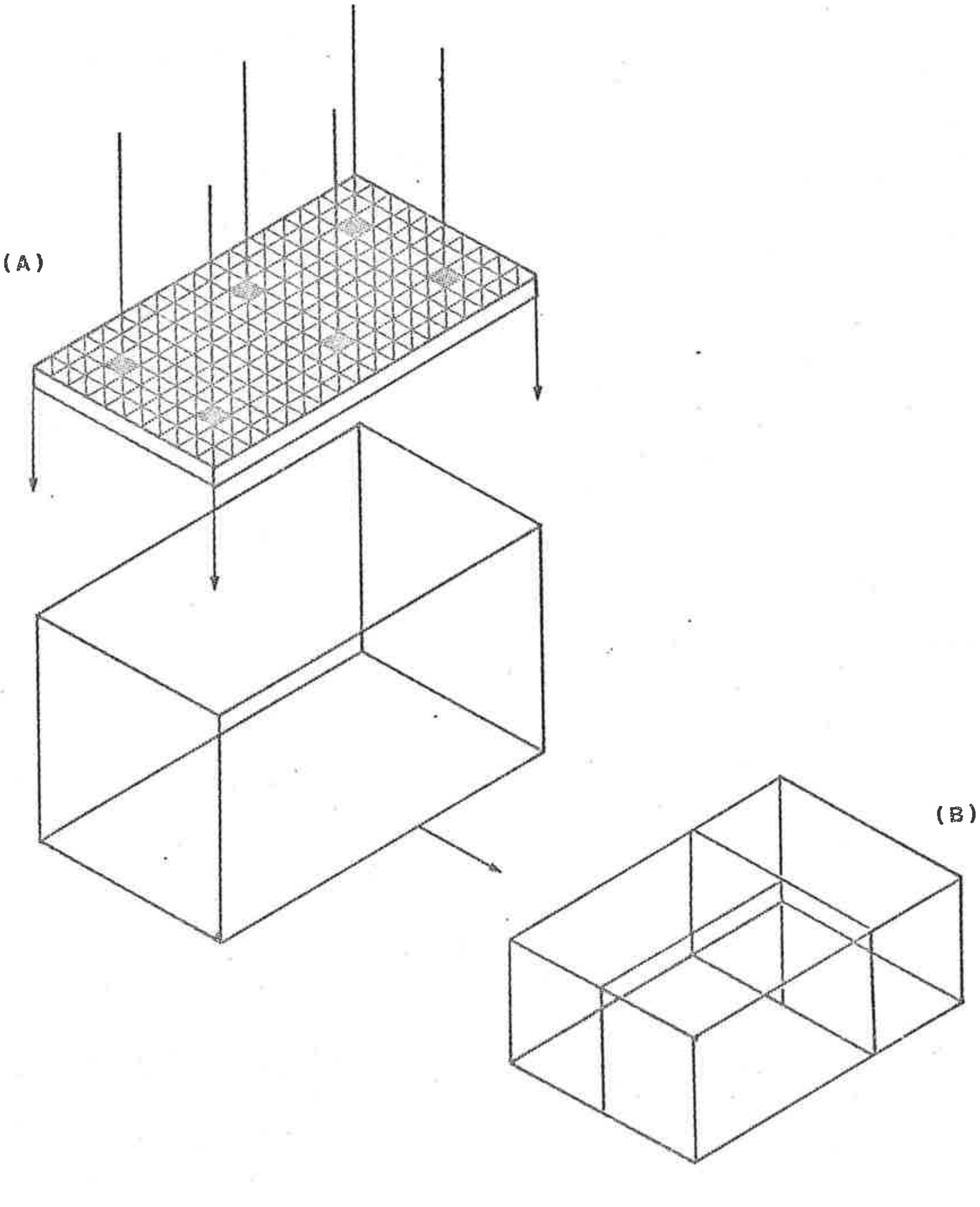
The basic unit of apparatus consisted of a glass aquarium (33 x 17.5 x 26.5 cm deep) with the vertical walls covered on the exterior surface with neutral translucent paper. A false floor of clear perspex with six foraging sites located vertically, 1 each 5.0 cm from each corner, the other 2 individually placed mid-way along each of the longest sides, 5.0 cm from the aquarium wall. The foraging sites were vertical dowelling rods, 0.5 cm diameter x 20 cm long. A 3-dimensional grid made from plastic grating was then lowered over the foraging sites onto the perspex floor (see Fig. 7:1A). Each square of the grid was 1 cm^3. This provided, not only a normal spatial identification aid, but the depth component of the grid acted as receptacles into which discarded prey could sink. This prevented them from being dislodged and relocated by the movement of the predator or prey and therefore could be used as a visual marker of foraging activity of the predator.

Three such tanks were arranged as shown in Fig. 7:1B on a 1 m^2 x 5 cm thick sheet of polystyrene. Four vertical Climplex® rods, 1 meter in length, located at each corner of the polystyrene sheet supported a 'tent' of black photographic curtaining that surrounded the apparatus on the four sides but remained open at the top. The tops of the vertical Climplex® also acted as anchor points for additional framework that supported a camera and flash attachments.

A Bauer cinecamera with time-lapse attachment was situated 1.5 m directly above the tanks, along with a rechargeable flash gun (Mecablitz 215 telecomputor model). The positioning of the camera was such that it provided the best field of view of all three tanks and a small electronic digital clock fixed to an outside wall of one tank. Preliminary trials identified not only the most suitable camera location but also the best angular position for the flash attachment to provide adequate illumination for all three tanks and clock without reflection or 'flash' zones from the glass.

Fig. 7:1A Diagram of glass tank, and plastic 3-D grid floor with wooden ambush sites.

Fig. 7:1B Arrangement of 3 glass tanks for camera observation.


(A)
(B)

The time interval between exposures was 60 secs. Super-8 reversal film (Kodak Tri-X) was used in all experiments, with the standard 15 m (50 ft) cartridge of film providing about 3600 exposures in 60 hours. Flash duration was set at 0.00002 sec. Controlled experiments beforehand in normal light (>2500 lux), dim light (15-20 lux) and darkness (<0.05 lux) using the characteristic leg extension or dive responses of R.dispar (see Chapter 3) as an indicator of 'fright' failed to show any observable effect of the 'flash' on the behaviour of the predator, likewise no significant effect on the prey was observed.

Experimental Procedure

Adult female R.dispar were fed abundant prey ad libitum for 2 days preceding the experiment. They were then subjected to a 48 hour fast, to 'standardize' their alimentary condition. For the last 4 hours of the fasting period the animals were transferred to the experimental tanks, one individual per tank, which had been filled with 10 litres of filtered, dechlorinated tap water. Animals were observed to 'settle down' within a few minutes and normally took up their characteristic prey capture posture (see Chapter 3) within 5-15 minutes.

Prey animals were adult A.deanei that were collected up to 48 hours before being used and maintained as outlined in Chapter 2. Three prey densities were used : no prey present (N = 0), medium density (N = 3/litre) and high (N = 15/litre).

The cinecamera was normally switched on 10 minutes before introducing the prey animals into the tanks, which in turn initiated the onset of the experiment. This was arranged to be as close to 1200 hours as possible. The lighting regime was 14L : 10D with lights on at 0600 h, off at 2000 h, which approximated the natural light conditions during the experimental period. A bank of 4 fluorescent lights (Phillips, 2 x 40 watt 'White', 2 x 60 watt 'Day Light') covered by a light diffusing panel was positioned 3 metres above the apparatus.

The tanks were inspected every 8 hours and the number and location on the grid of dead prey was noted and then an equal number of adult A. deanei were added. A fold-back window in the curtaining permitted easy access to the tanks without causing any apparent disturbance or fright reaction in the experimental animals. Observations during darkness (<0.05 lux) were carried out under Red Light (Phillips TL 40 watt/15 fluorescent tube). Preliminary studies in dim light (<2.0 lux) with and without the red light on levels of activity were not significantly different ($\chi^2 = 18.6$, $p<0.01$) and therefore it was assumed that the red light did not adversely affect or disturb the animals (see also Bailey 1981; Elliott 1968).

The duration of each experiment was 60 hours at the end of which the predators were returned to the holding tanks. Prey individuals, both dead and alive, were removed and counted in order to check against recorded observations.

The experiment was repeated five times between 22 January and 19 March, 1981, using new predators and prey individuals in each case.

Analysis of Films

Films were projected from a Kodak Ektagrafic MFS-8 Projector fitted with a single frame advance/reverse control, onto a screen.

For assessing movements between foraging sites each film was viewed and the number of site changes and duration of stay at each site was recorded. During the viewing of the film it was noticed that the angular position of the predator around the foraging site (in the horizontal plane) changed, and that there appeared to be different patterns exhibited in each of the treatments. In order to quantify this movement the following analysis schedule was adopted.

Movement around the foraging site was defined as the angular change of location of R.dispar each minute of the sample period (see below). It was by measured directly from the projected image by taking the compass location of the predator in relation to its own longitudinal body axis and the centre of the foraging site, a fixed point in each frame. This was done for frame 'x' and then re-measured for frame 'x + 1' (i.e. 1 minute later) and so on over a sample of 20 consecutive frames. By simple subtraction the angular movement could be calculated. Due to the volume of available data obtained (over 18000 frames collected from the 5 films) it was decided to subsample each film by analysing a block of 20 consecutive frames (i.e. 20 consecutive minutes) every 360 minutes. This therefore provided a total of 10 samples of 20 frames for each film, and were arranged to be taken from about the same time of day to allow for any diurnal rythms, etc. Table 7:1 shows the 10 time intervals used for each experiment.

TABLE 7:1 The time of the 10 observation periods for each experiment. (Starting at the time indicated a sample of 20 consecutive frames would be analysed for angular position change in *R.dispar*).

	OBSERVATION PERIOD NUMBER									
	1	2	3	4	5	6	7	8	9	10
DAY NUMBER	1		2				3			
Expt. 2*	1636h	2236	0436	1036	1636	2236	0436	1036	1636	2236
" 3	1515	2115	0315	0915	1515	2115	0315	0915	1515	2115
" 4	1620	2220	0420	1020	1620	2220	0420	1020	1620	2220
" 5	1738	2338	0338	0938	1738	2338	0338	0938	1738	2338

* Unfortunately the film from Expt. 1 was destroyed before this analysis could be undertaken.

7:2.2 Results

(A) Movement and Duration of Stay between Foraging Sites.

Tables 7:2 and 7:3 show the number of site changes for each of the prey treatments and the mean duration of stay at each site respectively over the five experiments. A 1-way ANOVA showed that a highly significant prey density effect was evident for both number of site changes ($F = 83.6$, df 2, 12, $p < 0.001$) and duration of stay ($F = 21.2$, df 2, 12, $p < 0.001$). While a one tailed t-test of comparison of means showed that predators changed foraging sites significantly more frequently when no prey were present compared with 3 prey per litre ($t = 8.13$, 4 df, $p<0.001$) or when only a few prey were present (i.e. 3/litre) compared with 15 prey per litre ($t = 2.48$, 4 df, $p<0.05$).

<u>TABLE</u> <u>7:2</u> The number of site changes of adult <u>R.dispar</u> when either no prey ($N = 0$), few prey ($N = 3\ 1^{-1}$) or many prey ($N = 15\ 1^{-1}$) are present over a 2.5 day observation period.

	EXPERIMENT NUMBER						
PREY DENSITY ($n.1^{-1}$)	1	2	3	4	5	$\bar{x}$	SD
0	39	47	31	33	48	39.6	7.8
3	6	3	11	2	8	6	3.6
15	2	1	4	3	1	2.2	1.3

In addition the absence of prey caused the predator to remain at a site for significantly less time compared to when 3 prey per litre were present ($t = 3.42$, 4 df, $p < 0.05$), while, comparison of means between the 3 prey per litre and 15 prey per litre treatments showed that the predator remained at the ambush site for less time when the prey density was low ($t = 2.63$, 4 df, $p<0.05$).

Figs 7:2A-C shows the mean duration of stay at each foraging site over the 5 replicates of each treatment. Initially, predators remain at foraging sites for significantly longer than later stays,

TABLE 7:3 The mean duration (min) of stay at each foraging site by adult *R.dispar* when either no prey, few prey or many prey are present.

PREY DENSITY		EXPERIMENT NUMBER						
		1	2	3	4	5	$\bar{x}$	SD
(n.l^{-1})								
0	$\bar{x}$	61.9	78	107	99	87	87	18
	SD	142.7	149	171	153	163		
	RANGE	1 to 696	1 to 722	1 to 624	1 to 750	1 to 648		
3	$\bar{x}$	514.2	900	300	1200	400	663	377
	SD	1010.7	1235	922	685	793		
	RANGE	97 to 2101	158 to 2807	27 to 1919	10 to 1418	211 to 2621		
15	$\bar{x}$	1537.2	1915	1216	834	1800	1469	394
	SD	1611.8	2505	801	511	2401		
	RANGE	200 to 2651	123 to 3477	79 to 1900	296 to 1315	300 to 3300		

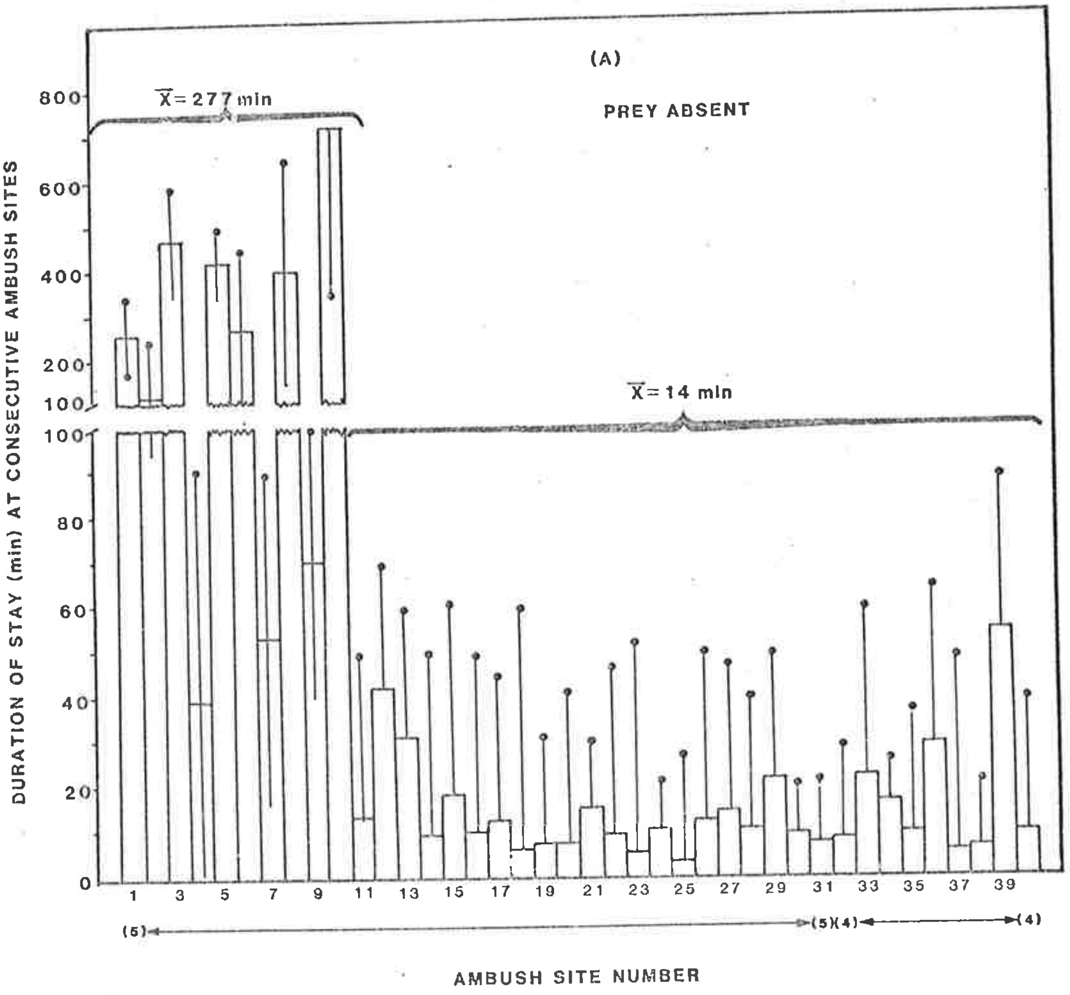
Fig. 7:2 The mean duration of stay (mins) at each ambush site before moving on to next site.

