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ON THE SEARCHING EFFICIENCY OF  
Rodolia cardinalis (MULSANT) (COLEOPTERA : COCCINELLIDAE),  
AND ITS RESPONSE TO PREY PATCHES.

by

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*A thesis submitted for the degree of Doctor of Philosophy  
in the Faculty of Agricultural Science to the  
University of Adelaide.*

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*I keep six honest serving-men  
(They taught me all I knew);  
Their names are What and Why and When  
And How and Where and Who.*

*-- Rudyard Kipling.*

◀ *A heavy infestation of cottony-cushion scale, Icerya purchasi,  
on Cootamundra wattle, Acacia baileyana.*

**TO  
MY PARENTS**

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## SUMMARY

A classical example of effective biological control is that of the control of the cottony-cushion scale, Icerya purchasi Maskell, by the Coccinellid beetle, Rodolia cardinalis and the Dipteran, Cryptochaetum iceryae (Williston). In the present study, experiments were conducted to test the effectiveness of Rodolia in the light of concepts generated by theoretical studies of predator-prey interactions, which suggest that, among other attributes, an effective predator should possess a high searching efficiency and an ability to exploit patches of prey differentially in relation to prey density.

A study of the changing numbers of the scale and its natural enemies on Wattle trees (Acacia baileyana) over two years indicated that their populations in Adelaide were extremely low throughout the year except for a brief period in the winter months (May to September) with a peak in June/July. Rainfall and wind disturbances were probably responsible for the decline in the scale numbers after the June/July peak, when the natural enemies were virtually inactive. From the month of October, Rodolia became very active in the field and, with the help of the green lacewing (Chrysopa spp.) and the parasites (Cryptochaetum iceryae and Euryschia spp.), it seemingly reduced the scale populations further, to levels so low that the scale numbers were able to attain their highest numbers again only by June of the following year. The role of natural enemies was further explored in experiments in which natural enemies were excluded from caged twigs on Acacia baileyana trees on which cohorts of scales were released once a month over a period of 12 months. The results indicated that the natural enemies were responsible for over 95% mortality of the scale population. The Weibull model and Manly's model for analysing survival data were used to describe trends in the survival-rate of the scales in each cohort. The settling rate of crawlers appeared to be influenced by seasonal changes, especially in that of temperature. It was not, however, affected by the location of their host plants.

Field experiments conducted to test the searching abilities of Rodolia supported the hypothesis that Rodolia had the potential to find its prey in isolated patches. Within a fortnight of the release of crawlers of Icerya, eggs and 1st instar larvae of Rodolia were noticed in patches about 500 m from the nearest known host plant of the scales and presumably from the natural enemies of the scales also. A large proportion of artificially

generated patches of prey were discovered and destroyed before the scales reached their reproductive stage.

In the laboratory, the searching behaviour of the beetle was studied at different levels of prey organization i.e., the beetle's response to a number of patches of different prey densities and also to prey in an individual patch.

In a small searching arena (270 x 410 x 120 mm), the beetle killed more prey, laid more eggs and spent more time at patches of higher prey densities. Also, it killed prey and laid eggs in a higher proportion of patches of higher prey densities.

The searching behaviour of the beetle was influenced by temperature and starvation. At 30° C, an Index of Activity which was measured as the number of flights per 5 mins was found to increase to a peak with starvation and later declined until death.

Attempts to evaluate the searching efficiency of the beetle led to the opinion that earlier concepts of searching efficiency were biologically unrealistic and misleading because they were only concerned with the process of attacking prey at a patch and they ignored the processes of a predator's immigration to and emigration from a prey patch. The term "searching efficiency" was therefore redefined as an overall response of a predator to patches of prey and it was considered to be a function of three distinct processes, viz. patch finding, attack rate and emigration from a prey patch. The new concept of searching efficiency evaluated a predator's response to both BETWEEN and WITHIN patches. The concept was dependent on a distinction between patches of prey that were VISITED (but no prey were eaten and no eggs were laid) and those that were ATTENDED (in which prey were eaten and eggs were laid).

Experiments with a single predator were conducted to evaluate this new concept of searching efficiency. The results demonstrated that the present concept was more realistic than those suggested in the literature on predation. Moreover, this method of evaluation of searching efficiency is simple and does not involve complex mathematical and statistical computations. This new concept is expected to have wide applicability in the field of applied biological control because it may allow the selection of the most effective predator by an experimental evaluation of different potential bio-control candidates.

A series of experiments conducted to test Rodolia's response to patches of different prey densities showed that, in all the different types of searching arenas tested, the beetle responded to spatial heterogeneity in the distribution of prey by exploiting differentially patches of different prey densities. Besides ATTENDING a higher proportion of patches of higher prey densities, the beetle killed more prey, laid more eggs, and spent more time on patches of relatively high prey densities. The estimates of searching efficiency of the beetle were described by two parameters :- one described its differential response in patch selection, and the other described its response to patches of lower prey densities.

Video equipment was employed to study the behaviour of the beetle in an individual patch. This method provided a detailed account of the activities of the beetle within patches of different prey densities. The results showed that patches of lower prey densities were actually VISITED more often than those of higher prey densities, which was interpreted as the beetle's greater persistence in searching for patches of lower prey densities. However, at patches of lower prey densities, a smaller proportion of VISITS resulted in patches ATTENDED. The data gathered were also in agreement with the general conclusions of Optimal Foraging theory, viz. an optimal forager ought to forage and spend a greater proportion of its foraging time in relatively more profitable patches. The beetle's searching behaviour in terms of patch time allocation appeared to follow Hassell and May's (1974) behavioural model. Green's (1984) "assessment rule" appeared to explain the beetle's decision to emigrate from a patch of prey. The entire searching behaviour of the beetle within a patch was described by a conceptual model. The feeding behaviour of the beetle could be described in terms of Holling's (1966) model of the feeding cycle of a mantid.

DECLARATION

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

.....  
(YUGAL KISHORE PRASAD)

March, 1985.

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**CHAPTER 1**  
**GENERAL INTRODUCTION**





## CHAPTER 1

### GENERAL INTRODUCTION

---

If a man will begin with uncertainties he shall end in doubts; but if he will be content to begin with doubts, he shall end in certainties.

-- Francis Bacon, The Advancement of Learning;  
Book I, Part v, Section B.

---

One of the most fundamental and difficult problems in ecology is the quantification of the influence of natural enemies on the abundance of animal populations (Kiritani and Dempster, 1973; Readshaw, 1973). In nature some animals are so numerous that they are given the status of pests, while others are so few that they go unnoticed. Successful biological control programmes show that many species of insects can be kept at extremely low levels of abundance by their natural enemies. In fact, the history of biological control of insects until 1974 indicates that a total of 223 species of insects were subjected to biological control through the importation of natural enemies; of this total, 42 species were completely controlled and some degree of success was noted with another 120 species (DeBach, 1974). More recently, Hall et al. (1980) evaluated the rate of success in classical biological control of arthropods from data provided by Clausen (1978) and found that "... there were no significant differences between the rates of success within the following categories : predators vs. parasites, islands vs. non-islands, and exotic natural enemies of native vs. exotic pest species."

Even though the reasons for the success of some biological control programmes and the failure of others are not well understood (Beddington et al., 1978), there is a general consensus among theoretical and applied entomologists about some of the necessary attributes of an efficient biological control agent (see van Lenteren, 1980 for review). Hassell (1978b), on the basis of theoretical studies of predator-prey interaction, recommends - "Other things being equal, an ideal parasitoid for biological control in a perennial crop system emerges as one with a high search rate and a marked ability to aggregate in patches of high host density." Beddington et al. (1978), considering the patchy distribution of hosts, suggest that parasitoids that can make good control agents should possess high aggregative responses to host patches, high powers of dispersal

between patches and high searching efficiencies. Applied entomologists also agree that a high searching capacity is the foremost attribute to be possessed by an ideal biological control agent (Flanders, 1947; Doult, 1964a; DeBach, 1974). This is because, in nature, prey populations are distributed in patches of varying sizes often spread far apart i.e., spatial heterogeneity is common. In fact, it has been suggested that ".....spatial heterogeneity, the patchy distribution of the host and the differential exploitation of these patches by the parasitoids provide the key in most cases of successful biological control....." (Beddington et al. 1978 ).

Formerly it was believed that predators searched for their prey at random but now there is considerable evidence to indicate that predators do not necessarily search for their prey at random and that parasitoids especially are attracted to their host's sex pheromones (Mitchel and Mau, 1971 and Sternlicht, 1973 ) or to prey-silk and associated faeces (Hislop and Prokopy, 1981) or to the host plants themselves (Read et al., 1970) or even to changes in the host plants brought about by the pest (Arthur, 1966; Camours and Payne, 1972).

Such directed searching behaviour should enhance the aggregative responses of predators to patches of high prey density. There are numerous examples of parasitoids and predators spending more time searching in areas of high prey density and Hassell (1978b) argues that "Prudent predators will spend more of their searching time where prey are abundant rather than scarce and hence be at a considerable selective advantage.". A positive relationship has also been found between the numbers of eggs laid and prey density (Clarke, 1963; Wratten, 1973).

An efficient natural enemy should thus possess a marked ability to aggregate in patches of high prey density. "The high search rate promotes low equilibrium host populations and the aggregation is necessary for this equilibrium to be stable. Such characteristics, it is argued, are likely to be most pronounced among relatively specific rather than polyphagous species" (Hassell, 1978).

Therefore, among other things, an ideal predator should possess (a) a high searching efficiency, and (b) an ability to distinguish between, and differentially respond to, patches of different prey density.

About a century back, in California, the cottony-cushion scale, Icerya purchasi Maskell (Homoptera : Margarodidae), was brought under successful

biological control by the vedalia beetle, Rodolia cardinalis (Mulsant) (Coleoptera : Coccinellidae). This was the first outstanding and now a classical example of biological control in the entomological literature. To quote DeBach (1974) "This project established the biological control method like a shot heard around the world.". Between 1889 and 1958 Rodolia has been introduced into 57 different countries, ranging from temperate or desert to tropical climates. Of these 57 attempts, 55 have been reported as producing successful establishment and good control (Bartlett, 1978). Hall et al. (1980) found that natural enemies introduced against Homoptera had the highest rate of success, and Rodolia was responsible for "an inordinate number of complete successes". They also point out that "one must be cautious when making generalizations about the rates of success without considering the impact of R. cardinalis on such rates."

The two organisms are believed to be natives of Australia (Maskell, 1887 (letter published in Pacific Rural Press, May 7, 1887); DeBach, 1974; Bartlett, 1978) from where the scale was accidentally introduced into California in 1868 (Doutt, 1964a). In Australia, the scale has never achieved the status of a pest, except for occasional patchy outbreaks following injudicious pesticide use. Rodolia cardinalis and a parasite, Chrytochaetum iceryae Williston (Diptera : Agromyzidae) are believed to be responsible for the obscure occurrence of the scale in Australia, though the former is thought to play the major role.

The apparent natural control of the scale in Australia and its successful biological control in many countries, have earned Rodolia cardinalis the reputation of a highly efficient and effective natural enemy in the entomological literature.

With this background information, a number of critical questions can be posed about the abundance of the scale and its natural enemies in Australia. Why is an organism that can achieve the status of a serious pest overseas relatively rare in Australia? Is it that the natural enemies are indeed, highly efficient in keeping the scale population very low? And if they are so efficient as appears to have been shown by their successful introductions to many countries, do they possess the attributes of an ideal natural enemy that have been enumerated by theoretical and applied studies of predator-prey interaction?

Rodolia cardinalis, the most popular choice for biological control

overseas, was selected for study. The investigations reported, herein, concentrated on the following :

- (1) The population dynamics of the scale and its natural enemies.
- (2) The role of Rodolia in prey-patch dynamics.
- (3) The ability of the beetle to differentially exploit prey-patches in relation to prey density.
- (4) A study of the prey finding abilities of Rodolia, which led necessarily to the quantification of its searching efficiency.
- (5) A novel concept of searching efficiency of predators is proposed because the earlier concepts were found to be biologically unrealistic.
- (6) The "optimal foraging" behaviour of the beetle.

**CHAPTER 2**  
**THE ICERYA - RODOLIA SYSTEM**

## CHAPTER 2

### THE ICERYA -- RODOLIA SYSTEM

---

Books must follow sciences,  
and not sciences books.

-- Francis Bacon.

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#### 2.1. A CLASSICAL EXAMPLE OF BIOLOGICAL CONTROL --- HISTORY

The history of the biological control of Icerya in California is described by DeBach (1974), and a summary of DeBach's account is given below.

The cottony-cushion scale, Icerya purchasi, was accidentally introduced into California in 1868 from Australia (Doutt, 1964b) and in the absence of any natural check it became very abundant, especially on citrus crops. By 1887 the scale infestations had become so massive that the local infant citrus industry, was on the verge of a total collapse.

The Convention of Fruit Growers meeting in Riverside, California in April 1887, invited as their principal speaker Charles Valentine Riley, Chief of the Division of Entomology of the federal government, to whom the citrus growers looked to provide a remedy. Riley suggested the introduction of natural enemies of the scale, and the convention adopted a resolution favouring the idea (Pacific Rural Press, January 7, 1888).

In the meantime, W.G. Klee, the State Inspector of the Fruit Pests, had been corresponding with W.M. Maskell in New Zealand and Frazer Crawford in Australia about the possible place of origin of the scale. In the May 7, 1887 issue of the Pacific Rural Press a letter, from Maskell to Klee, was published in which Maskell positively stated that the scale was a native of Australia. In the beginning, Riley was skeptical of Maskell's claim but in the March 4, 1888 issue of Pacific Rural Press he wrote that the view of Icerya being a native of Australia was probably true.

After some persuasion, the State Department agreed to bear the expense of sending an entomologist to Australia in search of natural enemies of the scale. Riley selected Alfred Koebele for the purpose. On August 25, 1888, Koebele sailed for Australia where he began his mission. He was not able

to find any natural enemies of the scale in Sydney and Melbourne so he came to Adelaide. From Adelaide he first sent a total of approximately 12,000 individuals of Cryptochaetum, but relatively little attention was paid to his discovery of vedalia feeding on scales in a north Adelaide garden on October 15, 1888. However, between November 1888 and January 1889, Koebele sent three consignments of a total of 129 specimens of vedalia. When received in California, these were placed under a tent on an Icerya-infested orange tree where they were allowed to breed, and by early April 1889, nearly all the scales on the enclosed trees had been destroyed. Accordingly, on the 12th of April, one side of the tent was removed, and the Coccinellids were permitted to spread to the adjoining trees. Later, the beetles were also distributed to various parts of the state. By 12th June that year, 10,555 of these Coccinellids had been distributed to 228 different orchardists and in nearly every instance the colonizing of these beetles proved successful. The further reports were only tales of successes, and vedalia was hailed as a miracle of entomology. The cost of the project was about \$ 1,500. The shipment of oranges from Los Angeles County jumped in one year from 700 to 2,000 cars (Doutt, 1964b).

Since then many biological control projects have been undertaken all over the world, and many have been equally successful but none has been so dramatic, with public involvement. It has remained an outstanding project in biological control and an important milestone in applied entomology (Doutt, 1964b).

Soon after vedalia was successfully established in California, attempts were made to transfer it to other countries where the scale was a problem. The beetle was introduced into Hawaii in 1890, into the Cape province in 1892, and into Europe in 1897. Between 1899 and 1958, vedalia was introduced into 57 different countries, ranging from temperate or desert to tropical climates. In 55 of these countries good control of the scale was achieved. In some colder areas, however, repeated releases were necessary where vedalia might have been eliminated because of severe winters (Bartlett, 1978).

## 2.2 THE COTTONY-CUSHION SCALE, *Icerya purchasi*.

### 2.2.1 GEOGRAPHICAL DISTRIBUTION

*Icerya purchasi* is now cosmopolitan in distribution, invading all the six continents of the world. Its distribution lies between latitudes 45 N and 45 S. Within Australia, it is present in all the eastern states (Queensland, New South Wales, Victoria and Tasmania) and South Australia in varying numbers (Commonwealth Institute of Entomology, Distribution Maps of Insect Pests, Series A, Map No. 51). In South Australia, the distribution of the scale extends from the colder, humid coastal areas to the relatively hot and dry interiors, though it is not common.

### 2.2.2 TAXONOMIC STATUS

The genus *Icerya* belongs to the Order Hemiptera, Sub-Order Homoptera, Super-Family Coccoidea, Family Margarodidae and Tribe Iceryini. It is represented by a number of species (Appendix Table 1) whose geographic distributions vary widely. Of all the species, *I. purchasi* is the most popular and widely distributed. An illustrated redescription of *I. purchasi* was recently published by Howell and Beshear (1981).

### 2.2.3 BIOLOGY OF *Icerya purchasi*

Since 1887 the biology of the scale has been extensively studied in California and other parts of the world. Quezada and DeBach (1973) provide an account of the work done on this species up to then. Unfortunately, in Australia, not much work has been done, perhaps because the scale has never been a pest. More recently, however, Heap (1980) conducted a short study of the biology of the scale in Adelaide, South Australia.

#### 2.2.3.1 HERMAPHRODITES

The so-called females of the scale are only protandric hermaphrodites capable of self-fertilization and reproducing hermaphrodite progeny. Unfertilized haploid eggs become males, which are alate and uncommon (Hughes-Schrader, 1930; Quezada and DeBach, 1973). However, Howell and Beshear (1981) believe that true males are produced by cross-fertilization of hermaphrodites by males.

The mature female scale is 5 to 6 mm long and is covered with wax which projects from the sides of its body as long filaments (Fig. 2.1).



Fig. 2.1

Photograph of the 2nd (a) and 3rd (b) instar, and the adult scales (both without ovisac (c) and with ovisac (d)); the pupa (e) and the adult (f) of Rodolia; and the parasitized scales showing emergence holes of the escaped parasites (g).

(Scale : 2 mm ).