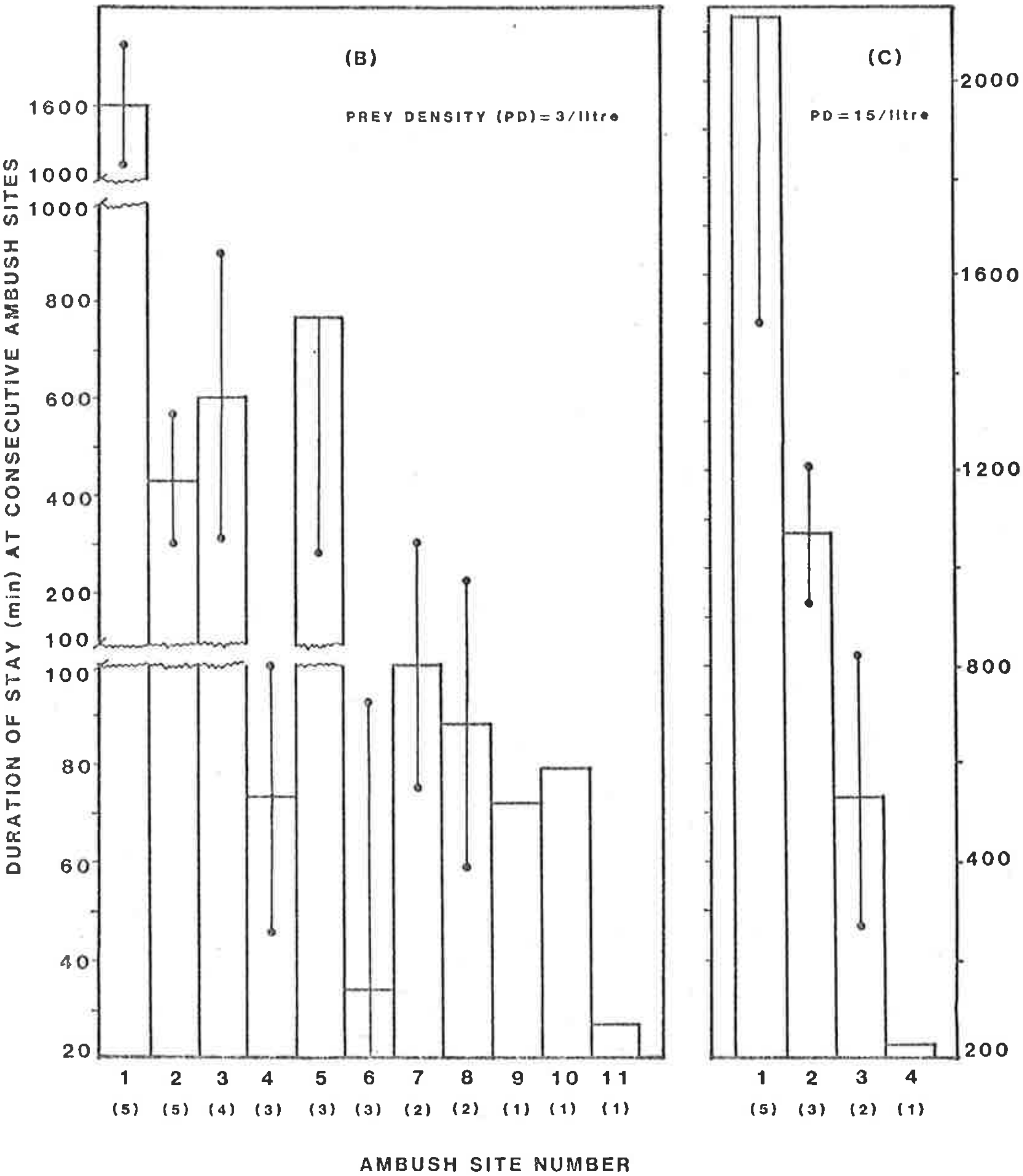
(A) Prey absent.

(B) Prey density 3 per litre.

(C) Prey density 15 per litre.

Vertical bars indicate Standard Error. Number in parenthesis is number of replicates mean and S.E. are based on.


(A)
PREY ABSENT
X̄ = 277 min
X̄ = 14 min
DURATION OF STAY (min) AT CONSECUTIVE AMBUSH SITES
800
600
400
200
100
100
80
60
40
20
0
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
33
35
37
39
(5)
(5)(4)
(4)
AMBUSH SITE NUMBER


(B)
PREY DENSITY (PD) = 3/litre
(C)
PD = 15/litre
DURATION OF STAY (min) AT CONSECUTIVE AMBUSH SITES
1600
1000
1000
800
600
400
200
100
100
80
60
40
20
2000
1600
1200
800
400
200
1 2 3 4 5 6 7 8 9 10 11
(5) (5) (4) (3) (3) (3) (2) (2) (1) (1) (1)
1 2 3 4
(5) (3) (2) (1)
AMBUSH SITE NUMBER

irrespective of the presence or absence of prey. In all three treatments there is a tendency for the duration of stay at a site to become shorter as the experiment progresses.

Because of the design of the experiment the hunger effect was continuously changing and could not really be controlled. To a certain extent this problem was alleviated in a second series of experiments discussed in Section 7:3. Nevertheless the results obtained over the 5 replicates are consistent and permit, it is believed, reasonable conclusions to be drawn.

When no prey are present R.dispar appears to follow two distinct movement patterns between foraging sites (Fig.7:2A). Initially, over the first 46 hours it remains at a site for a variable amount of time ($\bar{x}$ = 277, SD = 217.8, Range 39 to 720 mins., N = 50) it then switches into a second pattern of remaining at a site for a significantly shorter time ($\bar{x}$ = 14.2, SD = 11.4, Range 3 to 54 mins., N = 30 sites). When prey are present the predator remains at the initial site for significantly longer compared with the duration of stay at later sites. At the lower density (i.e. 3/litre) (Fig.7:2B) the variability in length of stay is more evident compared with the higher density (i.e. 15/litre) (Fig.7:2C), which exhibits a consistent trend of reducing the duration of stay at each consecutive site, although the low number of actual site changes, in particular the high density treatment, makes it difficult to identify long term effects or patterns. Ideally, the experiment needs to run over a much longer time to identify any real pattern, especially after the first 6 or so site changes in the high prey density treatment.

Significantly more prey were eaten (t = 2.59, 4 df, $p<0.05$) at the higher prey density than the low, while the distribution of dead prey carcasses on the grid floor of the tanks mirrors the movements between foraging sites by the predators.

(B) Movement Around the Foraging Site.

For each of the 10 periods per film a mean angular change per minute was calculated over the 20 consecutive frames, the data was log transformed and a 2-way ANOVA incorporating a repeated design (SPSS Update 9) was used to test for either a 'time of day' or 'prey density' effect on the mean angular movement per minute around the foraging site. Table 7:4 is the resultant ANOVA table and shows that the time of day had no effect on movement whereas prey density did.

<u>TABLE</u> <u>7:4</u> 2-way ANOVA to test the effect of either 'time of day' when sample was taken or prey density on mean angular movement per minute of adult <u>R.dispar</u> around a foraging site.

Source of Variation	SS	DF	MS	F	Signif
Time of Sample	1.8	9	0.20	0.784	NS
Error 1	18.4	71	0.26		
Prey Density	23.0	2	11.5	9.768	$p<0.05$
Error 2	7.0	6	1.2		
Time x Density	3.00	18	0.16	0.641	NS
<u>Total</u>	53.2	106			

This being the case the data over the different periods were combined to form one data-set. Fig. 7:3 shows the frequency distribution of the angular movement about the foraging site for predators at 3 different prey densities. The null hypothesis that there was no difference in the frequency of angular movements at each prey density was tested with a simple χ^2. A 3 x 6 contingency table was used to test the effect of density.

The results are summarized in Table 7:5. When no prey were present the predators remained stationary significantly more often than when prey were present, while the incidence of moving through relatively small angular changes occurs significantly more often when prey are present. Although not significant, the higher frequency of large angular movements observed when prey were absent merits some comment. After remaining stationary at a particular position for long periods (over one entire 20 minute observation in one instance) the predator would move through a large arc about the foraging site and thus be in a position to receive stimuli from a previously unscanned region of the surrounding water body.

Because of the resolution of the projected image it was not always possible to identify when a capture took place, and therefore I could not ascertain, with confidence, whether these small angular movements (when prey were present) were associated with orientation leading to a capture or whether a post capture behaviour which produced a 'sweeping' or 'searching' pattern of movements which caused the

Fig. 7:3 The effect of prey density on the frequency of angular movement around the ambush-site by adult R.dispar. The values given on the absicca are the means of each angular movement class.
See text for additional details.

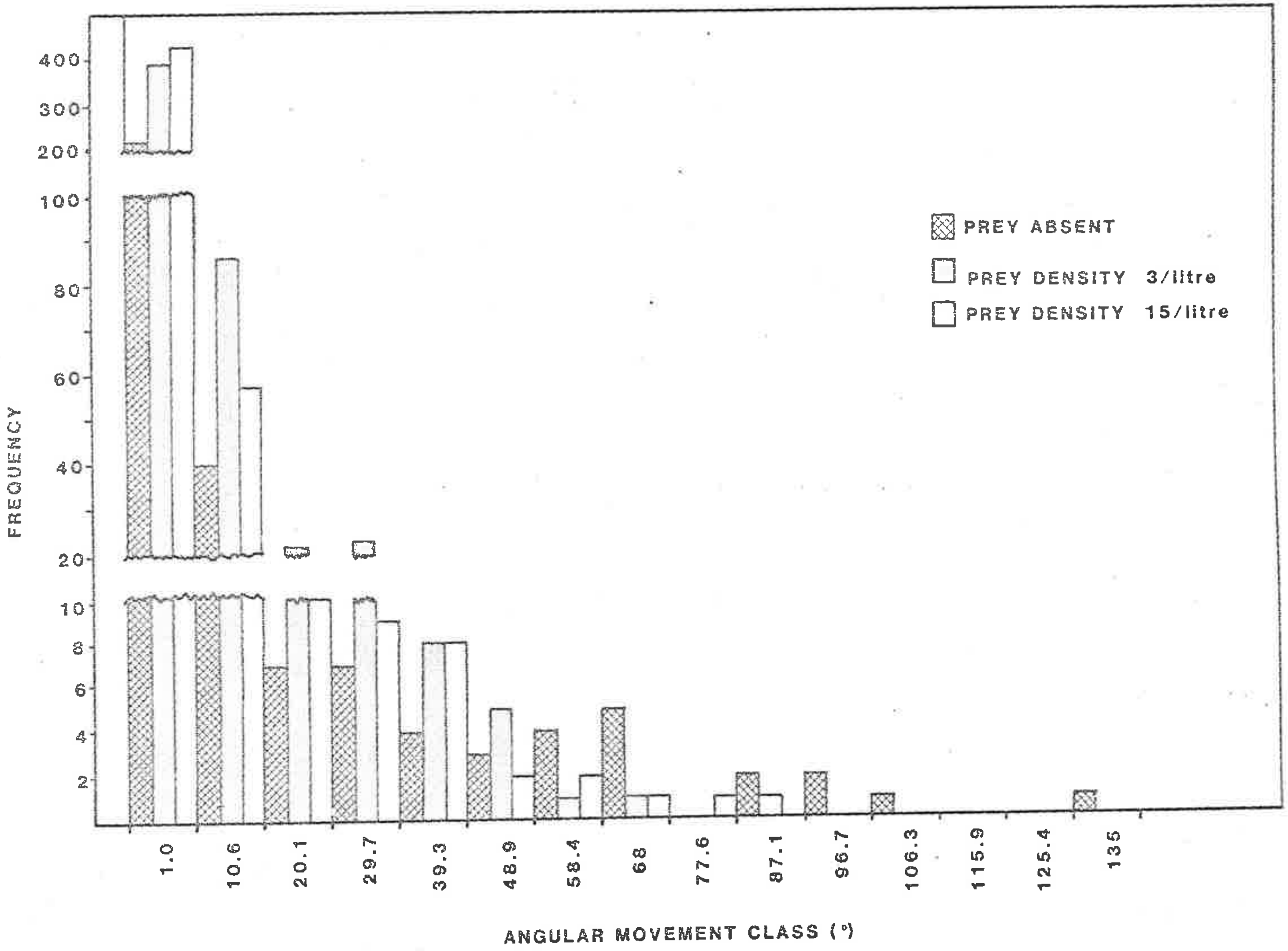

400
300
200
100
80
60
40
20
10
8
6
4
2
FREQUENCY
▨ PREY ABSENT
☐ PREY DENSITY 3/litre
☐ PREY DENSITY 15/litre
1.0
10.6
20.1
29.7
39.3
48.9
58.4
68
77.6
87.1
96.7
106.3
115.9
125.4
135
ANGULAR MOVEMENT CLASS (°)

TABLE 7:5 Effect of Prey Density on the frequency of the mean angular movement around the foraging site, as measured by degrees moved $\min^{-1}$. See text for details.

MEAN OF ANGULAR MOVEMENT CLASS (degrees moved $\min^{-1}$)	FREQUENCY OF MOVEMENTS AT			χ^2 Analysis			
	0	3	15 prey per litre	0 – 3		0 – 15	
0 (Predator stationary)	464	219	235	$\chi^2_1 = 43.9$	$p<0.05$	$\chi^2 = 37.5$	$p<0.05$
1	220	396	435	$\chi^2_1 = 25.1$	$p<0.05$	$\chi^2 = 35.3$	$p<0.05$
10.6	40	86	57	$\chi^2_1 = 8.4$	$p<0.05$	$\chi^2 = 1.5$	NS
20.1	7	20	10	$\chi^2_1 = 3.1$	NS	$\chi^2 = .3$	NS
29.7	7	23	9	$\chi^2_1 = 4.3$	$p<0.05$	$\chi^2 = .2$	NS
30	22	16	14	$\chi^2_1 = .48$	NS	$\chi^2 = .88$	NS

Effect of Density (3 x 6 contingency table) $\chi^2 = 236.6$, $p<0.05$, 10 d.f.

predator to be restricted to a 'small' area. Additional work is required with R.dispar in order to identify any significant pattern of behaviours.

In summary, the above experiments showed that both the number of site changes and the duration of stay at each site was significantly affected by the density of prey present. In addition, prey density also affected the extent of angular movements around the foraging site.

One question that arises from these results is whether the duration of stay at a foraging site (and the associated number of changes between sites) is dependent on the successful capture and subsequent nutritional reward whilst at a site, or does just encountering a prey affect the time spent at a site

In order to answer this the following experiment was carried out.

7:3 THE EFFECT OF PREY ENCOUNTER VERSUS FOOD INTAKE ON DURATION OF STAY AT AN AMBUSH SITE BY R.dispar

7:3.1 Material and Methods

Adult female R.dispar were fed a mixture of prey types and then fasted for 48 hours as outlined in Section 7:2. Individual predators were placed in a large glass aquarium (50 x 35 x 20 deep) filled with 20 litres of filtered dechlorinated tap water. The floors of the tanks were fitted with a plastic grid bottom (see Fig. 3:1) and 12 foraging sites constructed from 2 mm Dia. x 200 mm satay stick embedded into a weighted wax block that fitted into the grid floor. The 12 sites were allocated at random in the tank. Three such tanks were set up.

Predators were exposed to one of three treatments :

(i) Tank with No prey (NP)

(ii) Tank with Model prey - encounters only (EP)

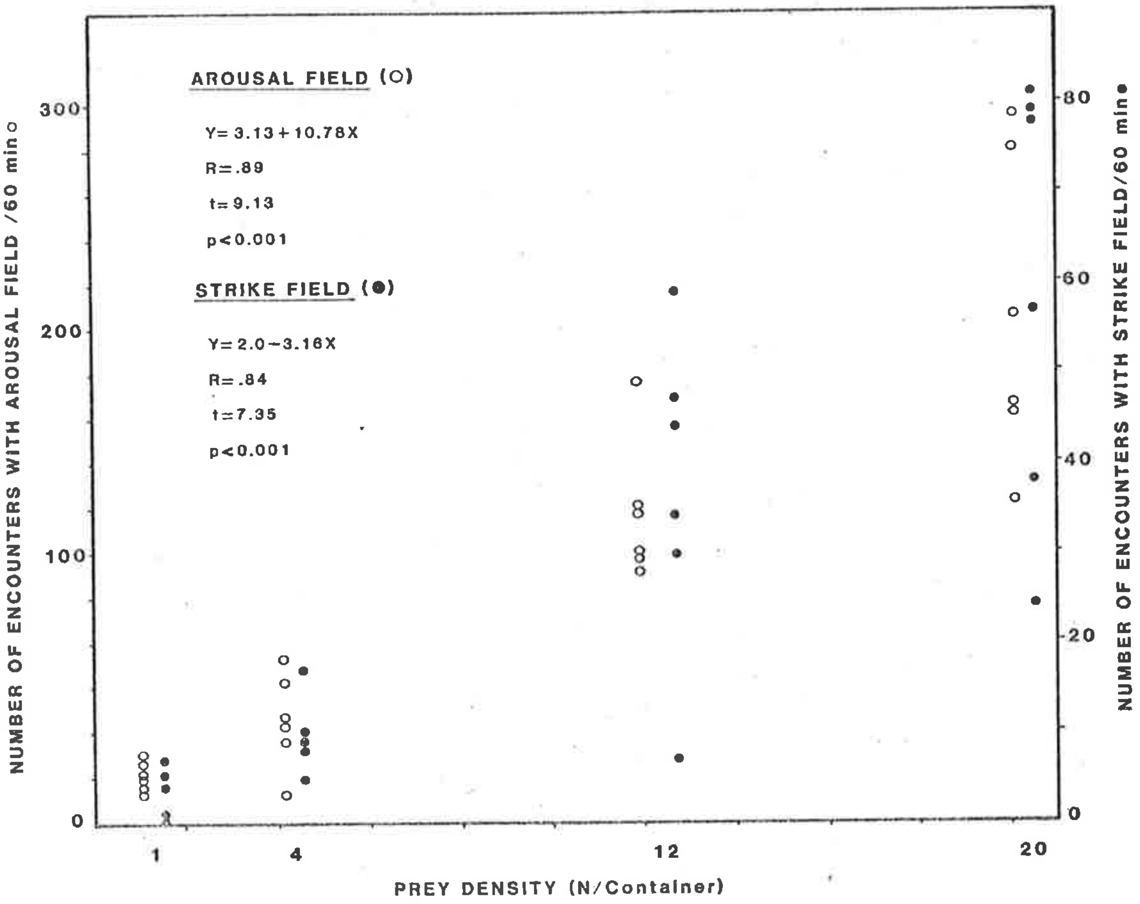
(iii) Tank with Live prey of known density (FP)

Two prey densities (with their associated encounter rates) were selected, these being High density (1.0/litre, i.e. 20 animals per tank) and Low density (0.2/litre, i.e. 4 animals per tank).

The encounter rates were calculated from the results of Chapter 6:4, pooling the data from the 20° and 25° experiments over the 4 densities. Although not strictly applicable, it was decided to plot encounter rate as a linear function of prey density to provide the theoretical encounter rate for use with the model prey. The resultant linear analysis is shown in Fig. 7:4.

By substitution into a polynomial equation a predicted encounter rate ± error could be computed for any prey density over the range used in the linear model. The calculated encounter rates for 4 and 20 prey per tank (0.2 and 1.0 prey/litre) were 1 and 4 encounters per minute for the arousal field and 1 and 10 encounters per 10 minutes for the prey capture field respectively. These encounter rates were used for the model prey to resemble, as closely as possible, the encounter rates that would occur with the live prey.

Fig. 7:4 Regressions of the number of prey encounters with either the predator's arousal field (○) or strike field (●) at four different prey densities during 60 minute observation period. (See text for definitions of arousal and strike fields and additional details). Regression statistics shown on figure.


AROUSAL FIELD (○)
Y= 3.13 + 10.78X
R=.89
t= 9.13
p<0.001
STRIKE FIELD (●)
Y= 2.0−3.16X
R=.84
t=7.35
p<0.001
NUMBER OF ENCOUNTERS WITH AROUSAL FIELD /60 min ○
NUMBER OF ENCOUNTERS WITH STRIKE FIELD/60 min ●
PREY DENSITY (N/Container)
0
100
200
300
0
20
40
60
80
1
4
12
20

PRESENTATION OF MODEL PREY AND EXPERIMENTAL PROCEDURE

Model prey, 6 mm in length (see Section 3:6) were suspended on fine nylon fishing line and presented to the predator as outlined in Chapter 3:4 at the above rates in such a fashion that the predator was clearly aroused towards the prey (in some instances predators struck at the prey) but was not permitted to capture or, in relation to the strike space, the predators were allowed to strike at and capture the model.

Predators were continuously observed for 12 hours and there were 3 replicates of each treatment using new predators in each case.

7:3.2 Results

Table 7:6 summarizes the results of the number of site changes and duration of stay over the three replicates for each treatment. It would appear that the mere fact of encountering a prey will result in the predator remaining at a 'potentially rewarding' foraging site. To test the null hypothesis that prey encounter does not significantly increase the duration of stay at a foraging site the raw data were analysed using the Mann-Whitney Test between each treatment. Because each experiment was run for a set period (i.e. 12 hours) it was decided to ignore the final duration of stay for each replicate, as this simply represented the experimental period minus the sum of the earlier durations and therefore had no real biological meaning in connection with the duration of stay at a foraging site. The result analysis summary is shown in Table 7:7.

TABLE 7:6 The number of site changes and mean duration of stay at a site by *R.dispar* in relation to density of prey.

PREY DENSITY (n.l^{-1})		REPLICATE NUMBER				
		1	2	3	$\bar{x}$	SD
0	# Site Changes	3	1	4	2.7	1.5
	$\bar{x}$±SD Duration	180 ± 145	360 ± 76	144 ± 107		
4	MODEL PREY					
	# Site Changes	1	2	1	1.3	.6
	$\bar{x}$±SD Duration	360 ± 209	240 ± 194	360 ± 341		
	LIVE PREY					
	# Site Changes	1	0	2	1.0	1.0
	$\bar{x}$±SD Duration	360 ± 396	720 ± 0	240 ± 308		
20	MODEL PREY					
	# Site Changes	2	1	0	1.3	1.1
	$\bar{x}$±SD Duration	240 ± 216	360 ± 56	720 ± 0		
	LIVE PREY					
	# Site Changes	0	0	1	0.3	.6
	$\bar{x}$±SD Duration	720 ± 0	720 ± 0	360 ± 483		

TABLE 7:7 The comparison of the duration of stay at each foraging site when either no prey were present or when the predators were stimulated with model prey at two different encounter rates.

DURATION OF STAY (mins)

LOW ENCOUNTERS	PREY ABSENT	HIGH ENCOUNTERS
508	372	489
410	208	130
281	40	400
601	306	720
	129	
	297	
	41	
	200	

U = 29 $p<0.05$ U = 29 $p<0.05$

U = 9

Not Significant

Clearly encounters cause the predator to remain at a potentially profitable site, even though no nutritional reward is forthcoming. The fact that the experiment was run over a relatively short period does affect the conclusion that can be drawn. In all likelihood, the pattern that has been observed would disappear after some time due to the predator's food deprivation time increasing, and the need to capture and feed becoming paramount. Nevertheless it is believed that this experiment illustrates that prey encounter, as distinct from feeding, is an important element in determining the time budgeting of sit-and-wait predators at foraging sites.

7:4 DISCUSSION

The results of the experiments described in this chapter support the hypothesis that prey density significantly affects the number of times that a sit-and-wait predator changes its foraging site, and the subsequent duration of stay at each site, and as such supports the findings of Formanowicz et al. (1982). Overall, more prey were eaten at the higher density and so capture-rate, or the amount of food in the predator's gut, may be used to assess the availability of prey. However, the second series of experiments, using model prey, clearly demonstrate that predators remain significantly longer at a foraging site after encountering a 'prey', compared with the mean site duration when no prey are present or when captures actually occur. The rate of model presentation nevertheless does not appear to affect the duration of stay.

Clearly this type of behavioural response should be adaptive, for on changing ambush sites, when prey density is low, the probability of encountering new prey increases (Łommicki and Slobodkin 1966). At higher prey densities the predators remain longer at a site and have therefore more time to engage in other activities, for example mate finding/mating. In addition, the lessening of open water swimming or movements amongst vegetation will reduce their exposure to predators (see Chapter 2). Andrews (1979) reported just such a case in the lizard, Corytophanes cristatus, where the risk of predation was minimized by adopting an extreme sit-and-wait predation technique coupled with the potential to capture and handle large arthropod prey, thus reducing the bouts of feeding activity. As mentioned in the introduction, a basic prerequisite of current optimal foraging theory involves the predator's ability to assess prey density, but there exists little empirical data on the possible mechanisms adopted by predators enabling them to do this.

It has been shown in Chapter 5 that the mean time between prey captures (i.e. mean intercatch interval) plays a significant role in the way that R.dispar subsequently utilizes individual prey items, which results in partial consumption of the prey. In addition however, the results presented in this chapter indicate that capture and feeding per se are not the only criteria used in assessing prey density but that stimuli from a prey encounter significantly affects the time that a predator will remain at a site. It would appear likely therefore that R.dispar utilizes more than one technique in assessing the prey density and that it can utilize this information in at least two behavioural responses, i.e. duration of stay at a foraging site and prey utilization.

Jaeger and Barnard (1981) suggested that the salamander, Plethodon cinereus Green, may use an encounter rate mechanism in determining search tactics and optimal diet, while recently Formanowicz (1982) reported that larvae of Dytiscus verticalis may be utilizing an encounter rate mechanism in assessing prey density and subsequently changing its search tactics. The initial selection of a foraging site by R.dispar, as an example of a sit-and-wait predator, probably does not include any assessment of prey availability but rather they depend on the spatial location of suitable objects on which to rest, submerged twigs or plants (and the associated water depth), from which they can capture prey. Depending on the current motivational state of the predator (i.e. how hungry it may be), in addition to other internal and external factors, the subsequent encounter rate and capture rate of prey will influence how long the predator will remain at the site before moving. Therefore the search mechanism of R.dispar involves the selection of a foraging site, suitably located, from which it can grasp prey. Once positioned it remains effectively motionless (see Table 7:5) until prey move into the vicinity, where arousal and capture takes place. Whether the change in frequency of angular movements around the foraging site is either orientation leading to capture or a post-capture behaviour which increases the probability of encountering additional prey, I am unable to say, as time did not permit additional experiments to be undertaken. The feeding time and subsequent utilization of the prey is affected in turn by the mean intercatch interval at least, with the possibility existing of encounter rate in addition to capture-rate providing further information to the predator enabling it to assess prey density.

If prey are not in the vicinity the predator adopts one of two movement patterns (see Fig. 7:3A) depending on, probably, the time since the last meal and therefore its present motivational state. It will move to another site and either remain there for between 40 minutes and 12 hours ($\bar{x} = 277$) or from 3 to 54 minutes ($\bar{x} = 14.2$) and therefore, in the second case, rapidly move between foraging sites, increasing the probability of locating and encountering more profitable ambush sites and thus prey. A similar hunger-dependent change in foraging site has been reported by Griffiths (1980a) who found that antlion larvae changed location of their ambush pits more often when starved than well fed.

In summary it can be seen that the assessment of prey density may involve a far more complex series of factors than have hitherto been reported, and that depending on the circumstances, predators may switch between different mechanisms or utilize information from several simultaneously. Clearly, for R.dispar, both prey encounter rate and prey capture rate appear to be important in determining the duration of stay at a foraging or ambush site (with the subsequent related rate of movement between sites) while the mean intercatch interval significantly affects the feeding time on an individual prey.

To what extent these factors are interrelated in so far as providing an overall 'picture' to the predator of the surrounding profitability of the habitat is concerned, cannot at present be determined. Recently, Formanowicz (1982) suggested that the encounter rate between predator and prey may be an overriding mechanism by which Dytiscus verticalis larvae decide which search tactic, either active search or ambush, to adopt at various prey densities, while Inove and Matsura (1983) working with the mantid, Paratenodera angustipennis, successfully correlated a switch in search tactics, from ambush to active forager, with an increase in hunger, although they were unable to identify the mechanisms underlying the reverse switching, from active search to ambush. Perhaps an encounter rate threshhold may be involved?

Unlike D.verticalis and P.angustipennis, R.dispar cannot capture prey while swimming and therefore the 'active search' component of its complete foraging response is concerned with locating an ambush site rather than prey items per se. Whether R.dispar randomly chooses ambush sites or uses far more subtle environmental cues is unknown, as is the relative energy expenditure. Morisita (1952) showed that ant-lions expend significant amounts of energy and time in locating suitable sites for their pitfall traps. Therefore, it can be seen that in addition to assessing the potential profitability of an ambush site the costs involved in moving between sites should be taken into account in some way by the predator. One would expect that selection would favour those predators that, when prey become scarce, move to a new, more favourable site rather than starve to death. However, it could be hypothesized that after prolonged periods of prey absence the optimal strategy to adopt, taking into account the costs involved in moving between sites, would be to remain stationary. This hypothetical adaptation remains to be tested.

CHAPTER 8

GENERAL DISCUSSION

This study has attempted to examine the ethology of a sit-and-wait predator, R.dispar, that is found in farm dams and other lotic water bodies in Australia. Emphasis has been placed on the importance of both the internal motivational level of the predator (as measured by food deprivation time) and the density of the prey, in affecting the various behavioural components that make up the predatory repertoire leading to capture; in addition to examining their effect on the way that individual prey are utilized during the feeding period.

Each chapter of this study has its own discussion section, where data are discussed and compared with the published literature. However, it would seem worthwhile at this point to examine several general points that have not been considered previously in detail and to mention others that may be of general interest to workers contemplating similar behavioural studies on such predators. In conclusion, aspects of this study that show promise as topics for future research work are discussed.

As mentioned previously, sit and wait predators are, by definition, reliant on the movement of the prey to bring about an encounter and a subsequent capture. Therefore, it is to be expected that natural selection would most certainly have the effect of concentrating the predatory effort in (1) the capture process per se and probably (2) the selection of a foraging site that increases the probability of an encounter taking place.

Data presented in this thesis show that R.dispar, as a sit and wait predator, certainly exhibits behaviours predicted from (1) above.

The actual behaviours involved in the selection of an ambush site (2) were not examined however. Whether *R.dispar* chooses sites at random within the pond or uses a far more elaborate system of cues is unknown. However, once positioned at an ambush site, its duration of stay is affected by the number of prey encountered~~s~~ and, in all likelihood, the number of captures and subsequent feeding. Clearly both the hunger level of the predator and the prey density play a significant part in determining the observed behaviours associated with rates of movement at and between ambush sites. Pianka (1974) characterized predators as ambush foragers or active foragers. Using this definition *R.dispar* would be categorized as an ambush forager. Inove and Matsura (1983) showed that in the similarly categorized mantid, *Paratenodera angustipennis*, hungry individuals start active search. They concluded that there is a phase of active search even in so-called ambush foragers. *R.dispar* does not have a searching component (for prey) in its predatory behaviour. However, the increased rate of moving between ambush sites, as demonstrated in this thesis, in association with hunger, is believed to constitute a 'searching' phase in the predatory process;. The 'searching' component being for a suitable ambush site rather than for prey.

If prey were randomly distributed and moving within the water body the selection of another ambush site by *R.dispar* would not necessarily increase the probability of encountering prey. However, the fact that prey are not distributed at random but tend to form aggregations often containing hundreds of individuals, and that certain areas of the dam seem to be 'preferred' by the prey, means that the probability of encountering prey can be increased. This is achieved by

R.dispar by increasing the rate of moving between ambush sites, thus increasing the likelihood of encountering a favourable site for prey encoumters.The interrelated prey encounter-rate and the predator's current hunger level are used as stimuli to estimate the profitability of a site. If prey are absent, and the hunger level high, the predator remains for a short period before moving off to another site; if prey are present and feeding commences, the hunger level drops and the predator remains at the site.