The eggs are laid in a white longitudinally grooved ovisac (characteristic of this species) which lifts the hind end of the body of the scale. A full grown female with the ovisac may be as long as 10 to 12 mm. Estimates of the fecundity of the scale vary widely, but between 600 to 800 eggs are produced over 2 to 3 months. The eggs are elongate, oval, pink, and smooth. Up to 76 % of the eggs hatch to produce crawlers (Quezada and DeBach, 1973). Following hatching, the life cycle of the scale has four distinct stages. Several good descriptions of the morphological characteristics of each stage exist (Gossard, 1901; Bodenheimer, 1951).

The crawlers are reddish with black legs and antennae, and are less than 0.5 mm in length (Fig. 2.2A). This is the only truly motile phase in the life of the scale. The crawlers remain mobile for a few days during which they wander to the apical areas of branches. During this period, the crawlers passively disperse on the wind. Only about 50 % of the crawlers are able to settle on their host plants and attain further development (Quezada and DeBach, 1973). The crawlers, which settle mostly along the leaf veins and twigs, become covered by yellowish-white wax plates shortly after settling. The insect remains in this stage for 2 to 3 weeks after which it moults. The second instar nymph is 1.5 mm long, reddish-brown in colour, with black antennae and legs (Fig. 2.1). This nymph settles at a short distance from its cast skin. It starts feeding again, becomes covered with wax plates, and gradually becomes more brownish in colour. After 2 to 3 weeks, it moults into the next stage. The third instar nymph is also reddish-brown and about 4 mm long (Fig. 2.1). The hairs on its integument, which are very small in the previous stages, become larger, darker and stout and they are grouped in tufts. This instar lasts between 2 to 3 weeks and moults to become the adult (Fig. 2.1).

#### 2.2.3.2 MALES

The second instar scales which are destined to become the winged males become larger and more elongate as they reach moulting. There is a clear dimorphism in the third instar stage between the would-be hermaphrodites and the males. The third instar male nymphs are about 5 mm long. They move to sheltered places where they spin white cocoons with a cottony secretion. The cocoons appear as elongated, white, fluffy cotton balls, from which the adults emerge in 2 to 3 weeks. The adult male is about 0.5 cm long, slow moving and has a pair of well developed and

Fig. 2.2

- (A) The adult scale with ovisac, the newly emerged crawlers, and the reddish oval eggs of Rodolia.
- (B) The 1st, 2nd, 3rd, and 4th instar larvae of Rodolia, including the 4th instar which is about to pupate.
- (C) The adult male of Icerya, which is winged.
- (Scale : 1 mm )



functional wings (Fig. 2.2C).

The life cycle of the scale in Riverside, California ranges from 96 days in the summer to 144 days in the winter and there are 3 generations in a year (Quezada and DeBach, 1973). All instars of the scale produce honeydew which attracts ants, flies and bees.

#### 2.2.4 HOST PLANTS OF *Icerya purchasi*

*I. purchasi* is highly polyphagous in habit. The list of host plants which are infested by the scale is very large (see Gossard, 1901; Bodenheimer, 1951; Subramaniam, 1954-55). In Adelaide, South Australia, I have found the scale feeding on over a dozen plant species (Appendix Table 2). The scales are more common on Acacias than on Citrus, and they do better on lemons than on oranges.

#### 2.2.5. NATURAL ENEMY COMPLEX

*Icerya purchasi* is attacked by a number of natural enemies (Appendix Table 3), but the most important are a Coccinellid predator *Rodolia cardinalis* and a Dipteran, *Cryptochaetum iceryae*. The two have been extensively used in biological control programmes and are of special significance in biological control, not only because of their effectiveness but also because they present a very good example in support of the concept of 'multiple introduction' of natural enemies for the control of a pest species (Quezada and DeBach, 1973). In California, though the distribution of *Rodolia* extends along with that of the scale, the beetle remains dominant all year in the warmer desert areas of the state. In the cooler coastal regions *Cryptochaetum* is dominant, and *vedalia* is common only during the summer months. In the areas in between, however, *vedalia* exists alongside *Cryptochaetum* (Quezada and DeBach, 1973), and the two organisms appear to share the responsibility of keeping the scale population within an appreciable density.

It would be interesting to compare the above findings with similar data collected from Australia, the home country of these organisms (Quezada and DeBach, 1973). Such a study has never been conducted. The geographic location and the climate of California are very similar to those of South Australia, so a similar distribution pattern of the scale and its natural enemies may be expected here. Indeed, the classical success of *Rodolia* in California, about a century ago, may be attributed to it being introduced

into an environment very similar to that of its endemic habitat.

An Aphelinid parasite, Euryschia spp. (Fig. 2.3) and the Green Lace Wing, Crysopa spp. were also found to attack the scale to a considerable degree. However, the present study was restricted mainly to the interaction of Icerya and Rodolia, and detailed information about natural enemies is restricted to that of Rodolia.

### 2.3. THE VEDALIA BEETLE, *Rodolia cardinalis*

#### 2.3.1. TAXONOMIC STATUS OF *Rodolia*

The genus Rodolia (Fig. 2.1) belongs to the Order Coleoptera, Sub-Order Polyphaga, Super Family, Cucojoidea, Section Clavicornia, Family Coccinellidae, Sub-Family Coccinellina, Tribe Noviini. It contains a number of other species ranging through Asia, Australia and Africa, which feed on monophlebine insects (Bartlett, 1978). Of these the vedalia beetle, Rodolia cardinalis, remains the most effective as a control agent due to reasons presented earlier.

#### 2.3.2. BIOLOGY OF *Rodolia cardinalis*

The biology of vedalia has also been extensively studied overseas (Coquillett, 1889; Kuwana, 1922; Bodenheimer, 1951; Priore, 1963; Quezada and DeBach, 1973; Matsuka and Watanabe, 1980). In Australia, such a study has not been undertaken.

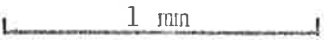
After a pre-oviposition period of 2 to 3 days, the adult female deposits her eggs on, under or close to the scales (Fig. 2.2A). The eggs are oval, red in colour and about a mm long. When deposited on the white ovisac of the scale, they are very conspicuous. A single female may lay 800 to 1,000 eggs although the average is usually about 300 (Bartlett, 1978). Eggs are laid on any stage of the scale, with the exception of crawlers, and the laying of more than one egg per scale is common. More than 12 eggs per scale has been recorded. Quezada and DeBach (1973) report a daily oviposition of one to 14 eggs, though I have found upto 52 eggs laid per day. The eggs hatch in 2 to 9 days in the open and the larvae start feeding on the scale on or under which the eggs were deposited.

There are four larval instars which have been well described by Coquillett (1889) and Priore (1963) (Fig. 2.2B). The larvae are dark



Fig. 2.3

Euryschia spp., the Hymenopteran parasitoid of  
Icerya, with two second instar scales.

(Scale :  ).



orange-red, covered with transverse rows of dark brown warts surmounted with white bristles. The full grown larva is covered with a greyish powder. For pupation, the full grown larvae attaches itself to leaves or bark by the pygidium and undergoes transformation into the pupa. The pupal skin splits longitudinally in a characteristic manner and the adult emerges in about a week's time. The newly emerged adult is bright red in colour and gradually changes to dark red with the characteristic black spots on the elytra. The adult measures slightly over 3 mm in length and is somewhat variable in size, some being very much smaller (Fig. 2.1). The head, central portion of the thorax, a broad stripe down the centre of the wing covers, and a c-like mark on the hind margin are black in colour, while the rest of the dorsal surface is bright red. The black markings are, however, very variable. Some specimens may have no black markings on the elytra, some only the median stripe down the back and a spot on either side, while in others the elytra are more black than red (Froggatt, 1902).

The duration of the life stages is temperature dependent and varies from season to season. The stage most prolonged during winter is the pupal stage. At 25°C the average developmental period (eggs to adult) was 19.7 days and the adult life span was 29.4 days (Matsuka and Watanabe, 1980).

### 2.3.3. SEX DIFFERENTIATION

Sex can only be determined with some difficulty in coccinellids. In general, Rodolia males are smaller than females, but the sexes can be differentiated with greater confidence by the structural differences of the last abdominal sternite which is emarginated to a different degree at the middle of the hind margin in the males than in females. Matsuka and Watanabe (1980) provide figures which are useful in sexing adults.

### 2.3.4. PREY SPECIFICITY

There are conflicting reports regarding the prey specificity of Rodolia. It is known to attack numerous members of the genus Icerya and some other Monophlebini (Bartlett, 1978). In France, it feeds on the eggs but not the other stages of Guerinella serratulae F. (Balachowsky, 1932); whereas in Japan Kuwana (1922) reports that it attacks Drosicha corpulenta (Kuw.) in addition to other Icerya. Vedalia has also been used in the successful control of Icerya seychellarum, I. aegyptiaca, I. montserrantensis, and I. palmeri (Bartlett, 1978). However, in California

*Rodolia* is virtually monophagous on I. purchasi (Cressman and Dumestre, 1930; Quezada and DeBach, 1973). There are no such reports from Australia and I have not noticed vedalia feeding on any other insect other than cottony-cushion scale. The high prey-specificity of the beetle leads, at times, to its local extinction due to lack of prey.

### 2.3.5. PREY CONSUMPTION

Cressman and Dumestre (1930) conducted intensive studies on the feeding rate of Rodolia adults and found that it was a function of temperature, age, seasonal change and sex. Temperature had an indirect effect through the response to thermal change of activities which condition feeding. The quantity of food consumed was the lowest during the first tenth of the adult life span, rose to a maximum during the third and then showed a slight decrease.

Matsuka and Watanabe (1980) studied the voracity of different larval instars of Rodolia on first instar crawlers of Icerya. They found that the fourth instar larva was the most voracious larval stage for it consumed about 80 % of the prey eaten during the whole larval period. However, compared to adult scales, the crawlers were not necessarily the best prey for the adult beetles.

### 2.3.6. EFFECT OF HOST PLANTS ON THE EFFICACY OF NATURAL ENEMIES

Host plants can have adverse effects on the insects that feed upon them but there are very few instances reported in which the effectiveness of the natural enemies of herbivorous insects is influenced by the host plants upon which the herbivores feed.

Quezada and DeBach (1973) report that both the scale and its natural enemies do very well on Pittosporum tobira but they were convinced that Icerya was immune to attack by Rodolia when the former developed on Cocculus laurifolius, Acer oblongum or Spartium juceum. Poutiers (1930) found that alkaloids such as spartein and a yellow pigment genestein, from Spartium juceum and Genista aethneuris respectively, were responsible for the unpalatability of Icerya to Rodolia. Quezada and DeBach (1973) believe that other alkaloids may be responsible for preventing vedalia from reproducing on Cocculus laurifolius and other plants in the Menispermaceae.

### 2.3.7. ATTRIBUTES AS AN EFFECTIVE NATURAL ENEMY

The following are some of the attributes which have enabled Rodolia cardinalis to maintain its reputation as a highly efficient natural enemy.

- (1) It has the ability to find isolated small colonies of the scale i.e., it has a high searching capacity. Also, the beetle disperses after almost completely destroying the scale colony (Coquillett, 1889; Kuwana, 1922; Bodenheimer, 1951; Quayle, 1938; Bartlett and Lagace, 1960; Priore, 1963; Quezada and DeBach, 1973 and others).
- (2) It is relatively prey-specific (see 2.3.4).
- (3) It has the ability to increase rapidly in numbers relative to that of the prey (Coquillett, 1889; Bodenheimer, 1934).
- (4) It has a wide climatic tolerance, though it does better in warmer areas. However, reports of its failure do exist (Kaussari, 1946) and there have been instances of the need of supplementation by other natural enemies for effective control of Icerya (Bennett and Hughes, 1959).
- (5) It has no natural enemies in California (Coquillett, 1889; Quayle, 1938; Quezada and DeBach, 1973). However, Subramanyam (1950) reports upto 100 % parasitization of Rodolia larvae in India by Homalotylus flaminus (Dalman).
- (6) It avoids eating scales which are parasitized by Cryptochaetum iceryae, thus not interfering with other natural enemies of the scale (Quezada and DeBach, 1973).

### 2.4. CLIMATE OF ADELAIDE, SOUTH AUSTRALIA

Adelaide is normally mild in the winter months and warm in the summer. Extreme cold is never experienced because the Southern Ocean effectively protects the state from the cold polar air masses. Occasionally, however, during the summer months, the very hot continental air masses drift down from the north and several days of unpleasantly hot weather result. Adelaide receives a mean annual rainfall of about 459 mm (for average meteorological data see Appendix Table 4).

**CHAPTER 3**  
**GENERAL MATERIALS AND METHODS**

## CHAPTER 3

### GENERAL MATERIALS AND METHODS

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Be not the first by whom the new are tried,  
Nor yet the last to lay the old aside.

-- Alexander Pope.

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The cottony-cushion scale has a wide range of host plants (Appendix Table 2) and it can be easily cultured on potted plants, or in cages on naturally growing trees, or on butternut pumpkins.

Because both Icerya and Rodolia are uncommon in the field in Australia, a continuous culture of both the organisms was maintained to satisfy the demand of insects for experiments. A stock culture and a laboratory culture were maintained in the field and in the insectary, respectively; and these two cultures were complementary to each other.

### 3.1 CULTURE OF SCALES

#### 3.1.1 STOCK CULTURE OF THE SCALES

The stock culture of the scale was maintained on 2 m high naturally growing trees of Acacia baileyana. Crawlers were released into plastic cages (Fig. 3.1) fitted to twigs on the trees. After 4 days, when the crawlers had settled down, the plastic cages were replaced by larger polyester voile sleeve cages (Fig. 3.1). The scales were allowed to develop in these cages till they became adults and started producing crawlers. These adults were collected when needed for the culture of Rodolia or for the collection of crawlers. Ten lots of similar releases were made every fortnight.

#### 3.1.2 LABORATORY CULTURE OF SCALES

Rearing Icerya on either potted plants, naturally growing trees, or butternut pumpkins involves using relatively large amounts of plant material and so was cumbersome for experimental work, especially when there was need to study the individual scales and also to manipulate their densities. The sedentary nature of the scales further aggravated the rearing problem when scales needed to be transferred from one place to

Fig. 3.1

The perspex cages (A), and the polyester voile cages (B) fixed on an Acacia baileyana tree for stock culture of the scales.





another. So a leaf-disc method with citrus leaves was developed which was extremely useful for experiments in which a large number of replicates were required, where space was limited, and where there was need to move scales from one place to another. Leaf-disc methods have been used for the culture of a number of homopterans, e.g. Brassica for aphids (Johnson and Birks, 1960; Hughes and Woolcock, 1965), eucalyptus for rearing psyllids (White, 1968), and citrus for rearing red-scales (Willard, 1976).

#### (A) THE LEAF-DISC PREY CULTURE SYSTEM

The leaf-disc culture system consisted of culture units (CU) and float valve units (FVU) all interconnected by means of clear vinyl tubing to a reservoir of distilled water (Fig. 3.2A). The units were arranged on shelves in an insectary room after the shelves were initially set horizontal by means of a spirit level. The levelling of the shelves was essential for the proper functioning of the system and for maintaining the same water level in all the units on a shelf. Each shelf had a separate FVU which was connected to the reservoir through the float valve on the one side and to the culture units on the other.

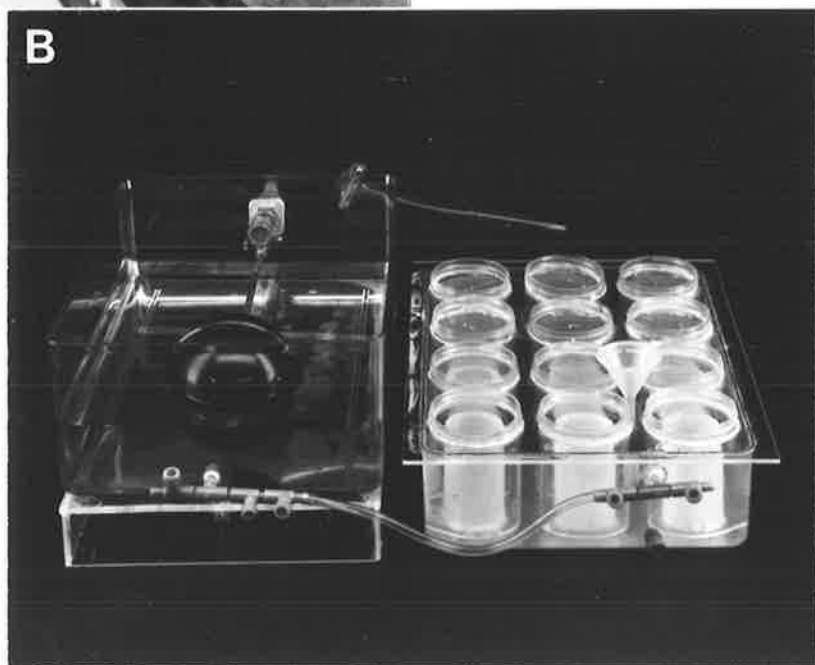
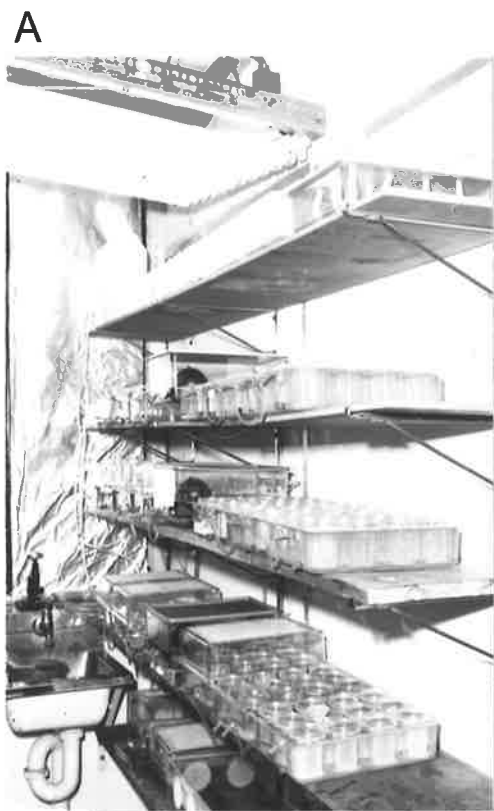
Each culture unit (CU) (Fig. 3.2B) was capable of supporting 12 citrus leaf-discs, each 50 mm in diameter. Its body comprised a clear plastic container (Decor<sup>1</sup>, clearseal-254; 265x195x65 mm), to the top of which was stuck a sheet of clear acrylic plastic (Perspex, 285x215x3 mm) with twelve 50.8 mm dia holes in three rows of four. A sub-unit for supporting a single leaf-disc was inserted into each hole. Each sub-unit consisted of two clear acrylic pharmaceutical vials, one placed inside another. The larger vial (70.9 ml) had two 8 mm dia holes on opposite sides towards the base on the walls to allow entry of water. A smaller vial (21.3 ml), whose base had been removed, was stuck into the larger vial. The small vial supported a circular piece of wire mesh (16 gauge, 18 mesh, 50 mm dia) which helped to prevent the edges of the leaf-disc from curling and kept it in position. The sub-units were lowered into the large plastic container

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1. (Decor; manufactured by Brian Davis & Co. Pty. Ltd., Australia)

Fig. 3.2

- (A) The leaf-disc insect culture system assembled on the shelves in an insectary cubicle
  
- (B) A part of the leaf-disc insect culture system comprising a float valve unit (FVU) and a culture unit (CU), showing their internal structure.
  