Bearing the above in mind, it would be expected that the sit-and-wait predator, like other predators, will at times be faced with an over-supply of prey, and that it could be expected that selection would favour those predators that can capitalize on such circumstances. R.dispar apparently proves to be just such a predator, having the capability to capture and hold more than one prey at the same time, in addition to being able, via its unusual extraction dynamics, to utilize prey in an optimal manner.

I have tended to discuss much of the data in the light of current optimal foraging theory. This is not to say that I believe optimal foraging to be without fault. Indeed, even if the models are successful in their predictions, they do not necessarily lead to the conclusion that animals are perfectly adapted to the natural environment. As has been pointed out, evolutionary adaptation lags behind environmental change (see Krebs et al. 1981; Maynard-Smith 1978). Nevertheless it has proved to be a valuable tool in the quantitative study of adaptation, especially in the field of decision-making processes by animals. A recent corollary in examining foraging patterns is the influence of other activities and how these activities are associated with foraging. For example, Milinski and Heller (1978) showed that the efficiency of foraging sticklebacks (Gasterosteus aculeatus) was reduced by the imposition of the need to watch for a predator, and there are numerous examples of birds interspersing their feeding with scanning to detect danger, at the expense of their food-gathering rate (for example, Barnard 1980; Bertram 1980; Elgar and Catterall 1981; Greig-Smith 1983; Inglis and Lazarus 1981; Lazarus 1978).

In R.dispar, it was shown that both the defensive or evasive behaviour associated with either predator threat or prey defence significantly influenced the predatory behaviour, principally the time-budgetting at foraging sites. I believe that the influence of such risk factors may prove worthwhile avenues of future research in predatory behaviour,and in particular, their effects on the interrelations between other components of the predation process, for example, feeding time and prey utilization.

This study has, it is believed, provided a number of potentially stimulating and useful areas of research that either may be continued or act as a starting point for future research. In addition to those already mentioned I believe others are worthy of note. Firstly, the age-dependent distribution in the field needs to be examined for evidence of the significance of oviposition- site selection, and/or support for the 'presence of prey' hypothesis. This may prove difficult since R.dispar proved to be a difficult animal to deal with in the field. Perhaps A.deanei may prove a better candidate for such studies.

The unusual feeding behaviour in regard to the extraction dynamics, and the associated diluting of prey contents by external water, may prove useful in investigating the way in which predators assess the quality of the prey. The whole area of prey- size selection by ambush predators, although only marginally touched on in this thesis, warrants further examination. Can ambush predators 'afford' to be as selective as actively pursuing predators, especially if prey are encountered infrequently? This is only one of the questions that come to mind in considering prey size selection.

Data show that both prey encounter and hunger level significantly affect the rate of change between, and the duration of stay at, an ambush site. Extension of this approach to examine the effect of feeding only, in isolation from a previous encounter, will probably provide valuable data in identifying the methods that predators use in assessing the profitability of an ambush site. The incorporation of a longer experimental period, in conjunction with the use of model prey will, no doubt, allow more conclusive statements to be made in assessing the importance of encounters only, without subsequent feeding. R.dispar would be a useful subject for such studies.

Finally, in a concluding statement to this study as a whole, I believe it appropriate to say that enquiry about predatory behaviour in general, and sit and wait predators in particular, is in its infancy. The importance of such knowledge in determining complex predator-prey relations has already been mentioned. In addition, such an approach may be useful not only in explaining the relationships but provides a better understanding of the way such associations may have developed.

BIBLIOGRAPHY

ABBOTT, C. (1940). Some reflex responses of *Ranatra fusca* to contact stimuli. *Bull. Brooklyn Ent. Soc.* 35:133-134.

ADAMS, J. (1980). The feeding behaviour of *Bdellocephala punctata*, a freshwater triclad. *Oikos.* 35: 2-7.

AKRE, B.G. and D.M. JOHNSON (1979). Switching and sigmoid functional response curves by damselfly naiads with alternative prey available. *J. Anim. Ecol.* 48: 703-720.

ALCOCK, J. (1978). *Animal Behaviour : An evolutionary approach.* Pub. Sinauer Associates, Inc. Sunderland, Massachusetts.

ALVEY, N.G. *et.al.* (1977). *GENSTAT 4.01. A general Statisical Program.* Published by The Statistic Department, Rothamsted Experimental Station .Hertfordshire England.

ANDORFER, B. (1980). The school behaviour of *Leucaspius delineatus* in relation to ambient space and the presence of a Pike, (*Esox lucius*). *Oecologia.*(Berlin) 47: 137-140.

ANDREWS, R. M. (1979). The lizard *Corytophanes cristatus* :an extreme 'sit-and- wait' predator. *Biotropica* 11: 136-139.

AOKI, I. (1980). Ananalysis of the schooling behaviour of fish : Internal organisation and communication process. *Bull. Ocean Res. Inst. Univ. Tokyo.* 0(12): 1-60.

ARNOLD, S.J. (1978). Some effects of early experience on feeding responses in the common Garter Snake, *Thamnophis sirtalis.* *Anim. Behav.* 26: 455-462.

ARNOUD, B. (1966). De Staafwants *Ranatra linearis.* *Nat. Historisch Maandblad.* 55:10, 151-155.

AUSLANDER, D., G. OSTER and C. HUFFAKER (1974). Dynamics of interacting populations. *Journal of the Franklin Institute.* 297: 345-376.

AUSTIN, A.D. and A.D. BLEST (1979). The biology of two Australian species of dinopid spider. *J. Zool. (Lond.).* 189: 145-156.

BAERENDS, G.P., R. BROUWER and H.Ty. WATERBOLK (1955). Ethological studies on *Lebistes reticulatus* (Peters) : I, An analysis of male courtship pattern. *Behaviour.* 8:249-334.

BAILEY, P.C.E. (1981). Diet activity patterns in nymphs of an Australian mayfly, *Atalophlebiodes* sp. (Ephemeroptera : Leptophebiidae). *Aust. J. Mar. Freshwater Res.* 32: 121-131.

BALAN, J. and N.N. GERBER (1972). Attraction and killing of the nematode *Panagrellus redivivus* by the predaceous fungi *Arthrobotrys dactyloides.* *Nematologica.* 18: 163-173.

BAN, Y. (1981). Some observations on the life cycle of the Water Scorpion, Ranatra unicolor (Hemiptera : Heteroptera : Nepidae) in Yamanoshita Bay, Lake Biwa, Japan. *Int. Ver. Theor. Angew. Limnol. Verh.* 21: 1621-1625.

BANKS, C.J. (1957). The behaviour of individual coccinellid larvae on plants. *Brit. J. Anim. Behav.* 5: 12-24.

BAQAI, I.U., P.A. SIDDIQUI and T. AKHTAR (1977). Description and habitats of some aquatic Hemiptera from Sind Pakistan. *Sind. Univ. Res. J. (Sci. Ser.).* 10: 31-36.

BARE, C.O. (1926). Life histories of some Kansas 'backswimmers'. *Ann. Entomol. Soc. Am.* 19: 93-101.

BARNARD, C.J. (1980). Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). *Anim. Behav.* 28: 295-309.

BARTON-BROWNE, L. (1975). Regulatory mechanisms in insect feeding. *Adv. Insect Physiol.* 11: 1-116.

BARTON-BROWNE, L., J.E. MOORHOUSE and A.C.M. van GERWEN (1975). Sensory adaptation and the regulation of meal size in the Australian Plague Locust, *Chortoicetes terminifera*. *J. Insect Physiol.* 21: 1633-1639.

BAUDRY, N. (1972). Comparison of the different types of perisympathetic organs of some families of heteroptera (Nepidae, Pyrrhocoridae, Coreidae and Pentatomidae). *C.R. Hebd. Seances Acad. Sci. Ser. D. Sci. Nat.* 275: 1535-1538.

BAUDRY-PARTIAOGLOU, N. (1978). Anatomy and histology of Neuro hemal organs of some Hemiptera. *Int. J. Insect Morphol. Embryol.* 7: 1-32.

BAUER, T. (1982). Prey capture in a ground-beetle larva. *Anim. Behav.* 30: 203-208.

BEARD, R.L. (1963). Insect toxins and venoms. *Annu. Rev. Entomol.* 8: 1-18.

BEGON, M. and M. MORTIMER (1981). *Population Ecology. A unified study of Animals and Plants.* Blackwell Scientific Publications, Oxford, London.

BEISSINGER, S.R. (1983). Hunting behaviour, prey selection, and energetics of Snail Kites in Guyana : Consumer choice by a specialist. *The Auk.* 100: 84-92.

BERNAYS, E.A. and S.J. SIMPSON (1982). Control of food intake. *Adv. Insect Physiol.* 16: 59-118.

BERTRAM, B.C.R. (1978). Living in Groups : Predators and prey. In : Behavioural Ecology an Evolutionary Approach. Eds. J.R. Krebs and N.B. Davis, Blackwell Scientific Publications, Oxford.

BERTRAM, B.C.R. (1979). Serengeti predators and their social systems. In : Serengeti : Dynamics of an ecosystem. Eds. A.R.E. Sinclair and M. Norton-Griffiths, University of Chicago Press, Chicago.

BERTRAM, B.C.R. (1980). Vigilance and group size in ostriches. Anim. Behav. 28: 278-286.

BEUKEMER, J.J. (1968). Predation by the three-spined stickleback (Gasterosteus aculatus) : The influence of hunger and experience. Behaviour. 31: 1-126.

BHATNAGAR, B.S. (1978). Comparative morphology of the spiracles in some aquatic and semi-aquatic heteroptera. Acta. Entomol. Bohem. 75: 25-31.

BIBEN, M. (1979). Predation and predatory play behaviour of domestic cats. Anim. Behav. 27: 81-94.

BLINN, D.W., C. PINNEY, and M.W. SANDERSON (1982). Nocturnal planktonic behaviour of Ranatra montezuma (Nepidae : Heteroptera : Hemiptera) in Montezuma Well, Arizona, U.S.A. J. Kans. Entomol. Soc. 55: 481-484.

BLOIS, C. and A. CLOAREC (1983). Density-dependent prey selection in the water stick insect, Ranatra linearis (Heteroptera). J. Anim. Ecol. 52: 849-866.

BREDEN, F. (1982). Body size and orientation in aggregations of Toad Tadpoles. Copeia. 1982(3): 672-680.

BRISTOWE, W.S. (1958). The world of Spiders. William Collins, London.

BROCK, V.E. and R.H. RIFFENBURGH (1960). Fish schooling : a possible factor in reducing predation. J. Cons. Perm. Intern. Explor. Mer. 25: 307-317.

BROOKE, M.M. and H.O. PROSKE (1946). Precipitin test for determining natural insect predators of immature mosquitoes. J. Nat. Malaria Soc. 5: 45-56.

BROWN, E.S. (1951). The relation between migration-rate and type of habitat in aquatic insects, with special reference to certain species of Corixidae. Proc. Zool. Soc. Lond. 121: 539-545.

BROWN, J.L. and G.H. ORIANS (1970). Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1: 239-262.

BROWN, H.D. (1974). Defensive behaviour of the wheat aphid *Schizaphis graminum* (Rondani) (Hemiptera : Aphididae), against coccinellidae. *J. Ent. (A).* 48: 157-165.

BROWN, L. (1977). *Birds of Prey : Their biology and ecology.* A. & W. Publishers, Inc. : New York.

BRUNS, D.A. and W.L. MINCKLEY (1980). Distribution and abundance of benthic invertebrates in the Sonoran Desert Stream. *J. Arid Environ.* 3: 117-131.

BUCHLI, H.H.R. (1969). Hunting behaviour in the Ctenizidae. *Amer. Zool.* 9: 175-193.

BURKHOLDER, B. (1959). Movements and behaviour of a Wolf pack in Alaska. *J. Wildl. Mgmt.* 23: 1-11.

BUTLER, E.A. (1918). On the association between the Hemiptera, Heteroptera and vegetation. *Ent. Month. Mag.* 54:132.

BUTLER, E.A. (1923). Nepidae. *In* : *A Biology of British Hemiptera.* Witherby, London. 682 pp.

CARLO, J.A.de (1968). Aparato genital femenino de *Ranatra*. *Physis, Sec. B.(Beunos Aires).* 28: 199-201.

CARLO, J.M.de and G.N. PELLERANO (1977). Compound eye of *Ranatra segrega* II. *Physis, Sec. B (Beunos Aires).* 37: 151-160.

CARLO, J.M.de and G.N. PELLERANO (1980). Microscopic anatomy of maxillary glands of *Ranatra* (Hemiptera : Heteroptera : Ranatridae). *Physis, Sec. B. (Beunos Aires).* 39: 9-15.

CERRI, R.D. and D.F. FRAZER (1983). Predation and risk in foraging minnows : balancing conflicting demands. *Amer. Nat.* 121: 552-561.

CHAPMAN, R.F. (1971). *The Insects. Structure and Function.* McGraw-Hill. London. New York.

CHARNOV, E.L. (1976a). Optimal foraging, the marginal value theorem. *Theor. Pop. Biol.* 9: 129-136.

CHARNOV, E. L. (1976b) Attack strategy of a Mantid. *Amer.Nat* 110: 141-151.

CHINERY, M. (1979). *Killers of the Wild : The technology of predation in the plant and animal world.* Salamander Books Ltd., London.

CHOWDHURY, S.H. and GULROO, B. (1974). Morphology and anatomy of the alimentary canal in *Ranatra chinensis*. *Bangladesh J. Zool.* 2: 53-63.

CLOAREC, A. (1969a). Contribution a l'etude des rythmes d'activite locomotrice de *Ranatra linearis*. *Rev. Comp. Animal.* 3:11-25 (1969).

CLOAREC, A. (1969b). Etude descriptive et experimentale du comportement de capture de *Ranatra linearis* an cours de son ontogenese. *Behaviour.* 35: 84-113.

CLOAREC, A. (1971a). Contribution a l'etude de la regulation du comportement alimentaire des insectes. Cas particuliar de *Ranatra linearis* (Insecte - Heteroptere aquatigue). These. Universite de Rennes, 251 pp.

CLOAREC, A. (1971b). Etude structurale de la deuxienne masse ganglionnaire du systeme nerveux central de *Ranatra linearis*. *Ann. Soc. Ent. Fr.* (New series) 7: 935-957.

CLOAREC, A. (1971c). Evolution de l'oeil compose de *Ranatra linearis* L. au cours du developpement larvaire. *Bull. Soc. Scient. Bretagne.* 46: 215-223.

CLOAREC, A. (1972a). Activite respiratoire de *Ranatra linearis* (Insecte, Heteroptere aquatigue). *Bull. Soc. Zool. France.* 97: 729-736.

CLOAREC, A. (1972b). Variations du comportement respiratoire au cours du developpement larvaire de *Ranatra linearis*. *Rev. Comp. Animal.* 6: 237-244.

CLOAREC, A. (1972c). Revue generale de comportements alimentaires d'insectes predateurs et de leur regulation. *Annee Biol.* 11: 257-290.

CLOAREC, A. (1973a). The sensory nervous structure of the Prothoracic leg of *Ranatra linearis* (Insecta Heteroptera). *Forma et Functio.* 6: 247-278.

CLOAREC, A. (1973b). Variations de la structure de la patte ravisseuse de *Ranatra linearis* L. au cours du developpement larvaire I. Morphogenese. *Bull. Soc. scient. Bretagne.* 48: 161-178.

CLOAREC, A. (1974a). A study of the postural variations in the foreleg of *Ranatra linearis* (Insect : Heteroptera). *Behaviour.* 48: 89-110.

CLOAREC, A. (1974b). Variations of the structure of the prothoracic leg of *Ranatra linearis* during nymphal development. II. Distribution of Sense Organs. *Forma et Functio.* 7: 201-240.

CLOAREC, A. (1975). Variations quantitatives de la prise alimentaire chez *Ranatra linearis*. *Ann. Nat. Alim.* 29: 245-257.

CLOAREC, A. (1976). Interactions between different receptors involved in prey capture in *Ranatra linearis* (Insect : Heteroptera). *Biol. Behav.* 1: 251-266.

CLOAREC, A. (1979). Estimation of hit distance by *Ranatra*. *Biol. Behav.* 4: 173-191.

CLOAREC, A. (1980a). Ontogeny of hit distance estimation in *Ranatra*. *Biol. Behav.* 5: 97-118.

CLOAREC, A. (1980b). Post-moult behaviour in the water-stick insect, *Ranatra linearis*. *Behaviour*. 73: 304-324.

CLOAREC, A. (1981). Effect on predatory performance of the presence of prey after moulting in the water-stick insect, *Ranatra linearis*. *Physiol. Entomol.* 6:241-249.

CLOAREC, A. (1982a). Predatory success in the water-stick insect - the Role of Visual and Mechanical Stimulations. *Anim. Behav.* 30: 549-556.

CLOAREC, A. (1982b). Influence of the duration of deprivation on the predatory performance of the water-stick insect. *Z. Tierpsychol.* 58: 217-230.

CLOAREC, A. (1983). Deprivation of prey during development of the water-stick insect, *Ranatra linearis*. *Biol. Behav.* 8: 141-158.

CLOUDSLEY-THOMPSON, J.L. (1980). *Tooth and Claw : Defence strategies in the animal world.* J.M. Dent & Sons Ltd. London : Melbourne.

COBBEN, R.H. (1968). *Evolution trends in Heteroptera Pt.1. Eggs, architecture of the shell, gross embryology and eclosion.* Centre for Agriculture Publishing and Documentation, Wageningen, Netherlands.

COBBEN, R.H. (1978). *Evolutionary trends in the Heteroptera Pt. II. Mouthpart-structures and feeding strategies.* Centre for Agriculture Publishing and Documentation, Wageningen, Netherlands.

COFRANCESCO, A.F. and F.G. HOWELL (1982). Influence of temperature and time of day on the ventilatory activities of *Erythemis simpliciocollis* Say (Odonata) naiads. *Environ. Entomol.* 11: 313-317.

CONNELL, J.H. (1961). Effects of competition, predation by *Thais lapillus* and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* 31: 61-104.

CONWAY, G.R.,.N. R. GLASS and D. WILCOX (1970). Fitting non linear models to biological data by Marquardt's Algorithm. *Ecology.* 51: 503-507.

COOK, R.M. and B.J. COCKRELL. (1978). Predation ingestion rate and its bearing on feeding and the theory of optimal diets. *J. Anim. Ecol.* 47: 529-547.

COPELAND, J. and A.D. CARLSON (1979). Prey capture in Mantids : A non-stereotyped component of lunge. *J. Insect Physiol.* 25: 263-269.

COTT, H.B. (1957). *Adaptive colouration in animals.* Methuen and Co., London.

COWIE, R.J. (1977). Optimal foraging in Great Tits. *Nature.*268: 137-139

COWIE,R. J. (19790 Foraging behaviour of the Great Tit (*Parusma jor*) in a patchy enviroment. Unpublished D. Phil thesis , Oxford University.

CROSS, J.L. (1972). New state records of aquatic insects from Virginia, U.S.A. *Proc. Entomol. Soc. Wash.* 74: 476.

CROWLEY, P.H. (1979). Behaviour of zygopteran nymphs in a simulated weed bed. *Odonatologica* 8: 91-101.

CURIO, E. (1976). *The Ethology of Predation.* Springer-Verlag : Berlin and New York.

DANIEL, C. and F.S. WOOD (1971). *Fitting equations to data. Computor analysis of multifactor data for scientists and engineers.* Wiley-Interscience Series in Probability and Mathematical Statistics. (Eds) R.A. Bradley, J.S. Hunger, D.G. Kendall and G.S. Watson. John Wiley & Son, New York.342pp.

DAVIS, C.C. (1961). Hatching in *Ranatra fusca* (Hemiptera : Nepidae). *Trans. Amer. Micro. Soc.* 80: 230-234.

DAWKINS, R. (1976). *The Selfish Gene.* Oxford University Press, Oxford.

DAWKINS, R. and J.R. KREBS (1979). Arm races between and within species. *Proc. R. Soc. Lond. B. Bio.* 205: 489-511.

DeBACH, P. (1974). *Biological control by natural enemies.* Cambridge University Press, London.

DESAI, V.R. and K.J. RAO (1972). Preliminary observations on use of Malarial B, a larvicidal oil in the control of aquatic insects in nursery ponds. *J. Bombay Nat. Hist. Soc.* 69: 214-217.

DESHEFY, G.S. (1980). Anti-predator behaviour in swarms of *Rhagovelia obesa* (Hemiptera : Veliidae). *Pan-Pac. Entomol.* 56: 111-112.

DESHPANDE, S.B. (1980). The thoracic functional myology of *Cyclopelta siccifolia* (Hemiptera : Heteroptera : Pentatomidae) and *Ranatra elongata* (Hemiptera : Heteroptera : Nepidae). *Entomol. Mon. Mag.* 116: 199-206.

DETHIER, V.G. (1973). Aquatic heteroptera from the Cerutti collection. *Mitr. Schweiz. Entomol. Ges.* 46: 297-312.

DETHIER, V.G. (1976). *The Hungry Fly. A physiological study of the Behaviour Associated with Feeding.* Harvard University Press. Cambridge, Massachussetts and London, England.

DETHIER, V.G. and D. BODENSTEIN (1958). Hunger in the Blowfly. *Z. Tierpsychol.* 15: 129-140.

DETHIER, V.G. and F.E. HANSON (1965). Taste papillae of the blowfly. *J. Cell. Comp. Physiol.* 65: 93-100.

DETHIER, V.G., R.L. SOLOMON and L.H. TURNER (1965). Sensory input and central excitation and inhibition in the blowfly. *J. Comp. Physiol.* 60: 303-313.

DEVONPORT, B.F. and M.J. WINTERBOURN (1976). The Feeding relationships of two invertebrate predators in a New Zealand River. *Freshwater Biology* 6: 167-176.

DIXON, A.F.G. (1959). An experimental study of the searching behaviour of the predatory coccinellid beetle, *Adalia decempunctata* (L.). *J. Anim. Ecol.* 28: 259-281.

DIXON, A.F.G. and R.J. RUSSELL (1972). The effectiveness of *Anthocoris nemorumand* and *A.confusus* (Hemiptera : Anthocoridae) as predators of the sycamore aphid, II. Searching behaviour and the incidence of predation in the field. *Ent. exp. and appl.* 15: 35-50.

DREES, O. (1952). Untersuchungen uber die angeborenen verhaltensweisen bei springspinnen (Salticidae). *Z. Tierpsychol.* 9: 169-207.

DUSSAULT, G.V. and D.L. KRAMER (1981). Food and feeding behaviour of the guppy, *Poecilia reticulata* (Pisces : Poecilliidae). *Can. J. Zool.* 59: 684-701.

EATON, R. (1970). Hunting behaviour of the cheetah. *J. Wildl. Mgmt.* 34: 56-67.

EBERHARD, W.G. (1967). Attack behaviour of diguetid spiders and the origin of prey wrapping in spiders. *Psyche.* 74: 173-181.

EDMUNDS, M. (1974). *Defence in animals.* Longman Group Ltd., Essex, England.

EDWARDS, J.S. (1963). Arthropods as predators. In : *Viewpoints in Biology.* 2: 85-114. Eds. J.D. Carthy and C.L. Duddington. Butterworth Inc. London.

EISENBERG, J.F. (1981). *The mammalian radiators : An analysis of trends in evolution, adaptation, and behaviour.* University of Chicago Press, Chicago.

ELGAR, M.A. and C.P. CATTERALL (1981). Flocking and predator surveillance in house sparrows : Test of an hypothesis. *Anim. Behav.* 29: 868-872.

ELLIOTT, J.M. (1968). The daily activity patterns of mayfly nymphs. *J. Zool. (London).* 155: 201-221.

ELLIS, R.A. and J.H. BORDEN (1970). Predation by *Notonecta undulata* (Heteroptera : Notonectidae) on larvae of the yellow-fever mosquito. *Ann. Entomol. Soc. Amer.* 63: 963-973.

EMLEN, J.M. (1973). *Ecology : An evolutionary approach.* Addison-Wesley : Reading, Mass.

ENOCH, F. (1900). On the oviposition of *Ranatra linearis.* *Ent. Month. Mag.* 36: 161.

ERIKSSON, M., L. HENRIKSON and H.G. OSCARSON (1977). Water bugs in some forest lakes in Bohuslan, Southwest Sweden. *Zool. Revy.* 39: 12-21.

ESSENBERG, C. (1915). Habits and natural history of the backswimmers. *J.Anim.Behav. (Cambridge)* 5: 381-390.

ESTES, R. and J. GODDARD (1967). Prey selection and hunting behaviour of the African wild dog. *J. Wildl. Mgmt.* 31: 52-70.

ETIENNE, A.S. (1972). The behaviour of the dragonfly larvae *Aeschna cyanea* M. after a short presentation of a prey. *Anim. Behav.* 20: 724-731.

EVANS, H.D. (1973). A study of the predatory habits of *Anthocoris* species (Hemiptera : Heteroptera). Unpublished D.Phil. thesis, University of Oxford.

EVANS, H.F. (1976). The role of predator-prey size ratio in determining the efficiency of capture by *Anthocoris nemorum* and the escape reactions of its prey, *Acyrthosiphon pisum.* *Ecol. Entomol.* 1: 85-90.

EVERSON, P. (1980). The relative activity and functional response of *Phytoseiulus persimilis* (Acarina : Phytoseiidae) and *Tetranychus urticae* (Acarina : Tetranychidae) : The effect of temperature. *Can. Entomol.* 112: 17-24.

EWER, R.F. (1973). The carnivores. Cornell University Press : Ithaca, N.Y.

FARMER, G.J. and F.W. BEAMISH (1973). Sea lamprey (Petromyzon marinus) predation on freshwater teleosts. J. Fisheries Res. Board Can. 30: 601-605.

FARUQUI, S.A. (1977). Histochemical observations on the Neuro Endocrine complex of Heteroptera. Part 2. The Endocrine Glands. Folia Histochem. Cytochem. 15: 259-266.

FERNANDO, M.H.J.P. (1977). Predation of the glasshouse red spider mite by Phytoseiulus persimilis A-H. Unpublished Ph.D. thesis, University of London.

FISHER, J. (1953). In : Evolution as a Process. (Eds. J. Huxley et al.) pp. 71-82. Allen and Unwin, London.

FORD, M.J. (1977a). Metabolic costs of the predation strategy of the Spider Pardosa amentata (Clerck) (Lycosidae). Oecologia (Berlin) 28: 333-340.

FORD, M.J. (1977b). Energy costs of the predation strategy of the Web-spinning spider Lepthyphantes zimmermanni Bertkan (Linyphiidae). Oecologia (Berlin) 28: 341-349.

FORMANOWICZ, D.R. (1982). Foraging tactics of larvae of Dytiscus verticalis (Coleoptera : Dytiscidae) : the assessment of prey density. J. Anim. Ecol. 51: 757-768.

FORMANOWICZ,D.R.M.S. BOBKA and E.D. BRODIE. (1982) The effect of prey density on Ambush- site Changes in an Extreme Ambush- type predator. Am. Midl. Nat 108: 250-255

FOX, L.R. (1975a). Cannibalism in natural populations. Ann. Rev. Ecol. Syst 6: 87-106.

FOX, L.R. (1975b). Some demographic consequences of food shortage for the predator, Notonecta hoffmañi. Ecology 56: 868-880.

FOX, L.R. (1975c). Factors influencing cannibalism, a mechanism of population limitation in the predator, Notonecta hoffmañi. Ecology 56: 933-941.

FOX, L.R. and W.W. MURDOCH (1978). Effects of feeding history on short-term and long-term functional responses in Notonecta hoffmañi. J. Anim. Ecol. 47: 945-959.

FRANTSEVICH, L.I. and V.E. PICHKA (1976). The size of the binocular zone of the visual field in insects. Zh. Evol. Biokhim. Fiziol. 12: 461-465.

GARDNER, B.T. (1964). Hunger and sequential responses in the hunting behaviour of Salticid Spiders. *J. Comp. Physiol. Psychol.* 58: 167-173.

GARTON, D. and W.B. STICKLE (1980). Effects of salinity and temperature on the predation rate of *Thais haemastoma* on *Crassostrea virginica* Spat. *Biol. Bull.* 158: 49-57.

GELPERIN, A. (1971). Regulation of feeding. *Ann. Rev. Entomol.* 16: 365-378.

GERRITSEN, J. (1980). Adaptive responses to encounter problems. *In* : *Evolution and Ecology of Zooplankton Communities.* Ed. W.C. Kerfoot. University Press New England, Hanover, N.H. pp. 52-62.

GERRITSEN, J. and J.R. STRICKLER (1977). Encounter probabilities and community structure in Zooplankton : A mathematical model. *J. Fish. Res. Board Can.* 34: 73-82.

GIBB, J.A. (1962). Tinbergen's hypothesis of the role of specific search images. *Ibis* 104: 106-111.

GILLER, P.S. (1980). The control of handling time and its effects on the foraging strategy of a heteropteran predator, *Notonecta.* *J. Anim. Ecol.* 49: 699-712.

GILLER, P.S. (1982). The natural diets of waterbugs (Hemiptera : Heteroptera) : electrophonesis as a potential method of analysis. *Ecol. Entomol.* 7: 233-237.

GILLER, P.S. and S. McNEILL (1981). Predation strategies, resource partitioning and habitat selection in Notonecta (Hemiptera : Heteroptera). *J. Anim. Ecol.* 50: 789-808.

GILMER, R.W. (1972). Free-floating mucus webs : A novel feeding adaptation for the open ocean. *Science.* 176: 1239-1240.

GITTLEMAN, S.H. (1973). The ecology of some Costa Rican backswimmers. *Ann. Entomol. Soc. Amer.* 68: 511-518.

GITTLEMAN, S.H. (1977). Leg segment proportions, predatory strategy and growth in Backswimmers (Hemiptera : Pleidae, Notonectidae). *J. Kan. Entomol. Soc.* 50: 161-171.

GITTLEMAN, S.H. (1978). Optimum diet and body size in Backswimmers (Heteroptera : Notonectidae, Pleidae). *Ann. Entomol. Soc. Am.* 71: 737-747.

GLASS, N.R. (1967). A technique for fitting non-linear models to biological data. *Ecology* 48: 1010-1013.

GLASS, N.R. (1970). A comparison of two models of the functional response with emphasis on parameter estimation procedure. *Can. Entomol.* 102: 1094-1101.

GLASSER, J.W. (1979). The role of predation in shaping and maintaining the structure of communities. *Amer. Nat.* 113: 631-641.

GLEN, D.M. (1975). Searching behaviour and prey-density requirements of *Blepharidopterus angulatus* (Fall.) (Heteroptera : Miridae) as a predator of the lime aphid, *Eucallipterus tiliae* (L.) and the leafhopper, *Alnetoidea alneti* (Dahlbom). *J. Anim. Ecol.* 44: 85-114.

GONSOULIN, G.J. (1975). Seven families of aquatic and semiaquatic Hemiptera in Louisiana. Pt.V. Family Nepidae. *Ent. News.* 86: 23-32.

GOSS-CUSTARD, J.D. (1977). The energetics of prey selection by Redshank, *Tringa totanus* (L.), in relation to prey density. *J. Anim. Ecol.* 46: 1-19.

GREIG-SMITH, P.W. (1983). Uses of perches as vantage points during foraging by male and female stonechats, *Saxicola torquata*. *Behaviour.* 86: 215-236.

GRESENS, S.E., M.L. COTHRAN and J.H. THORP (1982). The influence of temperature on the functional response of the Dragonfly *Celithemis fasciata* (Odonata : Libellulidae). *Oecologia (Berlin)* 53: 281-284.

GRIFFITHS, D. (1975). Prey availability and the food of predators. *Ecology.* 56: 1209-1214.

GRIFFITHS, D. (1980a). The feeding biology of Ant-lion larvae : Prey capture, handling and utilization. *J. Anim. Ecol.* 49: 99-125.

GRIFFITHS, D. (1980b). Foraging costs and relative prey size. *Amer. Nat.* 116: 743-752.

GRIFFITHS, D. (1982). Tests of alternate models of prey consumption by predators, using Ant-lion larvae. *J. Anim. Ecol.* 51: 363-374.

GRIFFITHS, K.J. (1969). The importance of coincidence in the functional and numerical responses of two parasites of the European pine sawfly, *Neodiprion sertifer*. *Can. Entomol.* 101: 785-818.