- (C) The specially designed punch used for cutting 5.08 cm dia citrus leaf-discs.



through the holes on the acrylic sheet and were stuck in position by glue<sup>2</sup>. The front end of the CU had two holes, one (5 mm dia) towards the base for drainage, otherwise plugged with a rubber stopper, and another (6 mm dia) towards the top into which was glued a small plastic tube (30x5 mm dia). To this tube was fitted a plastic T-control valve of the sort used in aquariums. Through a hole on the top of the CU was fitted a small funnell (35 mm dia) which assisted in manually maintaining the desired water level when the units were being used independently of the system.

The purpose of the float-valve unit (FVU) (Fig. 3.2B) was to regulate the level of water in all the culture units on a shelf. Each FVU consisted of a clear plastic container (Decor<sup>1</sup>, clearseal-253; 265x195x100 mm), into which is fitted a float valve (Ballcock, "Philmac", 80 mm proylene) on one side. The float valve was connected to the reservoir by means of clear vinyl tubing. On the opposite side, in the centre about 20 mm from the base, a plastic T-control valve was fitted in a manner similar to that of the CU. Normally this unit remained covered by its lid, but it could be opened to adjust the water level, which was done by bending the stem of the ballcock. Once adjusted, the water level did not need further attention unless disturbed. The FVU was placed on a platform, 35 mm high, in order to raise the level of water in the FVU to the CU.

The reservoir was a 4 litre plastic container kept at a level of about 50 cm above the topmost shelf of the culture units (Fig. 3.2A). One end of a vinyl tube was inserted into the container through a hole in its screw cap, while its other end connected to all the FVU by means of three-way connectors. From the reservoir, water flowed through the system by siphon action. Therefore, the portion of the tube in the container had to be freed of air bubbles each time an empty reservoir was replaced by another reservoir full of water. In the present set-up, distilled water was used but nutrients could also be added if necessary.

Since water remains stagnant in the system, with the passage of time, there was development of algae in the CUs. Every few weeks the CUs were cleaned by immersing them in a tank of 1 % sodium hypochlorite solution

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1. (Decor; manufactured by Brian Davis & Co. Pty. Ltd., Australia)

2. (IPS Weldon # 16, manufactured by Industrial Polychemicals Service (IPS), California, U.S.A.)

for 1-2 days and then rinsing with water.

By the help of a specially designed punch (Fig. 3.2C), large numbers of leaf-discs could be produced with ease. The citrus leaves used for making leaf-discs were collected from lemon trees in the experimental orchard of the institute.

The above system was very versatile. Not only could the individual CUs be dismantled and moved according to the needs of a particular experiment (e.g., keep in constant temperature cabinets), but also the individual leaf-discs could be moved without disturbing the sessile scale insects. The system did not need constant attention because the level of water was automatically regulated in all the CUs by the FVUs, and an empty reservoir needed to be replaced with a full one only once a week or so.

With minor modifications (depending on the width of leaves and the insect under study) the above apparatus could be used for the culture of a number of insects, such as scales, psyllids and aphids.

#### (B) CULTURE OF SCALES USING LEAF-DISC METHOD

The floating leaf-disc culture system, described in section 3.1.2(A), was employed to culture scales for use in experiments. Gravid adults were collected from the stock culture in crawler emergence cages (CEC) (Fig. 3.3A). Each crawler emergence cage (CEC) was made of a 70.7 ml plastic vial whose base was removed and replaced with polyester voile. The CECs with adult scales were placed in the insectary below a light source. The crawlers gathered towards the roof of each CEC from where they could be collected by tapping into a petri dish. They could then be counted and placed in individual plastic tubes by means of a camel hair brush (Fig. 3.3B). These crawlers could be introduced into the field or the laboratory culture itself, after an initial starvation of 24 h.

Twice a week, on Mondays and Fridays, an average of 50 crawlers per leaf-disc were released in two of the units of the culture system (i.e. 24 leaf-discs). After releasing the crawlers, each unit was covered with an inverted plastic container (Decor, clearseal 254; 265x195x100 mm), the bottom of which had been removed and replaced by polyester voile stuck with Weldon glue. This container was, in turn, covered by a piece of black cloth. The resultant darkening of the "arena" enhanced the percentage of crawlers that successfully settled on the leaf-discs. Without it, a large proportion of the crawlers would drown in the film of water around the

Fig. 3.3

(A) Four crawler emergence cages (CECs).

(B) Plastic tubes in which crawlers were collected after counting.

(C) Plastic container comprising individual tubes in which Rodolia pupae were isolated and in which adults later emerged.

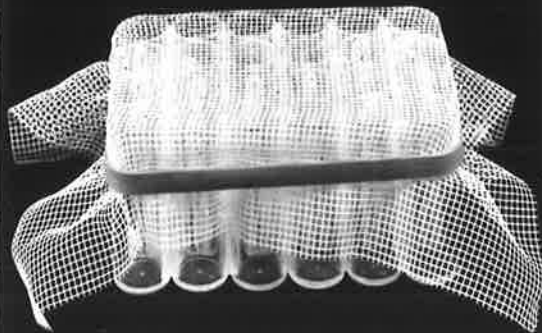
A



B



C





proportion of the crawlers would drown in the film of water around the leaf-discs.

After about 2 weeks, the first instars began to moult. Prior to their settling down again, they were removed with a camel hair brush into 70 mm dia plastic petri dishes. The newly moulted II-instar scales were starved for 24 h before being introduced on to a new set of leaf-discs. The number of II-instar scales per leaf-disc was controlled as per the requirements of a particular experiment. It usually ranged from 1 to 20 scales per leaf-disc. Generally 2 to 3 extra scales were introduced to allow for casualties due to various reasons. Before use in an experiment, the scale density was thinned to the desired level. Five to six days old II-instar scales were generally used in the experiments.

After another two weeks or so, the II-instar scales moulted into III-instars. Once again the scales were collected in petri dishes before they settled down starved for 24 h and reintroduced on a fresh set of leaf-discs. The III-instars moulted into adults in about 2 weeks. These were collected and transferred on to potted plants of citrus and Acacia baileyana where they grew to produce crawlers. Such adult scales were also used for the culture of Rodolia.

The above system provided a continuous supply of scales in the second and third instar for experimentation.

### 3.2 CULTURE OF Rodolia cardinalis

Adults of Rodolia were used in most experiments and a continuous culture of the beetle was maintained for the purpose. Newly emerged adults were sexed and confined in the crawler emergence cages (CEC) (Fig. 3.3A) for 2 days to facilitate mating. In each CEC, 2-3 females and 3-4 males were introduced. These beetles fed on both the crawlers and the adult scales (in fact the beetles feed on all the stages of the scales). The mated females from one of these CECs were then introduced into one of the units of the scale culture system. A single unit was covered with an inverted plastic container which had polyester voile netting on the top. The males were either used to mate with other newly emerged females, if there was shortage of them, or they were discarded. The females were allowed to lay eggs for 2-3 days. By this time they were 5 days old and

they were either used in experiments or transferred to new units or killed.

The eggs hatched in a week or so and the newly emerged larvae started feeding on the scales under which they were born. The adult beetle lays her eggs above, under or close to the scales. The number of I-instar larvae were later thinned to about a dozen i.e., an average of one per leaf-disc. They were checked daily to ensure that there was enough prey for them. From here they were later transferred into the CECs or onto the potted plants laden with the scales (section 3.3).

The larvae grew through four instars to become pupae. The pupae were collected and placed into another container (Fig. 3.3C) designed to isolate the individuals when they emerged. The excess larvae and adults were regularly discarded to avoid a shortage of prey. This measure was essential to prevent the predator culture from coming to a virtual halt. The predators consumed prey at a much faster rate than the prey population grew. Once every couple of months a few larvae or pupae were collected from the field and introduced into the laboratory culture so as to avoid the selection of a laboratory strain.

### 3.3 EXPERIMENTAL HOST PLANTS

Host plants of Acacia baileyana and citrus were maintained in pots in a shade house. Seedlings of these were purchased from a local nursery (Heyens & Co.) and potted in 150 mm dia plastic pots using recycled U.C. soil. The Acacia plants were staked by 12.3 mm dia dowell sticks to prevent them from lodging. More new seedlings were potted if older ones had grown too big for experimental purposes. The Acacia plants that were used in the experiments were pruned to leave only the main stem with leaves and no branches.

The potted plants kept in the shade house supported a reasonable population of scales and its natural enemies. These plants also served as a reservoir of insects when the main cultures were running low.

**CHAPTER 4**  
**SEASONAL ABUNDANCE OF ICERYA AND ITS NATURAL ENEMIES**

## CHAPTER 4

### SEASONAL ABUNDANCE OF ICERYA AND ITS NATURAL ENEMIES

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"...there is no generally accepted group of concepts with which population fluctuations can be described and some ecologists even wonder whether such concepts will ever be formulated. Bakker (pers. comm.) ..... : there is not only an ecological crisis, but also a crisis in ecology."

-- Professor J. C. van Lenteren (1980)

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#### 4.1 POPULATION ESTIMATES

##### 4.1.1 INTRODUCTION

A study of the population dynamics of an organism aims at identifying the causes of numerical changes in the population and provide an explanation of how these changes act and interact to produce the observed trends. It also helps elucidate when and how the regulatory mechanisms influence the dynamics of the organisms. The literature provides data on the population dynamics of Icerya purchasi and its natural enemies from Italy (Jannone, 1967), Hawaii (Hale, 1970), California (Quezada and DeBach, 1973) and Egypt (El-Saadany and Goma, 1974). However, estimates of the seasonal abundance of Icerya purchasi and its natural enemies is lacking in Australia, perhaps because their numbers are very low and the distribution very patchy, besides the scale being of little economic importance here. Since one of the objectives of this study was to find out why the scale was so uncommon in Australia, it was imperative to gather information on the natural abundance and seasonal dynamics of the scale and its natural enemies. Therefore, population sampling was conducted over a period of two years.

In Adelaide, South Australia, the summer, autumn, winter, and spring seasons comprise of the following months -- summer : December, January, and February; autumn : March, April, and May; winter : June, July, and August; spring : September, October, and November.

#### 4.1.2 MATERIALS AND METHODS

##### 4.1.2.1 SAMPLING SITE

Though the scale has a wide range of host plants (Appendix Table 2), in South Australia, only trees of Acacia baileyana harbour a sufficiently large population of the scale at certain times of the year to allow any worthwhile estimates of scale numbers. Thus, sampling was carried out at monthly intervals on two Acacia baileyana trees which grew along the northern perimeter of the institute beside "Cross Road". The two trees, larger Tree-A and smaller Tree-B, were about ten years old and approximately 30' and 20' high respectively, with a moderate canopy.

##### 4.1.2.2 SAMPLING PROCEDURE

In a preliminary sampling conducted to estimate the number of samples to be collected and sample variation, a stratified random sampling procedure was adopted. The tree canopy was divided into three levels in Tree-A and two levels in Tree-B. Each level was further divided into four aspects through cardinal directions (N, S, E & W). Each aspect was further divided into inner and outer sections. Thus the canopy in Tree-A had 24 strata (3 levels x 4 aspects x 2 sections) while the canopy in Tree-B had 16 strata (2 levels x 4 aspects x 2 sections).

Three samples were collected per stratum in Tree-A and four samples per stratum in Tree-B. Each sample was a twig which was randomly selected and was collected with a pole-pruner. The samples were placed in tagged polythene bags and brought to the laboratory where the insects were classified into different instars and counted. The insects were later incubated in plastic vials to check for emerging parasites.

In order to estimate the spatial distribution of different instars of the scales on the tree, data were also collected on the distance of the tip of the twig to the point where each scale had been feeding, the diameter of the twig at that point, and the number of nodes from the tip to that point.

Based on the results of the preliminary sampling and the cost involved, the number of samples was reduced in subsequent sampling occasions and only one sample was collected from each stratum. Also, in Tree-A subsequent samples were collected only from the lower two levels, for the sake of convenience. The samples were collected at monthly intervals for two years, beginning in July, 1981. They were collected during the last two days of every month.

### 4.1.3 RESULTS

#### 4.1.3.1 RESULTS OF PRELIMINARY SAMPLING

The data from the preliminary sampling (Appendix Table 5) were subjected to an analysis of variance in order to evaluate the effect of stratification. Prior to analysis, the data were transformed to  $\log(x+1)$  to homogenize the variances. The analysis is given in Tables 4.1.1 and 4.1.2.

In Tree-A, the interactions of the "factors" and the main effect of levels were not significant at  $P < 0.05$ , but the main effect of sections and aspects were significant (Table 4.1.1A). The means of the population estimates from the different strata from Tree (A) have been presented in Table 4.1.1B.

In Tree-B, on the other hand, the main effects of levels and of sections and the interaction of level and section were all significant (Table 4.1.2A). The means from the different strata for Tree (B) have been presented in Table 4.1.2B.

The analyses demonstrate that in both Tree (A) and Tree (B) a stratified random sample would be needed to allow for equal importance to levels, sections, and aspects.

The mean numbers of insects per sample in both the trees (A) and (B) were very low, 6.76 and 9.03 respectively (Table 4.1.3). With over 60 samples per tree, only a precision of about  $E=0.2$  (where  $E$  = standard error as a decimal of the mean) could be achieved as against the prescribed 0.05 (estimated by eq.(2.7) of Southwood, 1978). And to achieve this precision the cost (time) involved was much higher than could be spent in subsequent sampling. Since a detailed population dynamics study was not the sole aim of this project, a compromise was made between the cost and the precision by accepting a lower precision for a lower cost (Southwood, 1978). It was decided to collect one sample from each of the 16 strata, based on preliminary sampling data and accept a precision of about  $E=0.4$ .

Table 4.1.1A

ANALYSIS OF VARIANCE ON Log (x+1) TRANSFORMED PRELIMINARY SAMPLING DATA FROM TREE (A)

	D.F.	S.S.	M.S.S.	F	P
BETWEEN LEVELS	2	0.81	0.41	2.51	>0.05
BETWEEN SECTIONS	1	0.96	0.96	5.89	<0.05
BETWEEN ASPECTS	3	2.12	0.71	4.34	<0.01
LEVELS x SECTIONS	2	0.07	0.03	0.21	>0.05
LEVELS x ASPECTS	6	0.45	0.08	0.46	>0.05
SECTIONS x ASPECTS	3	0.24	0.08	0.50	>0.05
LEV. x SEC. x ASP.	6	1.08	0.18	1.11	>0.05
ERROR	48	7.80	0.16		
TOTAL	71	13.52	0.19		

(Cochran's Normality Test Statistic = 0.169; P= 0.345 approx.)

Table 4.1.1B

MEANS OF THE NUMBERS OF SCALES IN DIFFERENT SECTIONS, AND AT DIFFERENT LEVELS AND ASPECTS OF TREE (A) (ANOVA TABLE 4.1.1A)

ASPECT	INNER SECTION				OUTER SECTION			
	L1	L2	L3	MEAN	L1	L2	L3	MEAN
NORTH	0.92	0.67	0.64	0.74	0.52	0.82	0.51	0.62
SOUTH	0.80	1.02	0.40	0.74	0.20	0.26	0.52	0.33
EAST	0.81	1.29	1.06	1.05	0.62	1.12	0.68	0.81
WEST	0.56	0.58	0.53	0.56	0.49	0.69	0.10	0.43
MEAN	0.77	0.89	0.66	0.77	0.46	0.72	0.45	0.54

L1, L2, and L3 represent the LOWER, MIDDLE, and UPPER levels respectively.

Table 4.1.2A

ANALYSIS OF VARIANCE OF Log (x+1) TRANSFORMED PRELIMINARY SAMPLING DATA FROM TREE (B)

	D.F.	S.S.	M.S.S.	F	P
BETWEEN LEVELS	1	3.08	3.08	30.73	<0.0005
BETWEEN SECTIONS	1	4.87	4.87	48.55	<0.0005
BETWEEN ASPECTS	3	1.48	0.49	4.92	<0.005
LEVELS x SECTIONS	1	1.62	1.62	16.15	<0.0005
LEVELS x ASPECTS	3	0.56	0.19	1.85	>0.05
SECTIONS x ASPECTS	3	0.38	0.13	1.26	>0.05
LEV. x SEC. x ASP.	3	0.56	0.19	1.87	>0.05
ERROR	48	4.81	0.10		
TOTAL	63	17.35	0.28		

(Cochran's Normality Test Statistic = 0.215; P=0.19 approx.)