HAGUENDER, M. 91978). The aquatic Hemiptera : *Ranatra*. *Couvr. Nat.* 53: 35-36.

HALE, H.M. (1924). Studies in Australian aquatic Hemiptera. III. Nepidae. *Rec. S.Aust. Mus.* 2: 503-520.

HAMILTON, W.D. (1971). Geometry for the selfish herd. *J. Theor. Biol.* 31: 295-311.

HANSEN, L.P. and O.J. JACOBSEN (1978). New records of *Ranatra linearis* L (Hem. Het.) from Norway, with notes on its biology and distribution. *Norw. J. Ent.* 25: 39-40

HARDMAN, J.M. and A.L. TURNBULL. (1980). Functional response of the Wolf spider, *Pardosa vancouver*, to changes in the density of vestigial-winged fruit flies. *Res. Pop. Ecol.* 21: 233-259

HARP, G.L. and P.A. HARP (1980). Aquatic macro-invertebrates of Wapanocca National Wildlife Refuge, Arkansas, U.S.A. *Proc. Arkans. Acad. Sci.* 34: 115-117.

HASSELL, M.P. (1976). Arthropod predator-prey systems. *In Theoretical Ecology - Principals and applications.* Ed. R.M.May, Blackwells.Scientific Publications, pp. 71-93.

HASSELL, M.P. (1978). *The dynamics of arthropod predator-prey systems.* Princeton University Press.

HASSELL, M.P. and R.M. MAY (1973). Stability in insect host-parasite models. *J. Anim. Ecol.* 42: 693-736.

HASSELL, M.P. and R.M. MAY (1974). Aggregation in predators and insect parasites and its effect on stability. *J. Anim. Ecol.* 43: 567-594.

HASSELL, M.P. and T.R.E. SOUTHWOOD (1978). Foraging strategies of Insects. *Ann. Rev. Ecol. Syst.* 9: 75-98.

HASSELL, M.P., J.H. LAWTON and J.R. BEDDINGTON (1976). The components of arthropod predation I. The prey death-rate. *J. Anim. Ecol.* 45:135-164.

HASSELL, M.P., J.H. LAWTON and J.R. BEDDINGTON (1977). Sigmoid functional responses by invertebrate predators and parasitoids. *J. Anim. Ecol.* 46: 249-262.

HAYNES, D.L. and P. SISOJEVIC (1966). Predatory behaviour of *Philodromus rufus* (Araneae : Thomisidae). *Can. Entomol.* 98: 113-133.

HEILIGENBERG, W. (1965a). The suppression of behavioural activities by frightening stimuli. *Z. vergl. Physiol.* 50: 660-672.

HEILIGENBERG, W. (1965b). The effect of external stimuli on the attack readiness of a Cichlid fish. *Z. vergl. Physiol.* 49: 459-464.

HEILIGENBERG, W. (1966). The stimulation of territorial singing in house crickets (*Acheta domesticus*). *Z. vergl. Physiol.* 53: 114-129.

HEINRICH, B. and F.D. VOGT (1980). Aggregation and foraging behaviour of Whirligig Beetles (*Gyrinidae*). *Behav. Ecol. Sociobiol.* 7: 179-186.

HENNIG, E. (1968). Uber Beziehungen zwishen dem "Probieren" der schwarzen Bohrenblattlaus (*Aphis fabae* Scop.) und dem Stofftransport bei *Vicia faba* L. *Arch. Pflanzenschutz.* 4: 75-76.

HILDREW, A.G. and C.R. TOWNSEND (1977). The influence of substrate on the functional response of *Plechtronemia conspersa* larvae (Trichoptera : Polycentropodidae). *Oecologia.* 31: 21-26.

HILDREW, A.G. and C.R. TOWNSEND (1982). Predators and prey in a patchy environment : A freshwater study. *J. Anim. Ecol.* 51: 797-816.

HINDE, R.A. (1959). Unitary Drives. *Behaviour.* 7: 130-141.

HINDE, R.A. (1970). *Animal Behaviour : A synthesis of ethology and comparative psychology.* McGraw-Hill Book Co. New York. Sydney. 2nd Edition.

HINDE, R.A. (1982). *Ethology : Its nature and relations with other sciences.* Fontana Masterguides Series. Fontana Paperbacks.

HINTON, H.E. (1961). The structure and function of the egg-shell in the Nepidae (Hemiptera). *J. Ins. Physiol.* 7: 224-257.

HINTON, H.E. (1962). A key to the eggs of the Nepidae (Hemiptera). *Proc. R. Ent. Soc. Lond. (A).* 37: 65-68.

HODGES, C.M. (1981). Optimal foraging in bumblebees : Hunting by expectation. *Anim. Behav.* 29: 1166-1171.

HODGES, C.M. and L.L. WOLF (1981). Optimal foraging in bumblebees : Why is nectar left behind in flowers. *Behav. Ecol. Sociobiol.* 9: 41-44.

HOFFMAN, W.E. (1930). Notes on the life history of *Ranatra chinensis.* *Proc. Nat. Hist. Soc. Fukien. Christ. Uni.* 3: 31-37.

HOGAN, J.A. (1971). The development of a hunger system in young chicks. *Behaviour.* 39: 128-201.

HOLLING, C.S. (1959a). The components of predation as revealed by a study of small mammal predation of the European Pine Sawfly. *Can. Entomol.* 91: 293-320.

HOLLING, C.S. (1959b). Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91: 385-398.

HOLLING, C.S. (1963). An experimental component analysis of population processes. *Mem. Entomol. Soc. Can.* 32: 22-32.

HOLLING, C.S. (1964). The analysis of complex population processes. *Can. Entomol.* 96: 335-347.

HOLLING, C.S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45: 1-60.

HOLLING, C.S. (1966). The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.* 48: 1-86.

HOLLING, C.S.; R.L. DUNBRACK and L.M. DILL (1976). Predator size and prey size : presumed relationship in the mantid *Hierodula coaretata* Saussure. *Can. J. Zool.* 54: 1760-1764.

HOLMES, S.J. (1905). The reactions of *Ranatra* to light. *J. Comp. Neur. and Psych.* 15: 305.

HOLMES, S.J. (1906). Death-feigning in *Ranatra*. *J. Comp. Neur. and Psych.* 16: 200-216.

HOLMES, S.J. (1907). Observations on the young of *Ranatra*. *Biol. Bull. Woods Hole.* 12: 158-164.

HOLST, E. von (1948). Quantitative untersuchungen uber umstimmungsvorgange in Zemtral-nervensystem, I. Der influss des Appetit auf das Gleichgewichtsuerhalten bei *Pterophyllum*. *Z. vergl. Physiol.* 31: 134-148.

HOPPENHEIT, M. (1964). Untersuchungen uber den Einfluss von Hunger and Sattigung auf das Beutefanguerhalten der larva von *Aeschna cyanea* Mull. (Odonata). *Z. Wiss. Zool.* 170: 309-322.

HORN, H.S. and R.M. MAY (1977). Limits to similarity among coexisting competitors. *Nature* 270: 660-661.

HUNGERFORD, H.B. (1919). Family - Nepidae, from 'Aquatic Hemiptera'. *Kansas Uni. Sci. Bull.* 11: 151-164.

HUSSEY, P.B. (1926). Studies on the pleuropodia of *Belosoma flumineum* and *Ranatra fusca*. *Entom. Amer.* 7: 1-80.

INGLIS, I.R. and J. LAZARUS (1981). Vigilance and flock size in brent geese : the edge effect. *Z. Tierpsychol.* 57: 193-200.

INOVE, T. and M. MATSURA (1983). Foraging strategy of a Mantid, *Paratenodera augustipennis* S. : Mechanisms of switching tactics between ambush and active search. *Oecologia (Berlin).* 56: 264-271.

JACKSON, R.R. (1977). Comparative studies of *Dictyna* and *Mallos* (Araneae, Dictynidae) : III Prey and Predatory Behaviour. *Psyche.* 83: 267-280.

JACKSON, R.R. (1979). Predatory behaviour of the social spider *Mallos gregalis* :is it cooperative ? *Insectes Sociaux* 26: 300-312.

JAEGER,R,G. and D.E. BARNARD. (1981) Foraging tatics of a terrestial salamander:choice of diet in a structually simple enviroemnt. *Amer. Nat* 117:639-664

JANETOS, A.C. (1982) Foraging tatics of two guilds of Web- Spinning spiders. *Behav. Ecol. Sociobiol.* 10: 19-27.

JANETOS, A.C. and B.J. Cole. (1981) Imperfectly optimal aniamls. *Behav. Ecol. Sociobiol.* 9: 203-209.

JOHNSON, D.M., B.G. AKRE and P. CROWLEY (1975). Modeling arthropod predation : Wasteful killing by damselfly naiads. *Ecology.* 56: 1081-1093.

JUBB, C.A., R.N. HUGHES and T.A.P. RHEINALLT (1983). Behavioural mechanisms of size-selection by crabs, *Carcinus maenas* (L.) feeding on Mussels, *Mytilus edulis* L. *J. Exp. Mar. Biol. Ecol.* 66: 81-87.

JULKA, J.M. (1977). On the possible seasonal fluctuations in the population of aquatic bugs in a fish pond. *Oriental insects.* 11: 139-149.

KAISER, H. (1983). Small scale spatial heterogeneity influences predation success in an unexpected way : Model experiments on the functional response of predatory mites (Acarina). *Oecologia (Berlin.)* 56: 249-256.

KALMIJN, A.J. (1971). The elective senses of sharks and rays. *J. exp. Biol.* 55: 371-383.

KAMIL, A.C. and T.D. SARGENT (Eds) (1981). *Foraging Behaviour: Ecological, Ethological and Psychological Approaches.* Garland Series in Ethology, Garland STPM press, New York. 543pp.

KENWARD, R.E. (1978). Hawks and Doves : factors affecting success and selection in goshawk attacks on woodpigeons. *J. Anim. Ecol.* 47: 449-460.

KIDD, N.A.C. (1982). Predator avoidance as a result of aggregation in the Grey Pine Aphid, *Schizolachnus pineti.* *J. Anim. Ecol.* 51: 397-412.

KIRITSCHENKO, A.H. (1911). Mitteilung von einem Massenflug von *Ranatra linearis.* *Revue Russe d'Entomologie.* 11: 167.

KLOPFER, P. (1962). *Behavioural aspects of ecology.* Prentice-Hall Inc. Englewood Cliffs, New Jersey.

KNIPRATH, E. (1969). Nahrung und Nahrungserwerb des Eisvogels. *Vogelwelt.* 90: 81-97.

KOMNICK, H. (1976). Fine structure and function of the chloride cells of Nepa rubra and Ranatra linearis (Hemiptera : Nepidae). Microsc. Acta. 78: 312-327.

KOSICKI, S. (1958). Zagadnienne lota topielie Ranatra linearis. Polskie Archiwum Hydrobiologie. 5(28): 125-141.

KOSICKI, S. (1966). The mobility of Ranatra linearis and its thermal background. Ann. Univ. Mariae Currie - Sklodowska Sec. C. Biol. 21: 75-106.

KRAMER, S. (1960). Observations of prey capture in Mantids. J. New York Entomol. Soc. 68: 3-12.

KREBS, J.R. (1973). Behavioural aspects of predation. In : Perspectives in Ethology. Ed. P.P.G. Bateson and P.H. Klopfer, Plenum Press 1973, New York.

KREBS, J.R. (1977). Optimal foraging : theory and experiment. Nature. 268: 583-584.

KREBS, J.R. (1978). Optimal foraging : decision rules for predators. In : Behavioural Ecology an Evolutionary Approach. Eds. J.R. Krebs and N.B. Davis, Blackwell Scientific Publications, Oxford.

KREBS, J.R. (1979). Foraging strategies and their social significance. In : Social Behaviour and Communication. (Ed. by P. Marler and J. Vandenburgh), pp.225-270. Plenum Press, New York and London.

KREBS, J.R., A.I. HOUSTON and E.L. CHARNOV (1981). Some recent developments in Optimal Foraging. In : Foraging Behaviour. Ecological, Ethological, and Psychological Approaches. Eds. A.C. Kamil and T.D. Sargent. Garland Series in Ethology. Garland STPM Press, New York.

KREBS, J.R.,A. KACELNIK and P. TAYLOR. (1978) Test of optimal sampling by foraging Great Tite. Nature 275: 27-31.

KREBS, J.R., J.C. RYAN and E.L. CHARNOV (1974). Hunting by expectation or optimal foraging? A study of patch use by chickadees. Anim. Behav. 22: 953-964.

KRUSE, K.C. (1983). Optimal foraging by predaceous diving beetle larvae on Toad Tadpoles. Oecologia (Berlin). 58: 383-388.

KRUUK, H. (1972a). Surplus killing by carnivores. J. Zool. London. 166: 233-244.

KRUUK, H. (1972b). The spotted hyena. University of Chicago Press, Chicago and London.

KRUUK, H. (1975). Functional aspects of social hunting by carnivores. *In : Function and Evolution in Behaviour : Essays in Honour of Professor Niko Tinbergen.* Eds. G.Baerends, C. Beer, A. Manning, Oxford University Press, Oxford, New York.

KULLMAN, E.J. (1972). The convergent development of orb-webs in cribellate and ecribellate spiders. *Amer. Zool.* 12: 395-405.

LAKER, A.G. (1879). Note on the habits of *Ranatra linearis*. *Ent.* 12: 142-145.

LANSBURY, I. (1967). Comparative morphology of the male Australian Nepidae (Hemiptera : Heteroptera). *Aust. J. Zool.* 15: 641-649.

LANSBURY, I. (1972). A review of the Oriental Species of *Ranatra* (Hemiptera : Heteroptera : Nepidae). *Trans. R. Entomol. Soc. Lond.* 124: 287-341.

LANSBURY, I. (1974). Notes on *Ranatra compressicollis* with a review of its systematic position within the American Ranatra (Hemiptera : Heteroptera : Nepidae). *Zool. Scrip.* 3: 23-30.

LAPWORTH, K. (1978). Studies on a polymorphic backswimmer *Anisops thienemanni* Lundblad. Unpublished Honours Thesis, LaTrobe University.

LARSDEN, O. (1936). Zur Biologie von *Ranatra linearis*. *Opusc. Ent.* 1: 112-119.

LARSDEN, O. (1949). Die Ortsbewegungen von *Ranatra linearis*. Ein Beitrag zur Vergleichenden Physiologie der Lokomotionsorgane der Insekten. *Lunds Univ. Arsskrift N.F.* 45(6): 1-83.

LASZLO, M. (1977). Contributions to the knowledge of the bug fauna in bodies of water of Hortogaby Puszta (Heteroptera). *Folia Entomol. Hung.* 30: 77-82.

LAWTON, J.H. (1969). Feeding and food energy assimilation in larvae of the damselfly, *Pyrrhosoma nymphula* (Sulz.) (Odonata : Zygoptera). *J. Anim. Ecol.* 39: 669-889.

LAWTON, J.H., J.R. BEDDINGTON and R. BONSER (1974). Switching in invertebrate predators. *In : Ecological stability.* Eds. M.B. Usher and M.H. Williamson, Chapman & Hall, pp. 141-158.

LAZARUS, J. (1978). Vigilance, flock size and domain of danger size in the white-fronted goose. *Wildfowl* 29: 135-145.

LAZARUS, J. (1979). The early warning function of flocking in birds : an experimental study with captive *Quelea*. *Anim. Behav.* 27: 855-865.

LINDQUIST, S.B. and M.D. BACHMANN (1980). Feeding behaviour of the Tiger Salamander, *Ambystoma tigrinum*. *Herpetologica.* 36: 144-158.

LOCY, W.A. (1884a). Observations on the pulsating organs in the legs of certain Hemiptera. *Amer. Nat.* 18: 13-19.

LOCY, W.A. (1884b). Anatomy and physiology of the family Nepidae. *Amer. Nat.* 18: 250-255; 353-367.

LOMNICKI, A. and L.B. SLOBODKIN (1966). Floating in *Hydra littoralis*. *Ecology.* 47: 881-889.

LORENZ, K.Z. (1966). *Evolution and modification of behaviour.* Methuen, London.