Table 4.1.2B

MEANS SHOWING SIGNIFICANT DIFFERENCES IN THE NUMBERS OF SCALES SAMPLED FROM TREE (B) (ANOVA TABLE 4.1.2A)

ASPECT	INNER SECTION			OUTER SECTION		
	L1	L2	MEAN	L1	L2	MEAN
NORTH	1.43	0.33	0.88	0.19	0.31	0.25
SOUTH	1.31	0.89	1.10	0.45	0.29	0.37
EAST	1.34	0.91	1.13	0.62	0.54	0.58
WEST	1.15	0.08	0.62	0.49	0.12	0.31
MEAN	1.31	0.55	0.93	0.44	0.32	0.38

L1 and L2 represent the LOWER and UPPER levels respectively



Table 4.1.3

SUMMARY OF RESULTS FROM PRELIMINARY SAMPLING OF SCALES ON  
TREE (A) AND TREE (B) IN JULY, 1981

SITE	N	MEAN	S.E.	E	N *	E **	VAR.
TREE-A	72	6.76	1.15	0.171	16	0.362	95.82
TREE-B	64	9.03	2.12	0.235	16	0.471	288.98
POOLED	136	7.83	1.17				186.54

E = precision estimate.

\* = proposed sample size for subsequent sampling.

\*\* = corresponding precision accepted.

#### 4.1.3.2 SPATIAL DISTRIBUTION OF SCALES

Both the distances of different instars of the scales from the tip of the twig, and the diameters of the twig at that point, were allotted to class intervals. Their frequencies were transformed to percentages of the total for a particular instar and plotted against the class intervals in the form of histograms (Fig. 4.1.1).

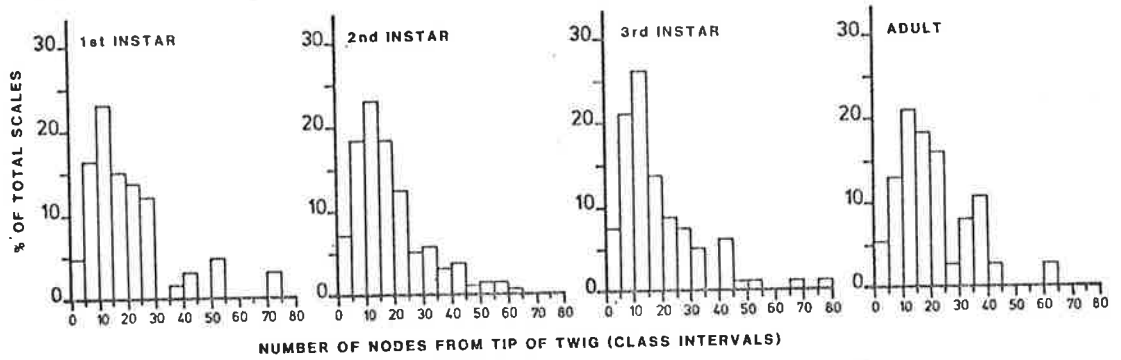
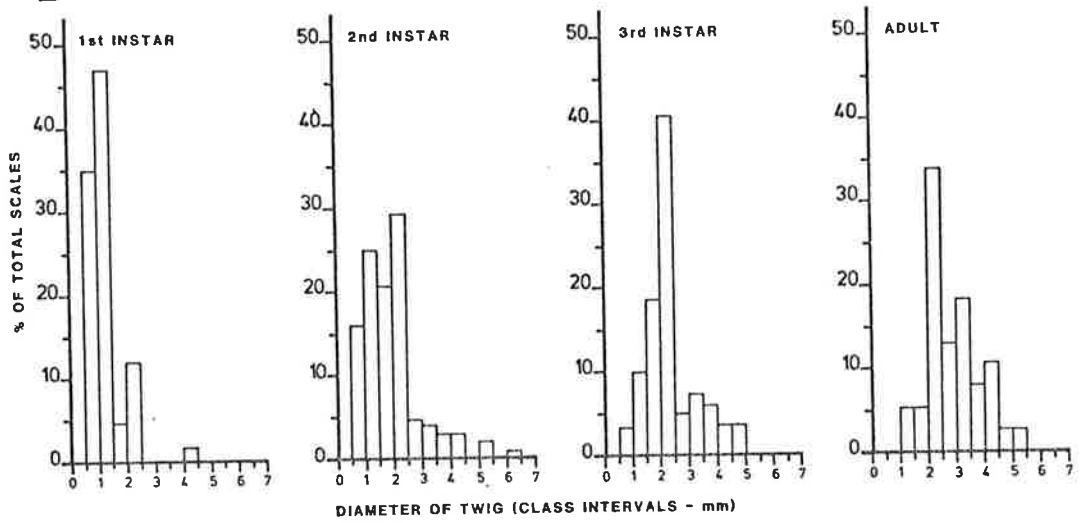
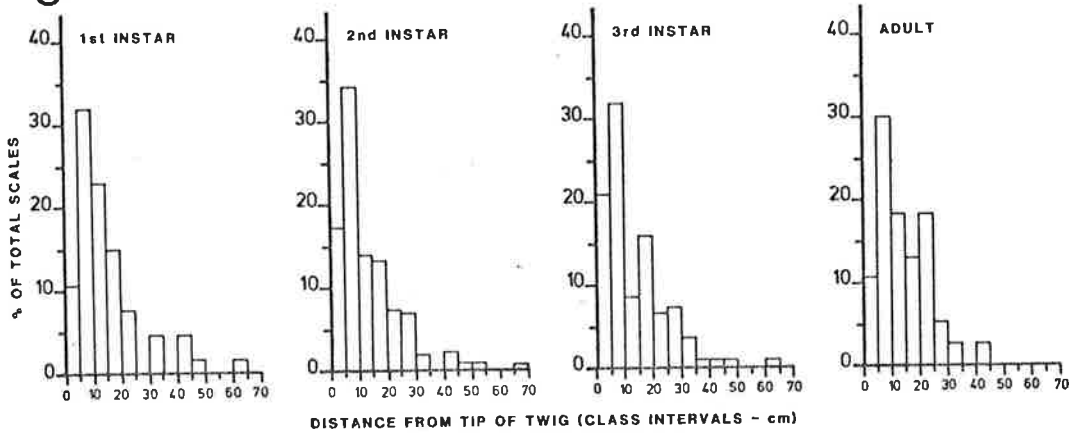
The spatial distribution of each of the four stages of the scales in terms of their distance from the tip of the twig followed a similar pattern (Fig. 4.1.1A). About 30 % of the total scales in each instar were located between 5 and 10 cm from the tip of the twig, and their distribution was skewed about this class interval. Only 2 % or less of the scales were located beyond 45 cm from the tip of the twig.

On the other hand, the spatial distribution of scales in relation to the diameter of the twig was not the same for different instars (Fig. 4.1.1B). Upto 35 and 47 % of the 1st instar scales were located on twigs in the diameter class (DC) 1 and 1.5 mm respectively. The percentage of 2nd instar scales in DC 1 mm was only about 10 % which increased to a peak of about 30 % in DC 2.5 mm. The percentage of 2nd instar scales in DC 1 mm was a low 4 % which gradually increased to a peak, again in DC 2.5 mm. After this it trailed off, till no insects were present beyond DC 5 mm. The adults, on the other hand, were only located above a twig dia of 1 mm and only 5 % of them were present in DC 1.5 and 2 mm. The adult numbers also peaked in DC 2.5 mm and upto 3 % of them were located above a twig dia of 5 mm. The spatial distribution of different instars of the scales in relation to the diameter of the twig, therefore, appeared to follow a wave like form; the waves for the preceding instar giving way to that of the succeeding instar. This would be expected because, after every moult, the otherwise sessile scale moves a short distance up the twig to settle down again and begin feeding.

The 1st instar scales were mostly found on the mid-rib and veins of the bipinnate leaves of Acacia baileyana, from where they generally moved to the stem after moulting into the 2nd instar. On the stem, they move a short distance upwards after every moult. Some adult insects have been found settled on comparatively thick woody branches of between 5 and 10 cm dia, though these represent a very small proportion of the whole population. Occasionally, a few adults have also been noticed on the main trunk of the tree which was over 50 cm in dia. Perhaps these were insects

Fig. 4.1.1

- (A) Frequency distribution of the percentages of the three different instars and of adults (based on the total scales) that were located in relation to the numbers of nodes from the tip of the twigs of Acacia baileyana.
  
- (B) Frequency distribution of the percentages of the three different instars and of adults (based on the total scales) in relation to the diameter of the twigs of Acacia baileyana where the scales were situated.
  
- (C) Frequency distribution of the percentages of the three different instars and of adults (based on the total scales) in relation to the distance from the tip of the twigs of Acacia baileyana to the point of location of the scales.

**A****B****C**

that were dislodged from the tree during their mobile phase and found their way to the tree trunk where they settled down.

The description of the spatial distributions of the scales suggest that a major proportion of scales of all stages were located within 50 cm of the tip of the twig. Thus, the insects gathered from the samples were truly representative of the total scale population on the tree.

#### 4.1.3.3 PHENOLOGY OF SCALES AND ITS NATURAL ENEMIES

The total numbers of all scales and of natural enemies (Appendix Tables 6 and 7) over a 24 month period for Tree-A and Tree-B have been plotted in Figs. 4.1.2 and 4.1.3, respectively as  $\log(\bar{x}+1)$  numbers. Figures 4.1.2A and 4.1.3A show that though the scales were present throughout the year, their total numbers remained very low on both the trees, especially during the summer months (November, December, January, and February). In spite of this, three peaks can be traced in each year in the graphs. The peaks, however, do not coincide for both the trees and there is a lag of about a month between trees which could have been due to the large intervals between successive samplings. Thus the first peak was found either in November or December, the second either in June or July and the third either in September or October. Of these the mid winter peak (in June or July) was the highest and most significant of all.

The age-specific population trends of the different stages of the scales have been presented in Figs. 4.1.2B and 4.1.3B. The results for both the trees showed 2 to 3 peaks in the population of 1st, 2nd, 3rd instars and adults. However, there was a time lag between the peak numbers for different stages, thus showing a succession; for example, the number of adults showed a peak in February/March, followed by a peak of 1st instars in April. This peak was in turn followed by a peak of 2nd instars in May, and was followed finally by a peak of the 3rd instar in July/August. Such a trend would be expected as insects develop through different stages.

The total numbers of natural enemies (two parasites, Cryptochaetum and Euryschia and two predators, Rodolia and Chrysopa) were so low that these species were not present in the sampling data for major part of the autumn and winter months (March, April, May, June, July, and August) and reappeared only in spring (September, October and November) with a peak in late spring and early summer, after which their numbers collapsed with the decline in the scale population (Figs. 4.1.2A & 4.1.3A).

Fig. 4.1.2

TREE (A)

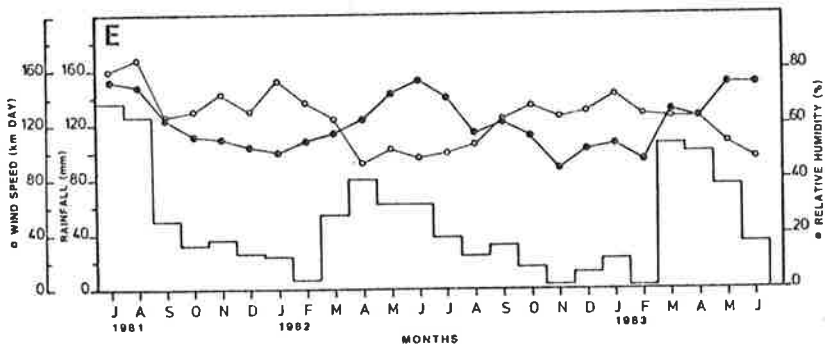
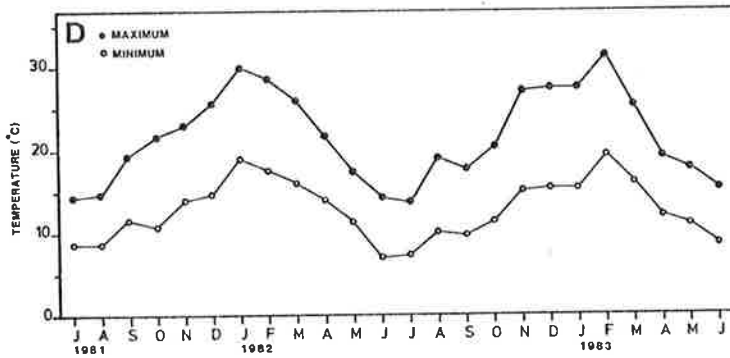
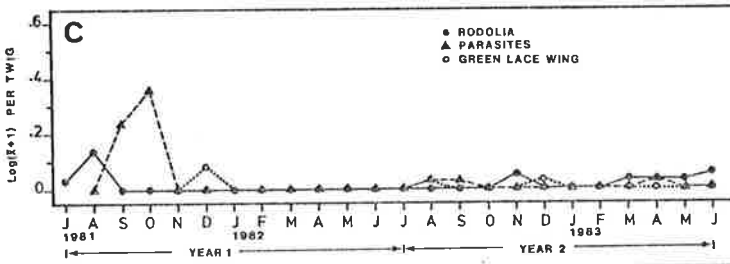
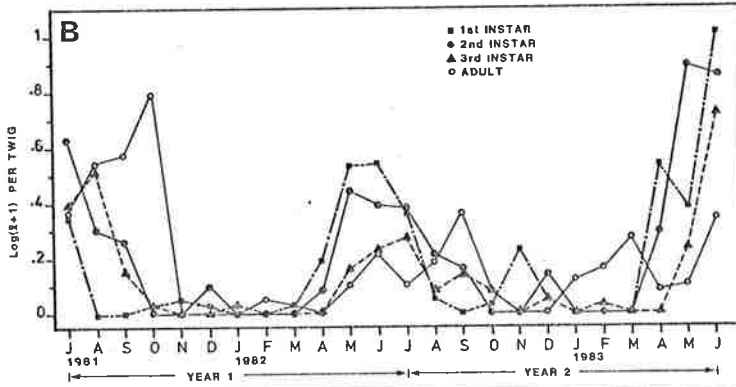
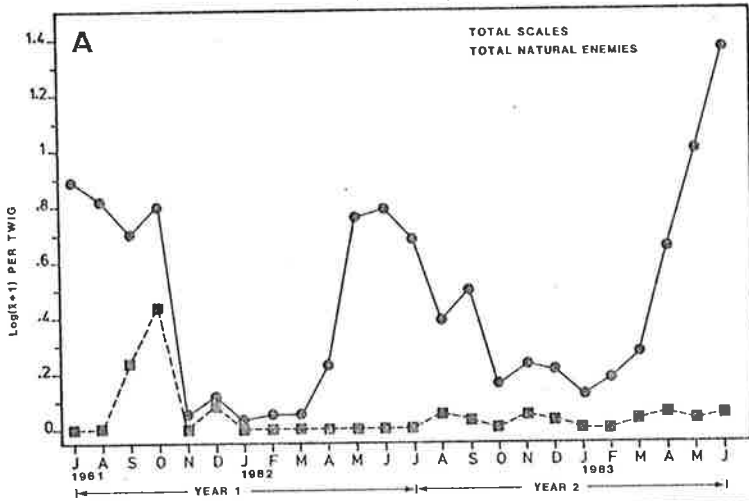
- (A) Numbers of total scales and of total natural enemies at monthly intervals over two years plotted as  $\text{Log}(x+1)$  of the mean numbers per twig. The first points are for July, 1981.
- (B) Numbers of the three instars of the scale and of the adults at monthly intervals over two years plotted as  $\text{Log}(x+1)$  of the mean numbers per twig.
- (C) Numbers of Rodolia, the parasites (Cryptochaetum spp. and Euryschia spp.) and of the green lacewing (Chrysopa spp.) at monthly intervals over two years plotted as  $\text{Log}(x+1)$  of the mean numbers per twig.
- (D) Monthly means of the daily maximum and minimum temperatures from July, 1981 to June, 1983.
- (E) Monthly means of the daily relative humidity (%) and wind-speed (km/day) and the total monthly precipitation (mm) during the 2 years of the field study.

Fig. 4.1.3

TREE (B)

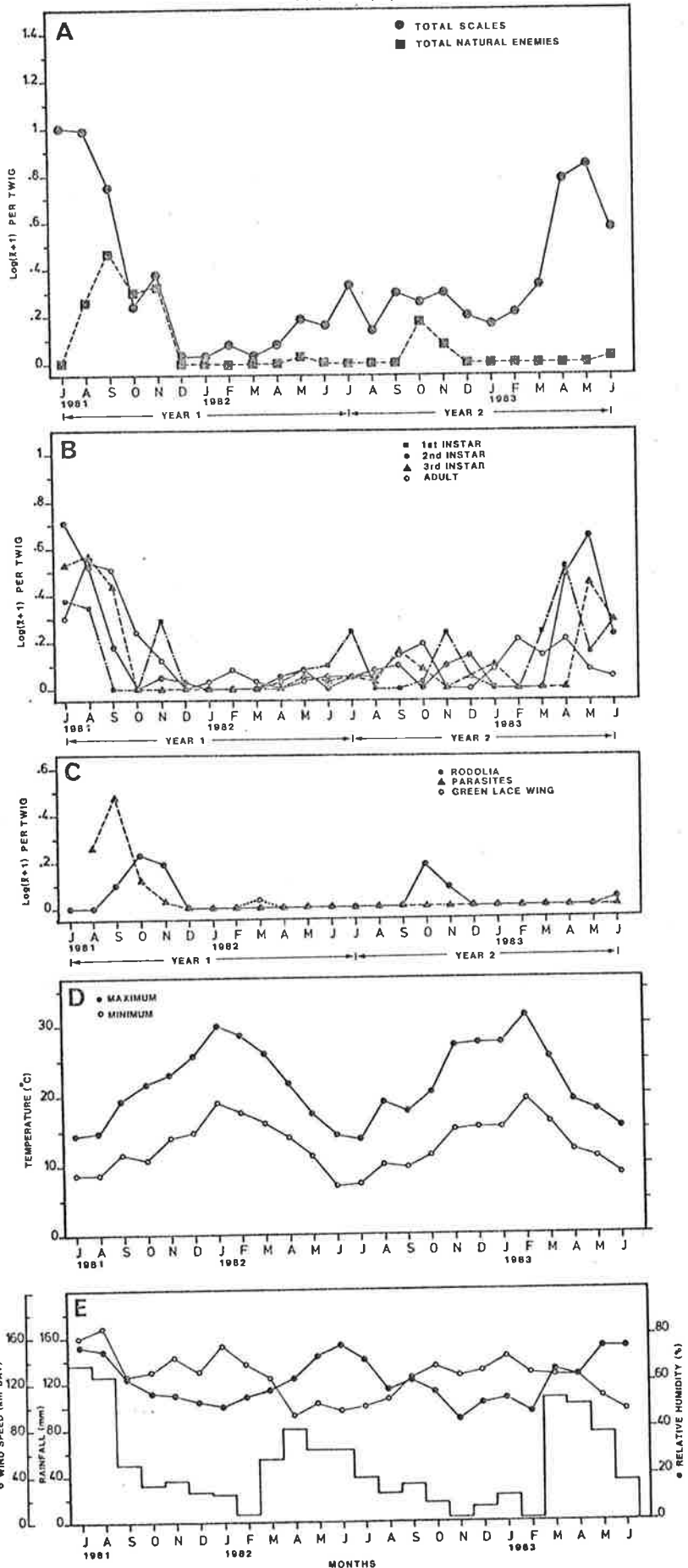
- (A) Numbers of total scales and of total natural enemies at monthly intervals over two years plotted as  $\text{Log}(x+1)$  of the mean numbers per twig. The first points are for July, 1981.
  
- (B) Numbers of the three instars of the scale and of the adults at monthly intervals over two years plotted as  $\text{Log}(x+1)$  of the mean numbers per twig.
  
- (C) Numbers of Rodolia, the parasites (Cryptochaetum spp. and Euryschia sp.) and of the green lacewing (Chrysopa sp.) at monthly intervals over two years plotted as  $\text{Log}(x+1)$  of the mean numbers per twig.
  
- (D) Monthly means of the daily maximum and minimum temperatures from July, 1981 to June, 1983.
  
- (E) Monthly means of the daily relative humidity (%) and wind-speed (km/day) and the total monthly precipitation (mm) during the 2 years of the field study.

TREE - (A)





TREE - (B)



The parasite population (the numbers of Euryschia and Cryptochaetum were pooled because the number of the former was very low) showed a single peak in October, 1981 in Tree-A and in September, 1981 in Tree-B (Figs. 4.1.2C & 4.1.3C). From December 1981, the parasite population remained unnoticed for most of the sampling period, except for a few that were observed in August and September in 1982 on Tree-A.

The numbers of Rodolia also showed one noticeable peak in a year; viz., in the spring, but their numbers were so low that it was difficult to assess when in spring their numbers were maximal. The numbers of another predator, the green lacewing, Chrysopa spp. also followed a trend similar to that of Rodolia, though its numbers were much lower than that of the latter. Though the population samples did not detect the presence of Rodolia during the winter months, a few larvae of Rodolia were noticed even during the winter, on potted plants and bushes. The green lacewing, however, was never found feeding on the scales at times other than the spring.

Figures 4.1.2D & 4.1.3D present the mean monthly maximum and minimum temperatures and precipitation data collected from the Waite Meteorological Observatory. The maximum temperatures ranged from a high of ca. 30° C in January/February to a low of ca. 14° C in June/July. However, during the summer months, daily maximum temperatures reached 40 - 43° C for a day or two. The mean minimum temperatures, on the other hand, ranged from a high of ca. 19° C in summer to a low of ca. 7° C in winter. During the winter months, daily minimum temperatures can drop as low as ca. 4° C.

The total monthly precipitation data showed that March/April were the wettest months and February the driest month (Figs. 4.1.2E & 4.1.3E). The mean monthly relative humidity also followed a trend similar to that of precipitation; highest in winter months and lowest in summer months. The mean monthly wind speed was, however, higher in the summer months and lower in the winter months.

#### 4.1.4 DISCUSSION

In Adelaide, South Australia, the cottony-cushion scale and its natural enemies are only noticed for a very short period during the year. The scale population rapidly builds up over the autumn months (April, May and June) when the numbers of their natural enemies remain extremely low. The scale population reaches its peak in early winter (June or July) when a large proportion of the scales are 1st and 2nd instars. Their numbers decline rapidly during the winter months, even with the lower activity of the natural enemies. The heavy rainfall, which might drown or dislodge the scales during the inter-moult period, could be the reason for such a decline during the winter months. The violent shaking of the branches resulting in the twigs banging against each other due to the wind disturbances could also dislodge the scales, especially those in their 1st and 2nd instars. Since the winter season can extend over 5 to 6 months beginning from March, the scale population may be exposed to a high risk of dislodgment over a considerable length of time. By the spring, when a greater proportion of the scale population is represented by the later instars and adults in already reduced numbers, the weather warms up and the natural enemies of the scale become active. This is a specially advantageous time for the parasites which oviposit in the late 2nd instars and later stages. The concerted efforts of both the parasites and the predators seemingly result in the collapse of the scale population by early summer. There is then a shortage of food for the natural enemies and the number of natural enemies decline rapidly as well. However, some 1st instar scales survive predation, possibly because of their small size, and establish new scale colonies. These insects develop very fast over the warm summer months and become adults by the end of summer when they start producing crawlers. At this time, large numbers of crawlers settle down and many new colonies are formed. In the virtual absence of the natural enemies and low rainfall, the scale population rapidly builds up until in winter rain/wind again take a heavy toll of a large proportion of the scale population. And the whole cycle is once again repeated.

It is difficult to know how the host-specific parasites and the monophagous Rodolia (Quezada and DeBach, 1973) survive the long period from late summer through the autumn and winter months. However, they may have alternate hosts in South Australia which we do not know about.

One of the reasons often forwarded in an attempt to answer why both

the scales and its natural enemies are uncommon in Australia, when the scales can become potential pests overseas, is that the natural enemies, especially Rodolia, are very efficient. That Rodolia alone, or in association with Cryptochaetum, has the potential to keep the scale population under commercial control, has been conclusively demonstrated by the numerous successes in biological control attempts overseas (see Chapter 2). The question arises -- is the same true for Australia too?

A study of the phenology of the scale and its natural enemies on Acacia baileyana shows that abiotic factors, such as precipitation coupled with wind disturbances, also play a vital role in reducing the scale population during the winter months when the natural enemies of the scale are virtually inactive. On the basis of laboratory studies in which crawlers died of drowning in 100 % relative humidity, Hale (1970) suggests that it is likely that nonsessile immature scales could easily be killed during periods of high precipitation. Wolcott and Sein (1933) also reported that practically all the scales were destroyed by a hurricane in Puerto Rico.

The low population of the scales is then severely attacked by the natural enemies in spring and early summer, when the numbers of natural enemies build up much rapidly due to their shorter generation times relative to that of the scales.

The sampling data, therefore, suggest that the abiotic and the biotic factors assist each other in keeping the scale population at low levels over the course of one year. The question then arises, which is more important -- the abiotic factors or the biotic factors? Also, do the biotic factors possess the potentiality to control the scale population on their own?

To evaluate the true impact of natural enemies on the seasonal abundance of the scales, natural enemy exclusion experiments were conducted. Twelve sets of such experiments were conducted over a period of 12 months in order to take into account the seasonal dynamics of the natural enemies (section 4.2).

## 4.2 NATURAL ENEMY EXCLUSION EXPERIMENT

### 4.2.1 INTRODUCTION

The assesment of natural enemy effectiveness can be undertaken either for (1) measurement of the beneficial results of colonization of newly imported exotic parasites or predators, or (2) measurement of the degree of biological control exerted by already established enemies (DeBach and Huffaker, 1971). The impact of natural enemies on the abundance of a prey population can be evaluated by a number of techniques. Periodic census and life table data provide much valuable information, but such quantitative methods, including regression and modelling techniques, have weaknesses for the adequate rating of the regulating or controlling power of the natural enemies (DeBach and Bartlett, 1964; DeBach and Huffaker, 1971; DeBach et al., 1976). The use of experimental comparison is considered to be the best (DeBach and Bartlett, 1964), though Legner (1969) argues that "The ultimate and probably only reliable method for judging a parasite's effectiveness is the reduction in host equilibrium position following liberation". Depending on the system under investigation, either of the three experimental comparison methods viz. (a) the addition method, (b) the exclusion (or subtraction) method, and (c) the interference method, can be employed. The exclusion method, which involves the initial elimination and subsequent exclusion of natural enemies either by mechanical or chemical means, is the most popular and has been successfully used by a number of workers in the past.

The population census data presented in Section (4.1) produced inconclusive results on the impact of natural enemies on Icerya purchasi populations, therefore, natural enemy exclusion experiments were conducted to determine the role of natural enemies.

### 4.2.2 MATERIALS AND METHODS

A typical experiment was set up on a small tree of Acacia baileyana, which was about 4 years old and located within the institute grounds. The experimental design consisted of three treatments (a) uncaged, (b) open-caged, and (c) caged, with each treatment replicated three times. Twelve experiments were conducted over a period of a year, each starting with cohorts of crawlers and beginning at each month from April 1982 to March 1983, in order to take into account the seasonal changes in the abundance of natural enemies.

Each cohort of insects was generated by releasing 100 crawlers in a tubular plastic cage (15 x 7 cm dia) (Fig. 4.2.1A) through the lid of which was inserted a twig. The crawlers had been starved for 24 h prior to release in order to stimulate settling. After four days, the numbers of crawlers which settled were counted and their numbers were thinned to 70 in those cohorts in which more than 70 had settled. The plastic cage only served to allow the the crawlers to settle on the twig, and it was then replaced by another larger cage which had a wire mesh frame (30 x 20 cm dia) and ployester voile covering. In the open cage treatment, the end of the cage which was away from the tree was left open (Fig. 4.2.1B) to allow the entry of natural enemies. In the caged treatment, both the ends of the cage was kept closed (Fig. 4.2.1C). The end of each cage away from the tree was suspended by string from higher branches to provide some stability. The uncaged treatment had no cage at all around the cohort of insects.

Data were collected every fortnight on the numbers of different instars surviving in each of the cohorts until all the surviving insects had become adults. Data were also gathered on the number of predators present while the parasitized scales were collected and incubated in the laboratory for adult emergence.

### 4.2.3 RESULTS AND DISCUSSION

#### 4.2.3.1 DURATION OF DEVELOPMENT

The duration of development of the different instars and resultantly the generation time of a cohort of insects would be expected to vary with the time of the year when it was introduced, and would depend largely on temperature. On a calender scale, in Fig. 4.2.2 are given :

- (i) the developmental time of the different instars of the scales (in A),
- (ii) the numbers of predators (in B), and
- (iii) the mean monthly maximum and minimum temperatures during the course of the 12 experiments (in C).

The results in Fig. 4.2.2A are based on the total number of insects in all the three replicates of the open-caged treatments. Since observations were terminated when all the surviving individuals in a cohort became adults, the data on the longevity of adults were incomplete. Also the results are based on fortnightly observations and so the estimates of

Fig. 4.2.1

- (A) Perspex cage in which crawlers were released to facilitate their settling on twigs.
- (B) Polyester voile cage which was open on one side and which was used for the open-caged treatment.
- (C) Polyester voile cage which was closed on both both ends and which was used for the caged treatment

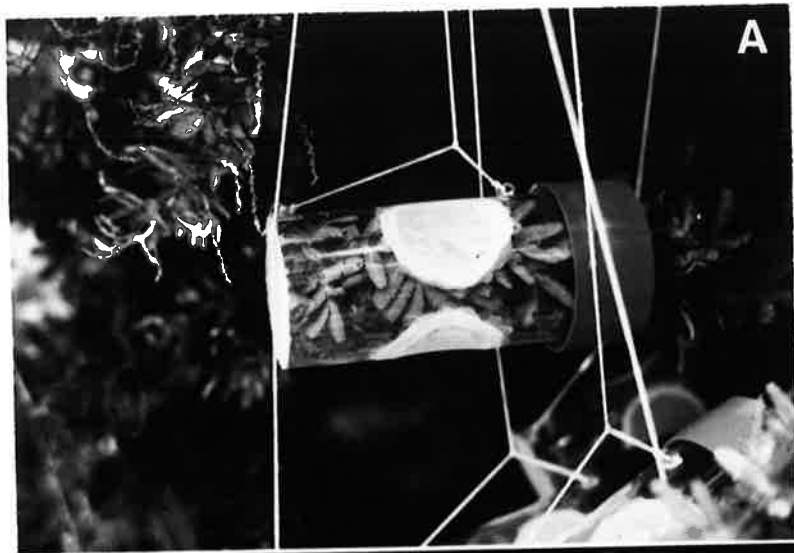
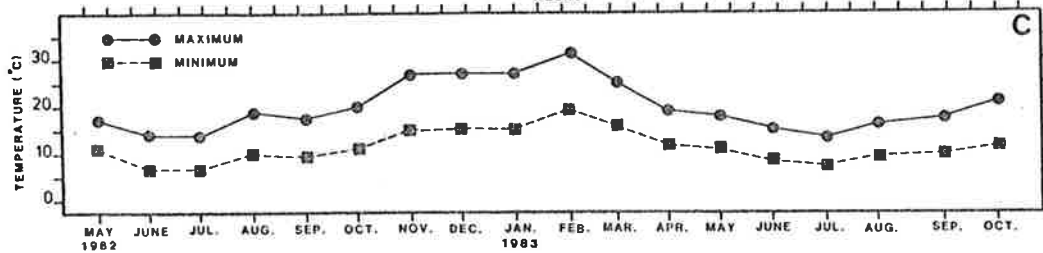
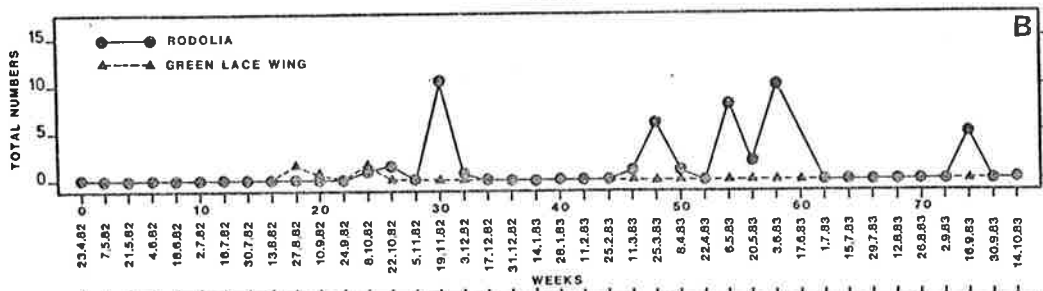
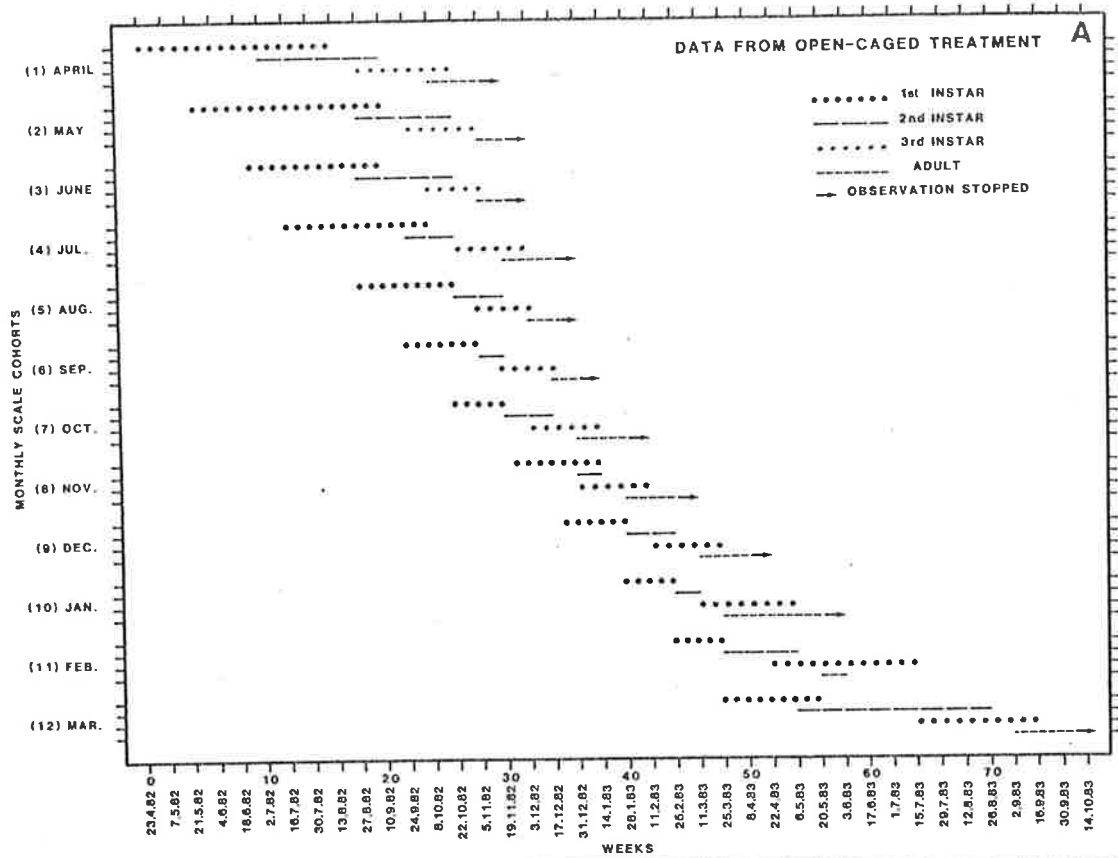




Fig. 4.2.2

- (A) Duration of development of each of the three instars and of the pre-reproductive period of the adult scales in weeks; based on the surviving scales in the open-caged treatment for each monthly cohort.
  