LOXTON, R.G. and J.NICHOLLS. (1979) The functional morphology of the praying mantids forelimb. (Dictyoptera,Mantodea). *Zool. J. Linn. Soc.* 66: 185-203.

LUBIN, Y.D. (1973). Web structure and function : the non-adhesive orb-web of *Cyrtophora moluccensis* (Doleschall) (Araneae : Araneidae). *Forma et Functio.* 6: 337-358.

LUBIN, Y.D. (1980). The predatory behaviour of *Cyrtophora* (Araneae : Araneidae). *J. Arachnol.* 8: 159-185.

LUCAS, N.J. (1900). *Ranatra linearis*, habitat. *Ento.* 33: 181. (London).

LUCAS CASTRO, M.T. and J.M. SALGADO COSTAS (1977/78). Aquatic heteroptera of the province of Leon, Spain. *Bol. Asoc. Esp. Entomol.* 1: 45-74.

LUNDBLAD, O. (1933). Zur kenntnis det aquatilen und semi-aquatilen Hemiptera von Sumatra, Java und Bali. *Arch. Hydrobiol. Suppl.* 12: 29-45.

McARDLE, B.H. and J.H. LAWTON (1979). Effects of prey-size and predator-instar on the predation of *Daphnia* by *Notonecta*. *Ecol. Entomol.* 4: 267-275

MacARTHUR, R.H. (1972). *Geographical Ecology.* Harper and Row, New York.

McCORMICK, S. and G.A. POLIS. (1982) Arthropods that prey on Vertebrates. *Biol. Rev.* 57 : 29-58.

McLEAN, D.L. and M.G. KINSEY (1968). Probing behaviour of the pea aphid, *Acyrthosiphon pisum* II. Comparisons of salivation and ingestion in host and non-host plant leaves. *Ann. Entomol. Soc. Amer.* 61: 730-739.

MACK, T.P., B.A. BAJUSZ, E.S. NOLAN and Z. SMILOWITZ (1981). Development of a temperature-mediated functional response equation. *Environ. Entomol.* 10: 573-579.

MAIORAN~~N~~A, V.C. (1981). Prey selection by sight : random or economic. *Amer. Nat.* 118: 450-451.

MALDONADO, H. and L. LEVIN (1967). Distance estimation and the monocular cleaning reflex in Praying Mantis. *Z. vergl. Physiol.* 56: 258-267.

MALDONADO, H., L. LEVIN and J.C. BARROS-PITA (1967). Hit distance and the predatory strike of the Praying Mantis. *Z. vergl. Physiol.* 56: 237-257

MALDONADO, H., E. RODRIGEZ and N. BALDERRAMA (1974). How mantids gain insight into the new maximum catching distance after each ecdysis. *J. Insect Physiol.* 20: 591-603.

MALMQUIST, B. and P. SJOTROM (1980). Prey size and feeding patterns in *Dinacras cephaletes.* *Oikos.* 35: 311-316.

MANDAL, B.K., A. HAKIM, S.P. ROY and J.S. DATTA MUNSHI (1974). Aquatic insect fauna of Bhagalpur, India. *Indian J. Zoology.* 15: 111-120.

MANNING, A. (1979). *An introduction to Animal Behaviour.* Arnold : London, 3rd Edition.

MARLER, P. and W.J. HAMILTON (1966). *Mechanisms of Animal behaviour.* John Wiley and Sons Inc. New York, London, Sydney.

MARSHALL, W.E. and SEVERIN, H. (1904). Some points in the anatomy of *Ranatra fusca.* *Trans. Wisc. Acad.* 14: 487.

MARTIN, J.B., N.B. WITHERSPOON and M.H.A. KEENLEYSIDE (1974). Analysis of feeding behaviour in the newt *Notophthalmus viridescens.* *Can. J. Zool.* 52: 277-281.

MATHAVAN, S., J. MUTHUKRISHNAN and G.A. HELEENAL (1980). Studies on predation on mosquito larvae by the fish *Macropodus cupanus.* *Hydrobiol.* 75: 255-258.

MAYNARD-SMITH, J. (1978). Optimization theory in evolution. *Annu. Rev. Ecol. Syst.* 9: 31-56.

MAYNARD-SMITH, J. and G.A. PARKER (1976). The logic of asymmetric contests. *Anim. Behav.* 24: 159-175.

MAYNARD-SMITH, J. and G.R. PRICE (1973). The logic of animal conflicts. *Nature (Lond.).* 246: 15-18.

MECH, L.D. (1970). *The wolf : The Ecology and Behaviour of an Endangered Species.* Natural History Press, Garden City, New York.

MENKE, A.S. and L.A. STANGE (1964). A new genus of Nepidae from Australia with notes on the higher classification of the family. *Proc. R. Soc. Qld.* 75: 67-72.

MESSENGER, P.S. (1968). Bioclimatic studies of the Aphid parasite *Praan exsoletum.* 1. Effects of temperature on the functional response of females to varying host densities. *Can. Entomol.* 100: 728-741.

MEYER, D.R. (1952). The stability of human gustatory sensitivity during changes in the time of food deprivation. *J. Comp. Physiol. Psychol.* 45: 373-376

MILES, P.W. (1972). The saliva of Hempitera. *Adv. Insect Physiol.* 9: 183-255.

MILINSKI, M. and R. HELLER (1978). Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus*). *Nature (Lond.).* 275: 642-644.

MILLER, N.E. (1957). Experiments on motivation. Studies combining psychological, physiological and pharmacological techniques. *Science.* 126: 1271-1278.

MILLER, P.L. (1966). Synchronised diving behaviour in flocks of *Anisops pellucens* (Hemiptera : Notonectidae). *Proc. R. Entomol. Soc. Lond.*(A) 41: 161-166.

MILLS, N.J. (1982). Satiation and the functional response : a test of a new model. *Ecol. Entomol.* 7: 305-315.

MITTELSTAEDT, H (1957). Prey capture in Mantids. *In* : *Recent Advances in Invertebrate Physiology.* (Ed. by B. Scheer) pp. 51-57. University of Oregon Publications, Oregon.

MOERMOND, T.C. (1981). Prey-attack behaviour of *Anolis* lizards. *Z. Tierpsychol.* 56: 123-136.

MOHAMED, U.V. (1977). Phospo-lipid content in Malpigian tubules and haemolymph of *Laccotresphes maculatus* and *Ranatra filiformis* (Heteroptera : Nepidae). *West Afr. J. Biol. Appl. Chem.* 20: 16-19.

MOLLES, M.C. and R.D. PIETRUSZKA (1983). Mechanisms of prey selection by predaceous stoneflies : roles of prey morphology, behaviour and predator hunger. *Oecologia (Berlin)* 57: 25-31.

MONTANDON, A.L. (1903). Trois nouvelles especes du genera *Ranatra* L. appartenant aux collections du Musee civique de Genes. *Bull. Soc. Ent. Ital.* 35: 20-24.

MORSE, D.H. (1983) Foraging patterns and time budgets of the crab spiders *Xysticus emertoni* Keyserling and *Misurnena vatia* (Clerk) (Araneae : Thomisidaeon flowers. *J. Arachnol.* 11: 87-94.

MORSE, D.H. and R.S. FRITZ. (1982) Experimental and observational studies of patch choice at different scales by the Crab Spider, Misumena vatia. Ecology. 63: 172-182.

MURDOCH, W.W. (1971). The functional response of predators. J. App. Ecol. 10: 335-342.

MURDOCH, W.W. and A. OATEN (1975). Predation and population stability. Adv. Ecol. Res. 9: 1-131.

MURDOCH, W.W. and A. SIH (1978). Age-dependent interference in a predatory insect. J. Anim.Ecol. 47: 581-592.

MURDOCK, G.R. and B.S. MURDOCK (1972). Tentacle length and prey capture as a function of starvation time in Hydra. Amer. Zool. 12: 719.

MURIE, A. (1944). The wolves of Mount McKinley. Fauna of the National Parks of the United States, Fauna Ser. No. 5.

NACHMAN, M. and C. PFAFFMANN (1963). Gustatory nerve discharge in normal and sodium-deficient rats. J. Comp. Physiol. Psychol. 56: 1007-1011.

NAKAMURA, K. (1974). A model of the functional response of a predator to prey density involving the hunger effect. Oecologia (Berlin). 16: 265-278.

NAKAMURA, K. (1977). A model for the functional response of a predator to varying prey densities : based on the feeding ecology of the Wolf Spiders. Bull. Nat. Inst. Agricul. Sci. 31: 29-89.

NAKAMURA, K. (1982). Prey capture tactics of a spider : An analysis based on a stimulation model for spider's growth. Res. Pop. Ecol. 24: 302-317.

NEILL, S.R. and J.M. CULLEN (1974). Experiments on whether schooling by the prey affects the hunting behaviour of cephalopods and fish predators. J. Zool. (Lond.). 172: 549-569.

NEISWANDER, C.R. (1926). On the anatomy of the head and thorax in Ranatra. Trans. Am. Entomol. Soc. 51: 311-320

NELSON, M.C. (1977). The blowfly's dance : role in the regulation of food intake. J. Insect Physiol. 23: 603-612.

NICHOLSON, A.J. and V.A. BAILEY (1935). The balance of animal populations. Part I. Proc. Zool. Soc. Lond. 114: 551-598.

NIESER, N. (1972). Faunistical notes on aquatic heteroptera, Part 5. Entomol. Ber. (Amst.). 32: 151-155.

OGORZALEK, A. (1974). Oogenesis in the water bugs. I. Cytochemical investigations of the follicular cells in Nepa cinerea L. and Ranatra linearis L. Zool. Pol. 24: 25-40.

OKLAND, J. (1977). Methods in bio-geographic research with examples from the distribution of *Ranatra linearis* and *Nepa cinerea* (Insecta : Hemiptera : Heteroptera) in Norway and Notes on European Invertebrate Survey. *Fauna (Oslo).* 30: 145-167.

OLDHAM, T.W. (1978). New records of aquatic and semi-aquatic Hemiptera in Kansas, U.S.A. *Tech. Publ. State Biol. Surv. Kans.* 6: 59-69.

OLIVE, C.W. (1980). Foraging specializations in Orb-weaving spiders. *Ecology.* 61: 1133-1144.

OMEROD, E.A. (1878). *Ranatra linearis* attacking small fish. *Ent.* 11: 119-120.

ORIANS, G.H. (1981) Foraging behaviour and the evolution of discriminatory abilities. *In: Foraging Behaviour :Ecological, Ethological and Psychological Approaches* Eds. A.C. Kamil and T. D. Sargent pp 389-406. Garland Series in Ethology, Garland STPM Press, NY.

OSTER, G. and Y. TAKAHASHI (1974). Models for age specific interactions in a periodic environment. *Ecol. Monogr.* 44: 483-501.

OWEN, J. (1980). *Feeding strategy.* University of Chicago Press, Chicago.

PARKER, G.A. and R.A. SMITH (1976). Animal behaviour as a strategy optimizer : evolution of resource assessment strategies and optimal emigration threshholds. *Amer. Nat.* 110: 1055-1076.

PARSONS, M.C. (1972a). Respiratory significance of the thoracic and abdominal morphology of *Belostoma* and *Ranatra*. *Z. Morphol. Tiene.* 73: 163-194.

PARSONS, M.C. (1972b). Morphology of the three anterior pairs of spiracles of *Belostoma* and *Ranatra*. *Can. J. Zool.* 50: 865-876.

PARSONS, M.C. (1973). Morphology of the eighth abdominal spiracles of *Belostoma* and *Ranatra*. *J. Nat. Hist.* 7: 255-265.

PARSONS, M.C. (1974). Anterior displacement of the metathoracic spiracle and lateral intersegmental boundary in the Pterothorax of Hydrocorisae (Aquatic Heteroptera). *Z. Morphol. Tiere.* 79: 165-198.

PASTOROK, R.A. (1980). Selection of prey by *Chaoborus* larvae : A review and new evidence for Behavioural Flexibility. *In : Evolution and Ecology of Zooplankton Communities.* Ed. W.C. Kerfoot. University Press New England, 1980. pp. 538-554.

PASTOROK, R.A. (1981). Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology.* 62: 1311-1324.

PAUL, A.J. and J.M. PAUL (1980). The effect of early starvation on later feeding success by King Crab zoeae. *J. Exp. Mar. Biol. Ecol.* 44: 247-251.

PEARSON, D.L. and S.H. STEINBERGER (1980). Competition, body size and the relative energy balance of adult Tiger Beetles. Amer. Midl. Nat. 104: 373-377.

PECKARSKY, B.L. (1980). Predator-prey interactions between Stoneflies and Mayflies : Behavioural observations. Ecology. 61: 932-943.

PECKARSKY, B.L. (1982). Aquatic insect predator-prey relations. Bio. Science. 32: 261-266.

PELLERANO, G.N. and J.M.de CARLO (1977). Compound eye of Ranatra segrega. I. Microstructure of Ommatidium. Physis, Sec. B (Beunos Aires). 37: 141-149.

PETTET, R.H. (1902). The eggs of the Water Scorpion, (Ranatra fusca). Can. Entomol. 34: 213.

PIANKA, E.R. (1974). Evolutionary Ecology. Harper and Row : New York, 2nd Edition.

POLHEMUS, J.T. (1976). Notes of North American Nepidae, Hemiptera, Heteroptera. Pan-Pac. Entomol. 52: 204-208.

POLHEMUS, J.T. and W.K. REISEN (1976). Aquatic Hemiptera, Heteroptera of the Philippines. Kalikasan. 5: 259-294.

POLLARD, D.G. (1973). Plant penetration by feeding aphids (Hemiptera : Aphidoidea) : A review. Bull. Ent. Res. 62: 63-714.

POWELL, G.V.N. (1974). Experimental analysis of the social value of flocking by starlings (Sturnus vulgaris) in relation to predation and foraging. Anim. Behav. 22: 501-505.

PRAMER, D. (1964). Nematode-trapping fungi. Science. 144: 382-388.

PUCHKOVA, L.V. (1978). Adaptive features of leg structure in the heteroptera. Entomol. Rev. 57: 189-196. (English transl. Entomol. Obozr. 57: 272-283).

PULLIAM, H.R. (1973). On the advantages of flocking. J. Theor. Biol. 38: 419-422.

PULLIAM, H.R. (1976). The principle of optimal behaviour and the theory of communities. In : Perspectives in Ethology, Vol. 2. (Ed. by P.P.G. Bateson and P.H. Klopfer), pp. 311-332. Plenum Press : New York.

PULLIAM, H.R. (1981) Learning to forage opitmally. In: Foraging Behaviour: Ecological, Ethological and Psychological Approaches. Ed. A.C. Kamil amd T.D. Sargent.pp.379-388. Garland Series in Ethology ,Garland STPM Press, NY.

PYKE, G.H., H.R. PULLIAM and E.L. CHARNOV (1977). Optimal foraging : A selective review of theory and tests. Q. Rev. Biol. 52: 137-154.

QUAYUM, M.A. (1975). Morphology and secretion of the salivary glands of *Ranatra filiformis*. *Bangladesh J. Zool.* 3: 49-54.

RADINOVSKY, S. (1964). Cannibal of the pond. New study elucidates biology and behaviour of water scorpions. *Natural History.* 11: 16-24.

RAGHUNATNA, T.K. (1962). On the biology of *Ranatra elongata* F. and *Sphaerodema annulatum* F. *Proc. Roy. Ent. Soc. Lond.* 37: 61-64.

RAGHUNATNA, T.K. (1976). Bio-ecological studies on some aquatic Hemiptera, Nepidae. *Entomon.* 1: 123-132.

RAND, D.M. and G.V. LAUDER (1981). Prey capture in the chain pickerel, *Esox niger* : correlations between feeding and locomotor behaviour. *Can. J. Zool.* 59: 1072-1078.

REES, A.R. and R.E. OFFORD (1969). Studies on the protease and other enzymes from the venom of *Lethocerus corclofanus*. *Nature.* 221: 675-677.

REYNOLDS, J. (1980). Size selective predation by the backswimmer *Anisops deanei* Brooks on different morphs of *Daphnia* from freshwater ponds. Unpublished Honours Thesis, University of Adelaide.

RICHARD, G. (1970). New aspects of the regulation of predatory behaviour of Odonata nymphs. *In* : *Development and Evolution of Behaviour. Essays in memory of T.C. Schneirla. Part IV. Social Behaviour.* Freeman & Co. San Francisco. pp. 435-451.