- (B) Total numbers of Rodolia and of green lacewings observed at fortnightly intervals in the three replicates in both the uncaged and the open-caged treatments in the natural enemy exclusion experiments.
  
- (C) Monthly means of the daily maximum and minimum temperatures between May, 1982 and October, 1983.



duration of development are rather crude; yet they provide an indication of the relative trend that would exist in natural populations in different times of the year.

If we consider the period from the introduction of the scales (crawlers) to the time when all the scales become adults as the total developmental time, we find that this developmental time varies considerably among the monthly cohorts (Fig. 4.2.2). The cohort with the longest developmental time, up to 28 weeks, is that started in April which develops right through the winter to become adults only in the middle of spring (in November). The cohort with the shortest developmental time, up to 14 weeks, is that started in November. In this cohort, the scales develop much faster over the warm summer months to become adults by the end of February.

Figure 4.2.2B shows the total numbers of predators (Rodolia and Green Lace Wing) observed in all the three replicates of both the uncaged and open-caged treatments. The activity of Rodolia can be traced for the major part of the year from Fig. 4.2.2B. During the wet winter months, they were present but their activity was very low. Their presence was more obvious in the spring and summer months. The Green Lace Wing, on the other hand, was only found active in the spring and summer months. These results are in agreement with those gathered from population sampling (section 4.1). It was not possible to plot the parasite numbers on a calendar scale in this manner as the data on them were available only from the emergence of parasitized scales. However, from general observations, it can be stated that they were active for a major part of the year but especially in the spring and summer months.

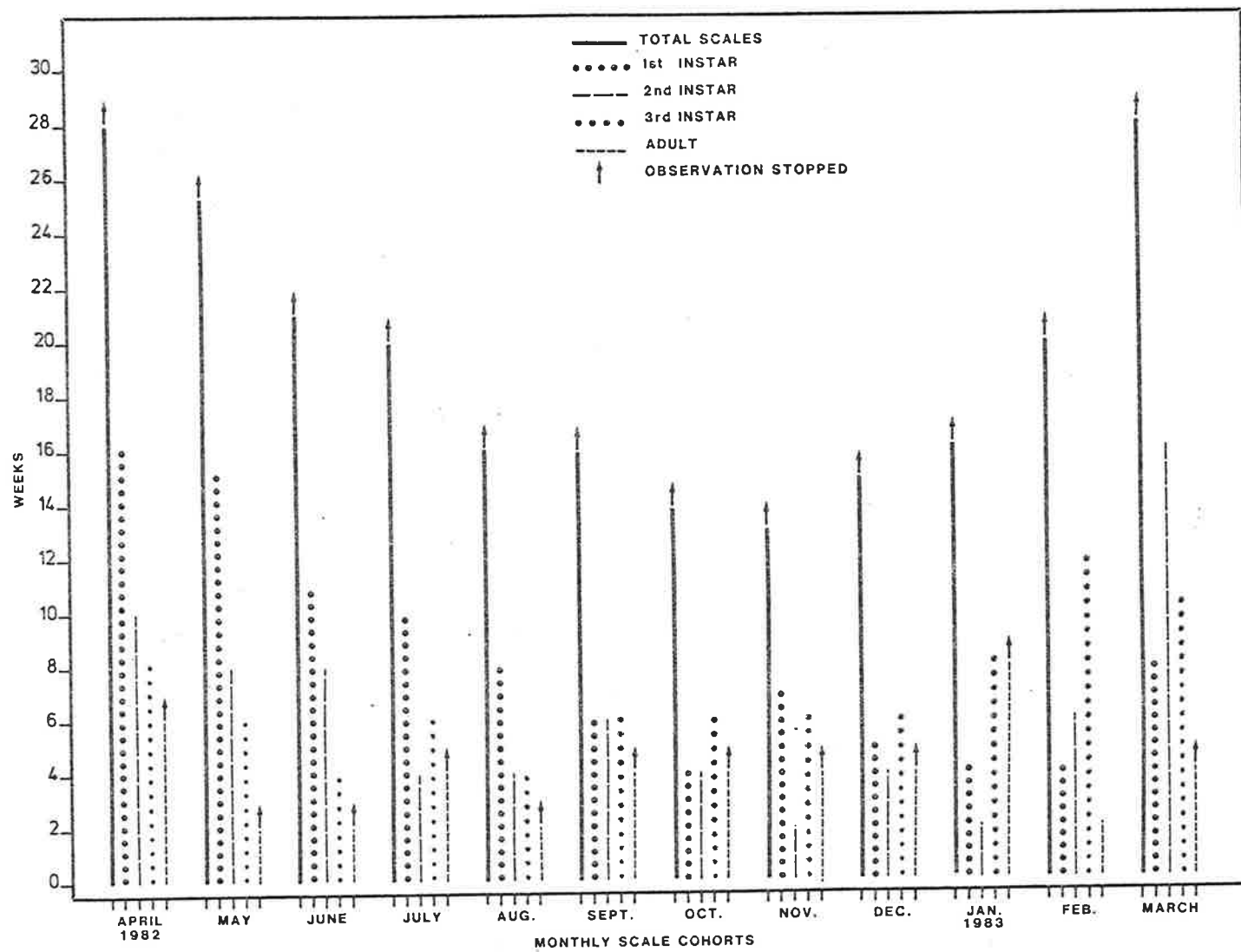
The mean monthly maximum and minimum temperatures plotted in Fig. 4.2.2C show, as expected, that the monthly cohorts that started when the temperatures were relatively high had much shorter developmental times than those started when the temperatures were relatively low.

In Figure 4.2.3, the results on the developmental time for the scales are plotted on a weekly scale to highlight the trends more clearly. If we had data over a few years, the trends in the developmental times in Fig. 4.2.3 would appear to follow a wave form, with autumn introductions (March, April and May) forming the crest and the late spring and early summer introductions (October, November and December) forming the trough.

If we followed any cohort for a few successive generations, we would

Fig. 4.2.3

Duration of total generation time and that of each of the three instars and of the pre-reproductive period of the adult scales; based on the surviving scales in the open-caged treatment for each monthly cohort.



find that only two generations can be successfully completed in a year, with only 4 to 5 weeks left for the third generation. The data also show that the November cohort took the shortest time and it still required from 14 to 16 weeks, yet the population sampling data (section 4.1) indicated that there could be three generations. Thus the third generation can only be produced if there were overlapping generations. This was quite possible since more than one stage of scales have been found in all the monthly population samples, though their proportions varied with the seasons (section 4.1).

Figure 4.2.3 also shows that, depending on the seasons, the different instars in different monthly cohorts took different durations to complete their development. The 1st instar in the April cohort took the longest time, up to 16 weeks to develop. There was a gradual reduction in the developmental time in the subsequent monthly cohorts till it reduced to a low of 4 weeks in the spring and summer cohorts; the exception being the November cohort in which this duration was unusually large, for some unknown reason. In later cohorts this duration started increasing again. The duration of development of the 2nd instar was the longest in the March cohort (16 weeks), from where it gradually declined, till it was lowest (2 weeks) in the November and January cohorts. The 3rd instar developmental period was the longest (12 weeks) in February cohort, from where it gradually declined to a minimum of 4 weeks in June and August cohorts.

When we consider the duration of development of different instars in the same cohort, we find that in the April, May and June cohorts, the duration of development of the 1st instar was the longest, followed by that of the 2nd instar, which was again followed by that of the 3rd. In the subsequent monthly cohorts, the degree of difference in the developmental periods among the different instars was reduced until in the September cohort all the three instars took the same time to develop. In cohorts following the September cohort, the later instars appeared to take longer than the early instars, thus reversing the trend and the maximum difference in the duration of development between instars being in the February cohort. These systematic changes in the duration of development of the different instars are mainly due to the changes in the seasonal temperatures.

#### 4.2.3.2 THE SURVIVAL OF SCALES

The numbers of scales surviving in the three treatments (uncaged, open-caged, caged) can be compared by considering either the end result i.e., the percentage of scales surviving to become adults, or by the rates of survival over the entire period of development. Though the former is a good enough test of the null hypothesis of no significant difference between treatments, the comparison of the rates of survival further substantiates the inferences drawn from a comparison of the end result. The data were therefore analysed by both methods. Student's t-Test of significance was used for the former, while the differences in rates were tested by fitting the Weibull Distribution as well as Manly's (1976) model to the survival data.

##### (A) PERCENTAGE OF SCALES SURVIVING TO ADULTS

The percentage of scales that survived to become adults in each of the treatments in each of the 12 monthly cohorts have been plotted in Fig. 4.2.4A. In all the sets of monthly cohorts, except that of April, the percentage of scales surviving to adults in the caged treatments were much higher than those in the open-caged treatments. Student's t-test conducted between the pairs of data for the caged and open-caged treatments showed that the differences between the means were highly significant ( $P < 0.01$  or  $P < 0.05$ ) in all, except the April and December cohorts (Table 4.2.1). The percentages for the open-caged treatment were the same as those of the uncaged treatment in all but the April, December and January cohorts in which the percentages were markedly higher.

The total number of natural enemies observed over three replicates in the open-caged and the uncaged treatments have been plotted in Figs. 4.2.4B and 4.2.4C respectively. The results show that the natural enemies have in general remained active over all the monthly cohorts except the April cohort and in this cohort, the percentage of scales surviving to adults were higher than that in the subsequent cohorts. This was perhaps because the experiment was set-up on a young tree which did not harbour any scales before, and so no natural enemies were present either. Thus the better survival of the scales, in the open-caged treatment in the April cohort set, could be attributed to the time lag in the natural enemies discovering the new colonies of scales. One of the important reasons for the better survival of scales in the open-caged treatment in December and January

Fig. 4.2.4

- (A) Mean percentages of scales surviving in each of the three instars of the three for the caged ( ■ ), open-caged ( ○ ), and the caged ( ● ) treatments of the natural enemy exclusion experiment.
- (B) Totals over three replicates of the numbers of parasitoids ( ■ ), of Rodolia ( ● ) and of green lacewings ( ○ ) in the OPEN-CAGED treatments.
- (C) Totals over three replicates of the numbers of parasitoids ( ■ ), of Rodolia ( ● ) and of green lacewings ( ○ ) in the UNCAGED treatments.



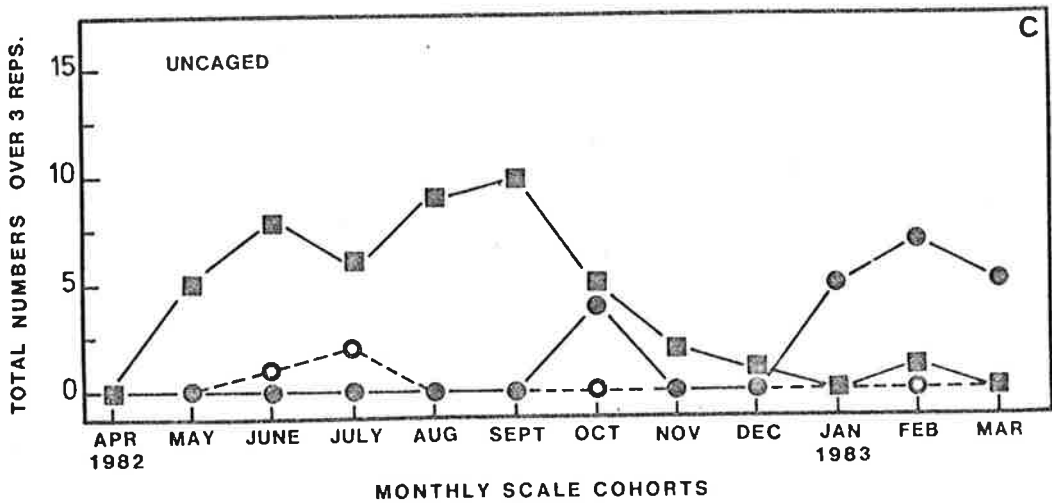
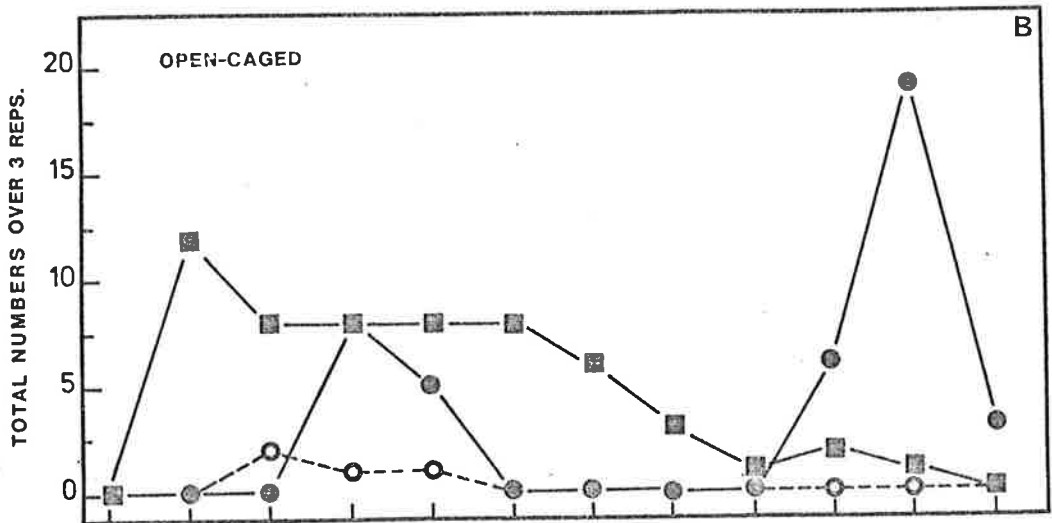
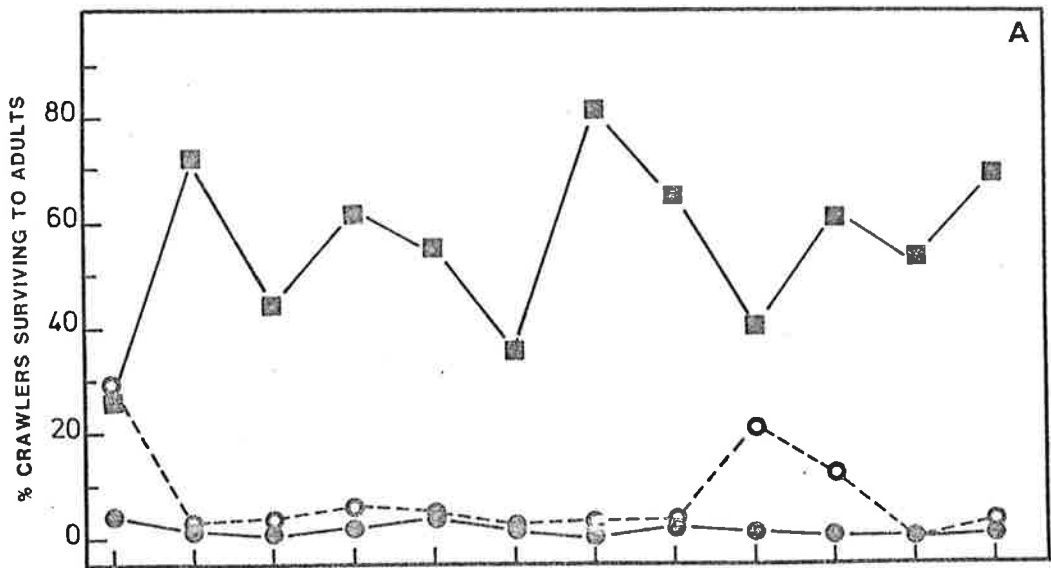


Table 4.2.1

PERCENTAGE OF SCALES SURVIVING TO ADULTS IN THE NATURAL ENEMY  
EXCLUSION EXPERIMENT AND TEST OF SIGNIFICANCE BETWEEN OPEN-CAGED  
AND CAGED TREATMENTS (\*\*)

MONTHL COHORT	UNCAGED MEAN $\pm$ S.E.	OPEN-CAGED MEAN $\pm$ S.E.	CAGED MEAN $\pm$ S.E.	"t" TEST **		
				t	D.F.	P
APRIL	3.8 $\pm$ 2.07	29.0 $\pm$ 3.91	25.7 $\pm$ 3.61	0.62	4	>0.05
MAY	1.0 $\pm$ 0.51	3.0 $\pm$ 3.03	72.6 $\pm$ 3.72	14.49	4	<0.001
JUNE	0.5 $\pm$ 0.47	3.5 $\pm$ 1.94	43.7 $\pm$ 9.63	4.09	4	<0.05
JULY	2.0 $\pm$ 2.03	6.1 $\pm$ 3.07	62.0 $\pm$ 5.72	8.60	4	<0.001
AUGUST	4.3 $\pm$ 2.17	4.8 $\pm$ 4.09	54.8 $\pm$ 4.99	7.76	4	<0.01
SEPT.	1.4 $\pm$ 0.84	2.4 $\pm$ 0.97	35.7 $\pm$ 5.77	5.69	4	<0.01
OCT.	0	2.9 $\pm$ 0.84	81.4 $\pm$ 4.59	16.84	4	<0.001
NOV.	2.4 $\pm$ 0.97	3.3 $\pm$ 1.72	64.3 $\pm$ 8.35	7.15	4	<0.01
DEC.	0.6 $\pm$ 0.57	21.1 $\pm$ 5.68	40.3 $\pm$ 10.51	1.60	4	>0.05
JAN.	0	11.9 $\pm$ 4.82	61.0 $\pm$ 4.54	7.41	4	<0.01
FEB.	0	0	52.8 $\pm$ 6.23	16.09	4	<0.001
MARCH	0.7 $\pm$ 0.70	2.8 $\pm$ 2.17	68.6 $\pm$ 2.48	19.94	4	<0.001

cohorts could also be due to the lower activity of the natural enemies; the decline in natural enemy numbers coinciding with the better survival in these cohorts (Fig. 4.2.4B). Though the parasite activity declined in December and subsequent cohorts, the influence of Rodolia increased considerably which, perhaps, kept the percentage of scales surviving to adults under control.

The numbers of natural enemies in the uncaged treatment followed the same general trend as that of the open-caged treatment, though being lower in magnitude (Fig. 4.2.4C). This could be because the natural enemies in the open-caged treatment were restricted by the confines of the cage and so were able to exert a more concerted impact on the scales. Also, in the uncaged treatment the natural enemies may have wandered away and escaped detection at the time of data collection. The similarity in the trends of the numbers of natural enemies and the percentage of scales surviving to adults in the uncaged and open-caged treatments and the latter being significantly different from the caged treatments are valid indications of the potentialities of the natural enemies in keeping the scale population under control.

## (B) THE RATES OF SURVIVAL OF THE SCALES

### (i) APPLICATION OF WEIBULL DISTRIBUTION TO SURVIVAL DATA

The Weibull frequency distribution is popular among engineers, who use it as a time-to-failure model for testing the life of ball-bearings, electron-tubes, relays, etc. (Hahn and Shapiro, 1967; Lawless, 1982). In biology, it has been considered as a model for human survivorship (Gehan and Siddiqui, 1973), and Pinder et al., (1978) proposed that survivorship data from animal populations could also be effectively described by it. Analysing data from the literature on birds, barnacles and rotifers, they found that generally the Weibull distribution fitted survival data very well.

The first application of the Weibull distribution to insect population data was made by Hogg and Nordheim (1983) who applied it to Heliothis spp. They found that the Weibull distribution was very useful as a survivorship model in an ecological context due to its great flexibility and the ability to draw statistically and ecologically meaningful inferences from the model parameters. The latter point was particularly important with regard to the shape parameter, because by describing the shape of the survivorship curve

the model described the distribution of mortality with age. The main limitation of the Weibull distribution, however, was that it was useful as a survivorship model only if mortality was a "monotonic" function of age (Hogg and Nordheim, 1983). When mortality is not a monotonic function of age, it is preferable to use a model that incorporates a mixture of distributions.

The Weibull parameters can also be used to compare a number of sets of lifetime data (Pinder et al., 1978; Hogg and Nordheim, 1983), and Lawless (1982) suggests that the estimates of the shape parameter ( $c$ ) ought to be compared first as a test of the null hypothesis of no difference between sets of data. Only if the estimates of the shape parameter are not significantly different, can estimates of the scale parameters be compared.

#### THE WEIBULL MODEL

The Weibull cumulative distribution function can be defined by the following expression :

$$F(t) = 1 - \exp [ -(t/b)^c ] \quad \dots\dots\dots(1)$$

( $t, c, b > 0$ )

$$S(t) = 1 - F(t) \quad \dots\dots\dots(2)$$

where :  $b$  = scale parameter

$c$  = shape parameter

$t$  = age at death

$F(t)$  = probability of dying at a given age ( $t$ )

$S(t)$  = probability of surviving at a given age ( $t$ )

There are two ways in which estimates of the shape and scale parameters can be obtained for any set of survival data. The first method, which is relatively simple but less precise, is obtained from a linear plot of the  $\ln \ln [1/(1-F(t))]$  values against  $\ln(t)$ , and estimates of " $c$ " and " $b$ " are obtained from least squares regression procedures (Hahn and Shapiro, 1967). The second method involves the use of maximum likelihood procedures. There are numerous ways of obtaining maximum likelihood estimates (MLEs) for the shape and scale parameters (see Lawless, 1982 for

review). However, as was found by Hogg and Nordheim (1983) and myself, one is confronted with the problem of finding the right procedure for obtaining the MLEs and the confidence intervals about these estimates.

Though the estimation of the shape and scale parameters using the linear regression procedure is relatively simple, there are no methods for calculating confidence intervals (Pinder et al., 1978). Also, appropriate goodness of fit tests for testing the fit of the Weibull model to the data, and appropriate methods of comparing the shape and scale parameters are available only for estimates obtained from maximum likelihood procedures (Lawless, 1982). Pinder et al. (1978) have suggested the use of Chi-square goodness of fit tests for testing the fit of the Weibull distribution to the data, and normal analysis of variance procedures for comparing shape parameters and scale parameters. However, in a comprehensive review of the Weibull distribution, Lawless (1982) makes no mention of such procedures, and statistical advice at the Waite institute also suggested that such statistical tests were inappropriate. Friedman's non-parametric analysis of variance was considered appropriate for analysing the shape and scale parameters and it was used.

## RESULTS AND DISCUSSION

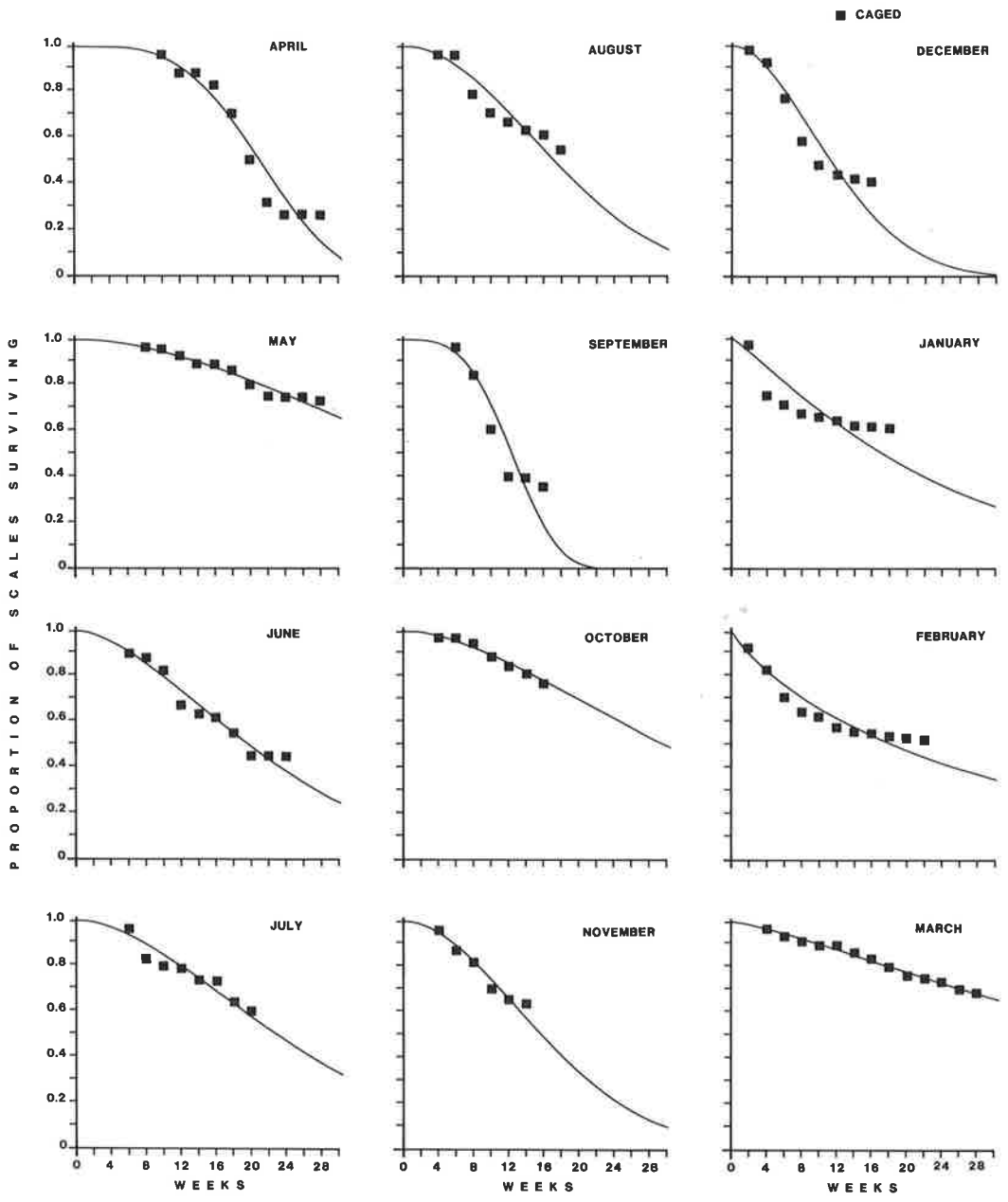
The numbers of scales surviving at fortnightly intervals in the three replicates of each of the uncaged, open-caged, and caged treatments have been presented in Appendix Tables 8A to 8L. The total number of scales surviving (not the means), summed up over the three replicates at each observation, was used in fitting the Weibull distribution to the data because the model can handle whole numbers only. The fitting of the Weibull distribution to the data was done by the help of a special programme used on the Apple IIe minicomputer, which also plotted the fitted Weibull curve (Fig. 4.2.5).

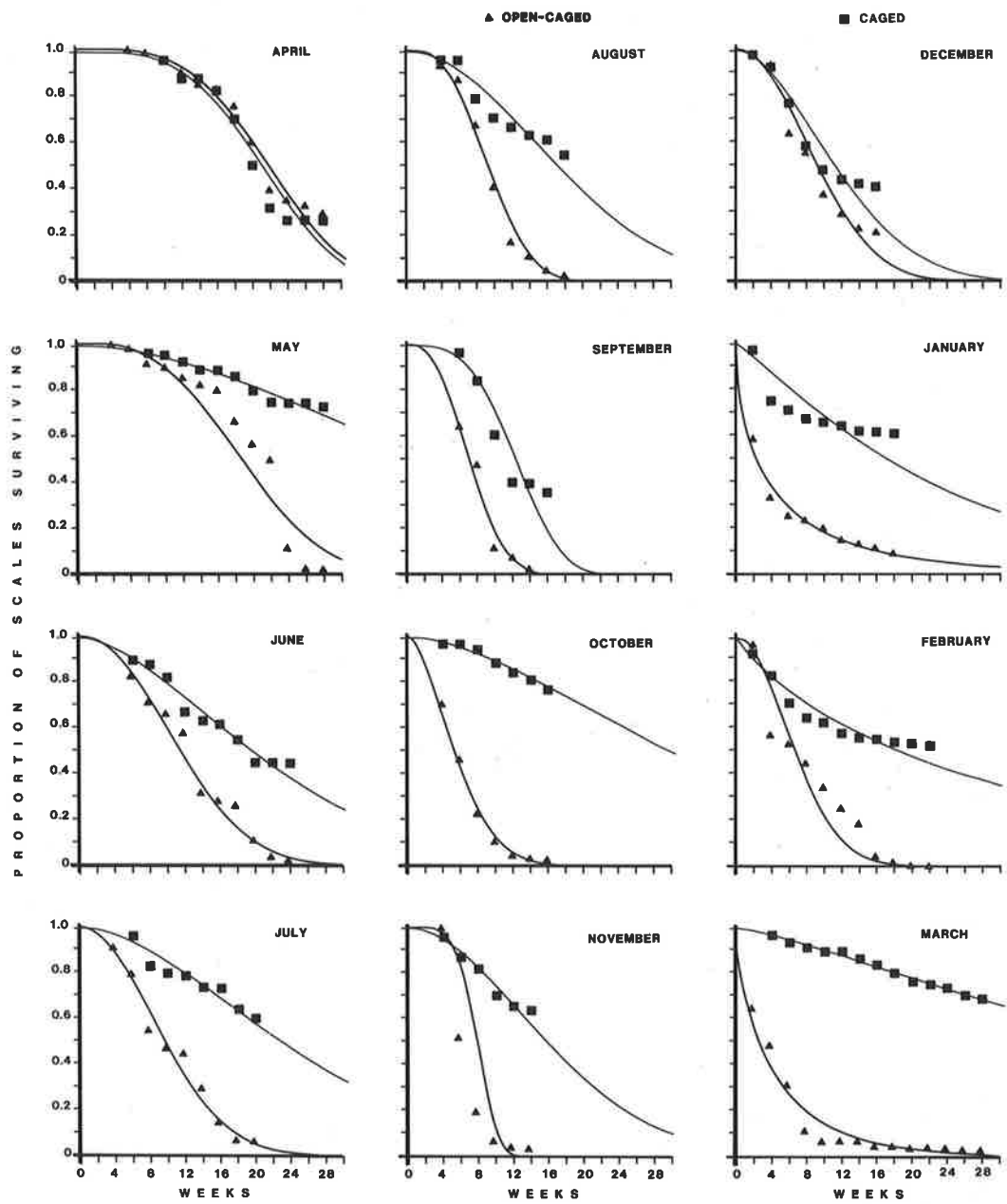
The proportion of insects surviving at fortnightly intervals in the different treatments in the 12 monthly cohorts have been plotted in Fig. 4.2.5 by means of a main figure (caged) and two overlays (one each for uncaged and open-caged treatments). The symbols in the figures represent the observed values and the lines represent plots of the fitted Weibull function.

Initially attempts were made to obtain MLEs for the shape and the scale parameters using Lawless's (1982) method, but plots of the fitted

Fig. 4.2.5

The proportion of the settled crawlers that survived over 28 weeks on Acacia baileyana in each of the uncaged ( ● ), open-caged ( ▲ ), and caged ( ■ ) treatments of each of the 12 monthly cohorts of the natural enemy exclusion experiment.









Weibull curves remained far away from a plot of the observed values (Fig. 4.2.6). Attempts were then made to fit the Weibull distribution using the BMDP-81 Statistical Software package, to the set of data for the uncaged treatment of the April cohort set using the maximum likelihood procedures. The rate of convergence was found to be very slow, and in fact, satisfactory convergence was not achieved. For the same set of data, the minimum Chi-square fitting criteria (asymptotically equivalent to the maximum likelihood) was also tried; and this method finally gave estimates but the fit was poor. The estimates obtained have been presented in the table below.

COHORT	PROCEDURE	SHAPE (c)	SCALE (b)	CHI-SQUARE
APRIL	MLEs	3.39	19.70	28.4 (minimum; 9 d.f.)
(UNCAGED)	REGRESSION	2.51	18.49	38.08 (not minimum; 9 d.f.)

The above table shows that the estimates obtained by the linear regression procedures produced a higher Chi-square value, inspite of the fact that graphically these estimates appeared to show a good fit (Fig. 4.2.5A). The test illustrated the dangers of using graphical cumulative distribution function plots to determine goodness-of-fit. A possible reason for not obtaining a good fit either numerically or statistically could be because the data set exhibited apparent bimodality. The maximum likelihood procedure of estimating the parameters was, therefore, abandoned.

Although the linear regression procedures produced imprecise estimates of the shape and scale parameters, it was still adopted and the apparent graphical fit of the model to the data was accepted as an adequate description of the data. Figure 4.2.5 shows that in most cases, graphically, the model fits the data satisfactorily. However, Kolmogorov-Smirnov and Chi-square goodness of fit tests showed that, statistically, the model did not fit all the sets of data (Table 4.2.2),

Fig. 4.2.6

The proportions of the settled crawlers that survived over 28 weeks in each of the uncaged, open-caged, and the caged treatments with the APRIL cohort set. The curved lines represent the plots of the fitted Weibull function using a maximum likelihood procedure for each of :

- (A) the UNCAGED treatment,
- (B) the OPEN-CAGED treatment,
- (C) the CAGED treatment.