RIECHERT, S.E. (1974) The pattern of local web distribution in a desert spider: mechanisms and seasonal variations. *J. Anim. Ecol.* 43: 733-746.

RILEY, C.F. (1921). Responses of the large Water-Strider, *Gerris regingis* Say, to contact and light. *Ann. Entomol. Soc. Amer.* 14:231-289.

RILLING, S., H. MITTELSTAEDT and K.D. ROEDER (1959). Prey recognition in the praying mantis. *Behaviour.* 14: 168-184.

ROBINSON, M.H. (1975). The evolution of predatory behaviour in spiders. *In* : *Function and Evolution of Behaviour.* Clarendon Press : Oxford. Chap. 14, pp. 292-312.

ROBINSON, M.H. and H. MIRICK (1971). The predatory behaviour of the Golden web spider, *Nephila clavipes* (Araneae : Araneidae). *Psyche.* 76: 487-501.

ROBINSON, M.H. and B. ROBINSON (1971). The predatory behaviour of the orge-faced spider *Dinopes longipes* (Araneae : Dinopidae). *Am. Midl. Nat.* 85: 85-96.

ROEDER, K.D. (1958). A physiological approach to the relation between predator and prey. *Smithson misc. (collections).* 137: 287-306.

ROEDER, K.D. (1959). The predatory and display strikes of the Praying Mantis. *Med. Biol. Illust.* 10:172-178.

ROGERS, D. (1972). Random search and insect population models. *J. Anim. Ecol.* 41: 369-383.

ROVNER, J.S. (1980). Morphological and ethological adaptations for prey capture in Wolf Spiders (Araneae, Lycosidae). *J. Arachnol.* 8: 201-215.

ROYAMA, T. (1971). A comparative study of models for predation and parasitism. *Res. Popul. Ecol. Supp. 1.* pp. 1-91.

RUBENSTEIN, D.I. (1978). On predation, competition and the advantages of group living. *In* : *Perspectives in Ethology,* Vol. 3. (Ed. by P.P.G. Bateson and P.H. Klopfer), pp. 205-231. Plenum Press : New York.

RUGGIERO, L.F., C.D. CHENEY and F.F. KNOWLTON (1979). Interacting prey characteristic effects on Kestrel predatory behaviour. *Amer. Nat.* 113: 749-757.

RUITER, L. de (1967). Feeding behaviour of vertebrates in the natural environment. *In* : *Handbook of Physiology. Alimentary Canal 7.* Ed. by C.F. Code. American Physiologist Society.

RUTTNER, F. (1974). *Fundamentals of Limnology.* University of Toronto Press, Toronto and Buffalo.

SABELIS, M.W. (1981) *Biological control of two-spotted spider mites using phytoseiid predators.* Part I. Centre for Agricultural Publishing Documentation, Wageningen.

SALT, G.W. (1967). Predation in an experimental protozoan population (Woodruffia paramecium). Ecol. Monogr. 37: 113-144.

SANDNESS, J.N. and J.A. McMURTRY (1972). Prey consumption of Amblyseius largoensis in relation to hunger. Can. Entomol. 104: 461-470.

SAUER, F. (1976). Animal growth on water lily leaves. Mikrokosmos. 65: 387-390.

SAVORY, T.H. (1952). The Spider's Web. Warne.

SCHALL, J.J. and E.R. PIANKA (1980). Evolution of escape behaviour diversity. Amer. Nat. 115: 551-566.

SCHALLER, G.B. (1967). The Deer and the Tiger. Chicago University Press, London.

SCHALLER, G.B. (1972). The Serengeti Lion. University of Chicago Press, Chicago, London.

SCHLEE, M.A. (1983). An experimental study of prey-attack behaviour in the European Blackbird, Turdus m. merula. Z. Tierpsychol. 61: 203-224.

SCHMIDT, J.O. (1982). Biochemistry of insect venoms. Annu. Rev. Entomol. 27: 339-368.

SCHOENER, T.W. (1971). Theory of feeding strategies. Annu. Rev. Ecol. Syst. 11: 369-404.

SHELDON, A.L. (1969). Size relationships of Acroneuria californica (Perlidae : Plecoptera). Hydrobiol. 34: 85-94.

SHELDON, A.L. (1980). Coexistence of Perlid Stoneflies : Predictions from multivariale morphometrics. Hydrobiol. 71: 99-105.

SHELLEY, T.E. (1982). Comparative foraging behaviour of light- versus shade-seeking adult Damselflies in a lowland neotropical forest (Odonata : Zygoptera). Physiol. Zool. 55: 335-343.

SHIRGUR, G.A. and H.G. KEWALRAMANI (1973). Observations on salinity and temperature tolerance of some of the freshwater insects. J. Biol. Sci. 16: 42-52.

SHUKLA, G.S. and K. GOPAL (1980). Malpighian tubules of Ranatra elongata (Hemiptera : Heteroptera : Nepidae). Zool. Beitr. 26: 227-230.

SIEGFRIED, W.R. and L.G. UNDERHILL (1975). Flocking as an anti-predator strategy in doves. Anim. Behav. 23: 504-508.

SIH, A. (1979). Stability and prey behavioural responses to predator density. J. Anim. Ecol. 48: 79-89.

SIH, A. (1980). Optimal foraging : partial consumption of prey. Amer. Nat. 116: 281-290.

SIH, A. (1981). Stability, prey density and age/dependent interference in an aquatic insect predator, Notonecta hoffmanni. J. Anim. Ecol. 50: 625-636.

SIH, A. (1982a). Optimal patch use : Variation in selective pressure for efficient foraging. Amer. Nat 120: 666-685.

SIH, A. (1982b). Foraging strategies and the avoidance of predation by an aquatic insect, Notonecta hoffmanni. Ecology. 63: 786-796.

SINGH, J. (1978). Proline metabolism in heteroptera from different environments. Biochem. Exp. Biol. 14: 181-184.

SMITH, J.M.N. and H.P.A. SWEATMAN. (1974) Food searching behaviour of titmice in patchy enviroments. Ecology. 55: 1216-1232.

SOLOMON, M.E. (1949). The natural control of animal population. J. Anim. Ecol. 18: 1-35.

SOUTHWOOD, T.R.E. (1978). Ecological Methods, with particular reference to the study of Insect Populations. Chapman and Hall (Halsted Press Book), London : New York.

SPENCE, J.R. (1980). Density estimation for Water-Striders (Heteroptera : Gerridae). Freshwater Biol. 10: 563-570.

SPENCE, J.R. and J.F. STUCLIFFE (1982). Structure and function of feeding in larvae of Nebria (Coleoptera : Carabidae). Can. J. Zool. 60: 2382-2394.

STREAMS, F. and S. NEWFIELD (1972). Spatial and temporal overlap among breeding populations of New England Notonecta. Univ. Conn. Occ.as Papers Biol. Sci. Ser. 2 pp. 139-157.

STREAMS, F.A. and T.P. SHUBECK (1982). Spatial structure and intraspecific interactions in Notonecta populations. Environ. Entomol. 11: 652-659.

SWAMMERDAM, J. (1737). Bijbel der Natuure. Historie der insecten. Leyden. 910 pp.

SWYNNERTON, C.F.M. (1919). Experiments and observations on the explanation of form and colouring. J. Linn. Soc. Lond. 33: 203-285.

TANAKA, Y. and M. HISADA (1980). The hydraulic mechanism of the predatory strike in dragonfly larvae. J. Exp. Biol. 88: 1-19.

TAWFIK, M.F.S. and K.T. AWADALLAH (1975). The Biology of the Water Scorpion *Ranatra vicina*. *Dtsch. Ent. Z.* 22: 229-240.

TAYLOR, D. (1968). Coexistence and competitive interactions in fall and winter populations of six sympatric *Notonecta*. *Univ. Conn. Occas. Papers Biol. Sci. Ser. 1*, pp. 109-139.

TAYLOR, R.J. (1976). Value of clumping to prey and the evolutionary response of ambush predators. *Amer. Nat.* 110: 13-29.

THOMPSON, W.R. (1924). La theorie mathematique de l action des parasites entomophages et le facteur du hassarol. *Ann. Fac. Sci. Marseille.* 2: 69-89.

THOMPSON, D.J. (1975). Towards a predator-prey model incorporating age structure : The effects of predator and prey sizes on the predation of *Daphnia magna* by *Ischnura elegans*. *J. Anim. Ecol.* 44: 907-916.

THOMPSON, D.J. (1978a). Towards a realistic predator-prey model : The effect of temperature on the functional response and life history of larvae of the Damselfly, *Ischnura elegans*. *J. Anim. Ecol.* 47: 757-767.

THOMPSON, D.J. (1978b). Prey-size selection by larvae of the damsel fly, *Ischnura elegans*. *J. Anim. Ecol.* 47: 769-785.

THORPE, W.H. (1979). *The origins and rise of Ethology*. Heinemann : London.

TOLBERT, W.W. (1975). Predator avoidance and web defensive structures in the orb weavers, *Argiope aurantia* and *A.trifasciata* (Araneae : Araneidae). *Psyche.* 82: 29-52.

TORRE-BUENO, J.E. de la (1903). Notes on the stridulation and habits of *Ranatra fusca*. *Can. Entomol.* 35: 235-237.

TORRE-BUENO, J.E. de la (1905a). The tonal apparatus of *Ranatra quadridentata* stal. *Can. Entomol.* 37: 85-87.

TORRE-BUENO, J.E. de la (1905b). The three Ranatras of the N.E.U.S. *Can. Entomol.* 37: 187.

TORRE-BUENO, J.E. de la (1906). Life-histories of North American water bugs. II. *Ranatra quadridentata*. *Can.Entomol.*38: 242-252.

TOTH, R.S. and R.M. CHEW (1972). Development and energetics of *Notonecta undulata* during predation on *Culex tarsalis* (Diptera : Culicidae). *Ann. Entomol. Soc. Amer.* 65: 1271-1279.

TREHERNE, J.E. and W.A. FOSTER (1980). The effect of group size on predation avoidancer in a marine insect. *Anim. Behav.* 28: 1119-1122.

TREHERNE, J.E. and W.A. FOSTER (1981). Group transmission of predator avoidance behaviour in a Marine insect : The Trafalger Effect. *Anim. Behav.* 29: 911-917.

TREHERNE, J.E. and W.A. FOSTER (1982). Group size and anti-predator strategies in a Marine insect. *Anim. Behav.* 30: 536-542.

VERMEIJ, G.J. (1982). Unsuccessful predation and evolution. *Amer. Nat.* 120: 701-720.

VINE, I. (1971). Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *J. Theor. Biol.* 30: 405-422.

VISSER, M. and L.J. REINDERS (1981). Waiting time as a new component in functional response models. *Netherl. J. Zool.* 31: 315-328.

VISSER, M. (1982). Prey selection by the 3-spined Stickleback. *Oecologia (Berlin).* 55: 395-402.

VITA, J. de; D. KELLY and S. PAYNE. (1982). Arthropod encounter rate: A null model based on random motion. *Amer. Nat.* 119: 499-510.

VYAS, A.B., P.L. BHATT and A.U. BUCH (1972). Aquatic heteroptera of Ahmedabad. *Ind. Sci. Cong. Assoc. Proc.* 59(Part 3): 433.

WAAGE, J.K. (1979). Foraging for patchily distributed hosts by parasitoid, *Nementis canesceus.* *J. Anim. Ecol.* 48: 353-371.

WAITZBAUER, W. (1974). Die larvalentwicklung einiger aquatischer Wanzenarten (Heteroptera, Hemiptera); *Naucoris cimicoides, Notonecta glauca, Ranatra linearis.* *Anz. ost. Akad. Wiss. math.-nat. KI. Abt. I.* 182: 77-102.

WAITZBAUER, W. (1976a). Energieumsatz aquatischer Hemiptera (*Naucoris cimicoides* L., *Notonecta glauca* L., *Ranatra linearis* L.). *Oecologia.* 22: 179-209.

WAITZBAUER, W. (1976b). Methoden zur Abundanzerhebung aquatischer Insekten. *Anz. ost. Akad. Wiss. math. -nat. KI. Abt. I.* 185: 259-276.

WANKOWSKI, J.W.J. (1981). Behavioural aspects of predation by juvenile Atlantic Salmon (*Salmo salar* L.) on particulate, drifting prey. *Anim. Behav.* 29: 557-571.

WASSERSUG, R.J. et al (1981). An analysis of school structure for Tadpoles (Anura : Amphibia). *Behav. Ecol. Sociobiol.* 9: 15-22.

WARD, J.V. and J.A. STANFORD (1982). Thermal responses in the evolutionary ecology of aquatic insects. *Annu. Rev. Entomol.* 27: 97-117.

WATT, K.E.F. (1959). A mathematical model for the effect of densities of attacked and attacking species on the number attacked. *Can. Entomol.* 91:129-144.

WELLS, M.C. and M. BEKOFF (1982). Predation by wild coyotes : Behavioural and ecological analyses. *J. Mammal.* 63: 118-127.

WHEELER, W.M. (1930). Demons of the Dust. W.W. Norton, New York.

WHITE, C.M. and R.B. WEEDEN (1966). Hunting methods of gyrfalcons and behaviour of their prey (Ptarmigan). *Condor.* 68: 517-519.

WHITFIELD, P. (1978). *The Hunters.* New York : Simon and Schuster.

WHITNEY, R.J. (1939). Thermal resistence in Ephemeroptera nympths. *J. Exp. Biol.* 21: 97-114.

WIGGINS, G.B. et al (1980). Evolutionary and ecological strategies of animals in annual temporary pools. *Arch. Hydrobiol./Suppl.* 58: 97-206.

WILLIAMS, D.S. (1979). The feeding behaviour of New Zealand *Dolomedes* species (Araneae : Pisauridae). *N.Z. J. Zool.* 6: 95-105.

WILLIAMS, G.C. (1966). *Adaptation and natural selection.* Princeton University Press : New Jersey.

WILMOTT, C. (1889). *Ranatra linearis*, Habits and Transformation. *Sci. Gossip.* 15: p.252.

WILSON, D.S. (1974). Prey capture and competition in the Ant-lion. *Biotropica.* 6: 187-193.

WILSON, D.S. (1975). The adequacy of body size as a niche difference. *Amer. Nat.* 109: 769-784.

WILSON, E.O. (1972). *The insect societies.* Cambridge, Mass. Belknap Press, Harvard Univ. Press.

WILSON, E.O. (1975). *Sociobiology : The new Synthesis.* Belknap Press, Cambridge, Mass.

WINFIELD, I.J., G. PIERSON, M. CRYER and C.R. TOWNSEND (1983). The behavioural basis of prey selection by underyearling bream (*Abramis brama* (L.)) and roach (*Rutilus rutilus* (L.)). *Freshwater Biology.* 13: 139-149.

WINTERBOURN, M.J. (1974). The life histories, trophic relations and production of *Stenoperla prasina* (Plecoptera) and *Deleatidium* sp. (Ephemeroptera) in a New Zealand river. *Freshwater Biology.* 4: 507-524.

WISE, D.H. (1979). Effects of an experimental increase in prey abundance upon the reproductive rates of two Orb-weaving spider species (Aranea : Araneidae). *Oecologia (Berlin.)* 41: 289-300.

WRATTEN, S.D. (1973). The effectiveness of the coccinellid beetle, *Adalia bipunctata* (L.), as a predator of the lime aphid, *Eucallipterus tiliae* L. *J. Anim. Ecol.* 42: 785-802.

WYMAN, J. (1967). The jackals of the Serengeti. *Animals (London).* 10: 79-83.

WYNE-EDWARDS, V.C. (1962). *Animal dispersion in relation to social behaviour.* Oliver and Boyde : Edinburgh.

ZALOM, F.G. (1978). Backswimmer prey selection with observations on cannibalism (Hemiptera : Notonectidae). *Southw. Nat.* 23: 617-622.

ZAR, J.H. (1974). *Biostatistical Analysis.* Prentice-Hall Inc., Englewood Cliffs, New Jersey.

ZETTLER, F.W. (1967). A comparison of species of Aphididae with species of three other aphid families regarding virus transmission and probe behaviour. *Phytopathology.* 57: 398-400.