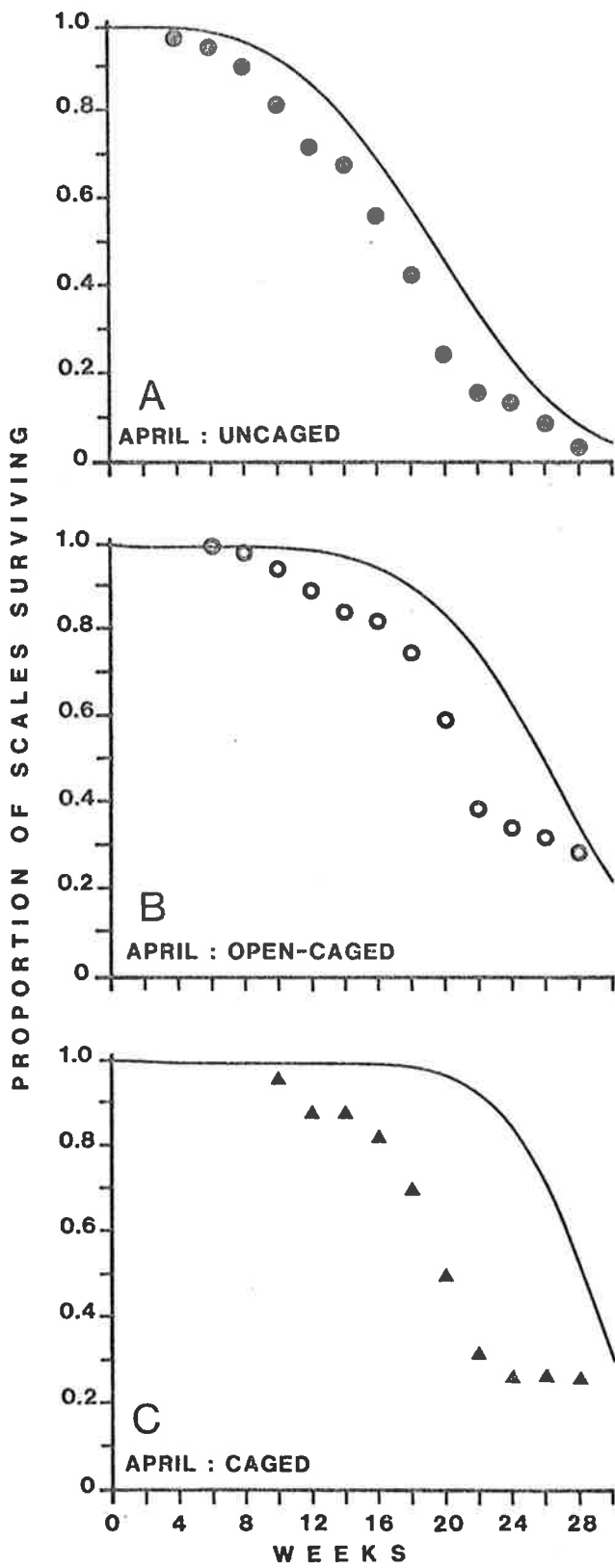


Table 4.2.2

CHISQUARE AND KOLMOGOROV-SMIRNOV GOODNESS OF FIT TESTS ON FITTED WEIBULL DISTRIBUTION TO DATA FROM NATURAL ENEMY EXCLUSION EXPERIMENTS

MONTHLY COHORTS	UNCAGED						OPEN-CAGED						CAGED					
	KOL-SMIR TEST			$\chi^2$ TEST			KOL-SMIR TEST			$\chi^2$ TEST			KOL-SMIR TEST			$\chi^2$ TEST		
	N	D(i)	FIT	$\chi^2$	D.F.	FIT	N	D(i)	FIT	$\chi^2$	D.F.	FIT	N	D(i)	FIT	$\chi^2$	D.F.	FIT
APRIL	210	.068	NS	10.4	10	NS	210	.108	*	21.7	9	*	210	.135	*	30.2	7	*
MAY	181	.194	*	98.9	10	*	194	.159	*	87.1	10	*	174	.039	NS	0.94	8	NS
JUNE	202	.094	NS	36.7	7	*	215	.097	NS	21.8	7	*	173	.051	NS	3.9	7	NS
JULY	238	.262	*	63.2	7	*	212	.092	NS	11.7	6	NS	210	.066	NS	2.7	5	NS
AUGUST	210	.099	NS	9.39	5	NS	210	.084	NS	8.9	5	NS	210	.084	NS	7.9	5	NS
SEPT.	210	.034	NS	3.4	4	NS	210	.081	NS	10.3	3	*	210	.159	*	39.6	3	*
OCT.	210	.04	NS	4.5	2	NS	210	.036	NS	8.8	4	NS	210	.021	NS	0.3	4	NS
NOV.	210	.034	NS	5.1	4	NS	210	.347	*	2561.6	3	*	210	.066	NS	2.2	3	NS
DEC.	200	.307	*	94.1	4	*	208	.121	*	23.0	5	*	203	.142	*	24.5	5	*
JAN.	210	.109	*	94.5	4	*	210	.054	NS	4.2	6	NS	210	.125	*	18.7	6	*
FEB.	185	.333	*	319.3	7	*	212	.221	*	120.3	8	*	225	.075	NS	8.6	8	NS
MARCH	210	.257	*	136.8	11	*	210	.094	NS	35.4	11	*	210	.018	NS	0.3	10	NS

N = NUMBER OF SCALES RELEASED

NS = NOT SIGNIFICANT AT P<0.05 (GOOD FIT)

\* = SIGNIFICANT AT P<0.05 (NOT GOOD FIT)

and much less in the uncaged and open-caged treatments. In the caged treatment, however, where the influence of natural enemies was eliminated, the model fitted the data in 8 out of 12 monthly cohorts. These results suggest that the Weibull distribution would show a better fit to survival data if the numbers of animals surviving were indeed a monotonic function of age (Hogg and Nordheim, 1983), e.g. when the influences of biotic factors, which often tend to be more sporadic, are absent.

The shape (c) and scale (b) parameters for each set of data have been tabulated in Table 4.2.3, and plotted in Fig. 4.2.7A and 4.2.7B respectively. The estimates of the shape parameters do not appear to be different, and indeed, Freidman's test of non-parametric analysis of variance conducted on the estimates of the shape parameters showed that the the three treatments (uncaged, open-caged, and caged) were not significantly different (Table 4.2.3). These results suggest that the distribution of mortality with age is not different among the treatments.

A plot of the scale parameter (Fig. 4.2.7B), on the other hand, showed that it followed a consistent trend in that, in each of the monthly cohorts, the estimates of the scale parameters were consistently higher in the caged treatments, while the values for the open-caged treatments were close to but higher than those of the uncaged treatments; except for the April cohort in which the scale parameter for the open-caged treatment was slightly higher than for the caged treatment. Freidman's Test of non-parametric analysis of variance on the scale parameters showed that the difference between the treatments were highly significant (Table 4.2.3). Interestingly, the trends in the scale parameter are very simmlar to that of the percentage of scales surviving to adults (Fig. 4.2.7C).

Thus, if we accept that the shape and the scale parameters describe the survival data sets, we may conclude that the caged treatments were significantly different from the uncaged and the open-caged treatments on the basis of the scale parameters, and we may attribute these differences to natural enemies. The results also suggest that the differences between treatments are a difference in magnitude (scale parameter) and not in the distribution of mortality with age (shape parameter).

Fig. 4.2.7

- (A) The estimates of the shape parameter (c) (Fig. A) and the scale parameter (b) (Fig. B) by the log-log regression method of fitting the Weibull distribution to the proportion of scales surviving over two weeks in the uncaged ( ● ), open-caged ( ○ ) and the caged ( ■ ) treatments with each of the twelve monthly cohorts.
- (C) Mean percentages of scales surviving in each of the three instars for the uncaged ( ● ), open-caged ( ○ ), and the caged ( ■ ) treatments of the natural enemy exclusion experiment.

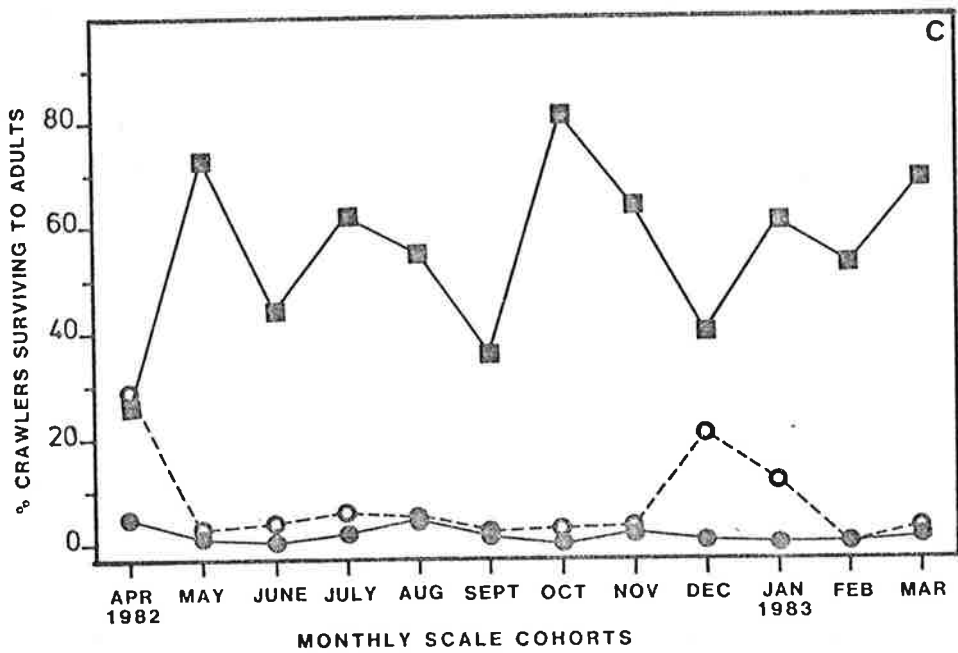
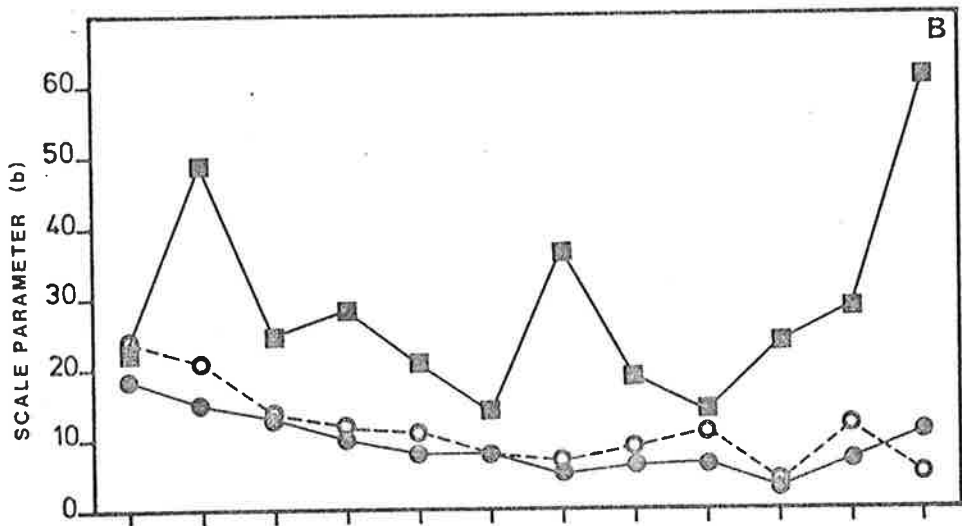
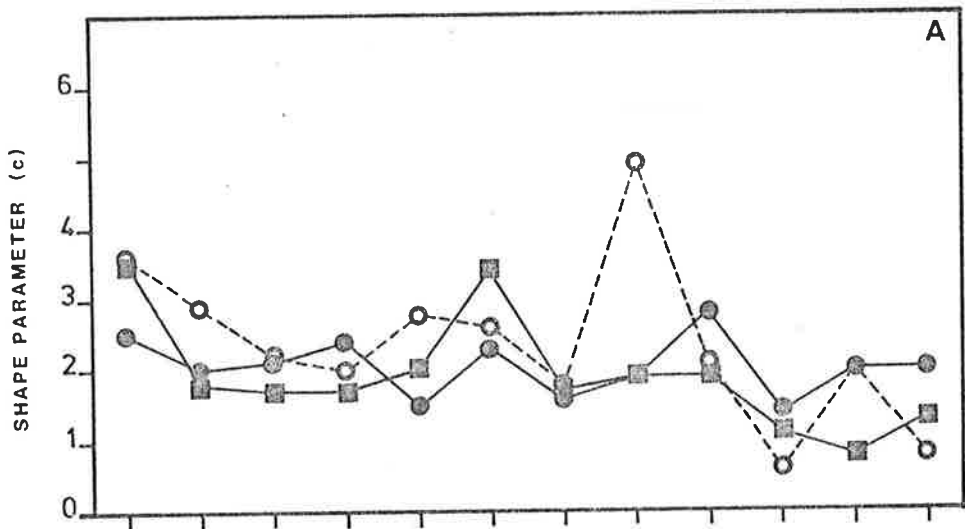




Table 4.2.3

ESTIMATES OF THE SHAPE (c) AND SCALE (b) PARAMETERS FROM FITTING OF THE WEIBULL DISTRIBUTION TO DATA FROM THE NATURAL ENEMY EXCLUSION EXPERIMENT BY LINEAR REGRESSION METHOD, AND FREIDMAN'S NON-PARAMETRIC ANONA ON THE ESTIMATES

MONTHLY COHORTS	SHAPE PARAMETERS			SCALE PARAMETERS		
	UNCAG	OPCAG	CAG	UNCAG	OPCAG	CAG
APRIL	2.52	3.64	3.54	18.49	24.19	23.52
MAY	1.96	2.88	1.81	15.35	21.24	49.25
JUNE	2.11	2.16	1.65	13.27	13.83	24.63
JULY	2.41	2.03	1.73	9.67	11.87	28.46
AUGUST	1.48	2.77	1.99	8.08	10.68	20.81
SEPT.	2.32	2.60	3.41	8.16	8.28	13.89
OCT.	1.64	1.78	1.67	5.04	6.77	37.22
NOV.	1.86	4.86	1.87	6.32	8.85	19.27
DEC.	2.84	2.06	1.86	6.54	11.12	13.78
JAN.	1.39	0.63	1.14	3.27	4.44	23.90
FEB.	1.97	1.99	0.84	6.85	8.30	28.70
MAR.	2.02	0.81	1.26	10.55	4.57	60.56

FREIDMAN'S TEST (NON-PARAMETRIC ANOVA)

RANK SUMS	22	29	21	13	24	35
	$\chi^2 = 3.17$ (D.F.= 2) ; $P > 0.05$			$\chi^2 = 20.67$ (D.F.=2) ; $P < 0.005$		

UNCAG = UNCAGED TREATMENT  
 OPCAG = OPEN CAGED TREATMENT  
 CAG = CAGED TREATMENT

(ii) APPLICATION OF MANLY'S MODEL TO SURVIVAL DATA

(a) INTRODUCTION

Insect population ecologists have for long struggled to accurately estimate the stage-specific survival rates from estimates of the numbers of insects in each stage for various points in time drawn from a population containing several stages (Kiritani and Nakasuji, 1967; Manly, 1974b, 1976, 1977; Ruesink, 1975; Birley, 1977; see Southwood, 1978 for review). These methods of estimation are based on many assumptions, and so the results obtained can only be considered within the constraints of those assumptions. For example, the method of Kiritani and Nakasuji (1967) assumes a constant survival rate in all stages and can only be used if samples are taken at regular intervals of time until all insects have disappeared from the population.

Manly (1974a) conducted a comparative study of the then existing models for analyzing stage frequency data which shared an assumption of constant daily mortality rates, and found that the method of Kiritani and Nakasuji (1967) was more favourable than the rest, though it too was plagued with the constraints mentioned above. Manly (1976, 1977) produced a modified version of the Kiritani and Nakasuji's model which overcame the limitation of sampling at regular intervals in time.

Later workers have attempted to develop models which include variable mortality rates. Birley (1977) developed a model in which several formulations can be used for age dependency in mortality rates, and Bellows and Birley (1981) produced a model in which mortality varies between stages but is constant within a stage. More recently, Bellows et al. (1982) developed a model in which the mortality rate of a population changes markedly at some fixed point in time, possibly due to predation or other means in a similar manner; and van Straalen (1982) produced a model which, he claims, is an extension of the models produced by Manly (1974b) and Birley (1977).

Bishop and Maelzer (1982) also undertook a comparative study of the models produced by Ruesink (1975), Manly (1976, 1977), and Birley (1977), using computer-simulated populations and found that "none of the methods was robust when the main assumption was false, and the statistics were also influenced by the frequency of sampling "incorrect" durations of development of different stages, variations in the daily survival-rate etc.". They also mention that "to get good estimates, one not only has to

estimate the survival-rate for each of the many cohorts starting at different times but also to choose the individuals in each cohort so that they are distributed at random within the population". Bishop and Maelzer further point out that "such cohort survival-rates can be obtained but their cost -- in terms of time spent in estimating them -- is high".

Bishop (pers. comm.) suggested that Manly's model could be satisfactorily applied to data gathered from the natural enemy exclusion experiment for the estimation of survival rates, especially because observations on numbers of insects surviving were made at regular intervals of time. Ready access to Manly's own program, which had been acquired by Bishop and Maelzer (1982), was an added incentive in using Manly's model.

#### DESCRIPTION OF MANLY'S MODEL

As mentioned above Manly (1976) produced an improved version of Kiritani and Nakasuji's (1967) model in order to overcome the latter's restrictions like (a) taking samples at regular intervals of time, and (b) numbers entering stage one to be known independently. The theory behind Manly's model is as follows :-

If we consider a large insect population developing through (q) stages, then the expected number of insects in the stage at time (t) will be those individuals that entered in the time interval (t-a, t) and the survival to time (t), and will be given by --

$$N(t) = M \int_{(t-a)}^t f(x) \cdot e^{-\theta(t-x)} \cdot dx \quad \dots\dots\dots (1)$$

where :

- M = total number of insects entering the stage,
- a = the duration of the stage (measured in days and assumed to be the same for all insects),
- $e^{-\theta}$  = the daily survival rate,
- f(x) = the probability density function for the distribution of the time of entry to the stage.

Now suppose that the ith stage is observed for a time period covered by n samples, possibly with varying time intervals between them. Suppose

also that estimates  $\hat{f}_1, \hat{f}_2, \dots, \hat{f}_n$  are available for  $N(t)$  at times  $t_1, t_2, \dots, t_n$  for the  $i$ th stage, then area under the frequency curve according to the trapezoidal rule is :-

$$\hat{A}_i = 1/2 \sum_{j=1}^n (h_j + h_{j+1}) \hat{f}_j \quad \dots \dots \dots (2)$$

where :  $A_i$  = Area under the frequency curve for the  $i$ th stage  
 $h_i = t_i - t_{i-1}$   
 $\hat{f}_j$  = the number of the  $i$ th instar estimated from the samples.

The survival rate of the  $i$ th stage is estimated by the following expression :-

$$\phi_i = | -A_i | \sum_{j=1}^q A_j \quad \dots \dots \dots (3)$$

where :  $j$  = next stage,  
 $q$  = last stage.

Manly (1976) has shown that estimates of other parameters can be obtained if the median stage (instar value, which will not, of course, normally be a whole number) is plotted against time so that the time for a "median" animal to pass from one stage to another can be read off. Now the daily survival rate raised to the power of the duration of the stage should equal the stage specific survival rate as determined above.

$$\hat{\phi}_i = \hat{\phi}_d^{\hat{a}_i} \quad \dots \dots \dots (4)$$

where :  $\hat{\phi}_d$  = daily survival rate,  
 $a_i$  = duration of the  $i$ th stage as determined above.

From equation (4) we have :

$$\text{Log } \hat{\phi}_d = \text{Log } \hat{\phi}_i / \hat{a}_i \quad \dots\dots\dots (5)$$

From equation 4 the following expression is derived for estimating the numbers of insects entering each stage.

$$\hat{N}_{oi} = -\text{Log}_e \phi_d \left[ \sum_{j=i}^q A_j \right] \quad \dots\dots\dots (6)$$

where :  $N_{oi}$  = the number entering the  $i$ th stage

#### (b) RESULTS AND DISCUSSION

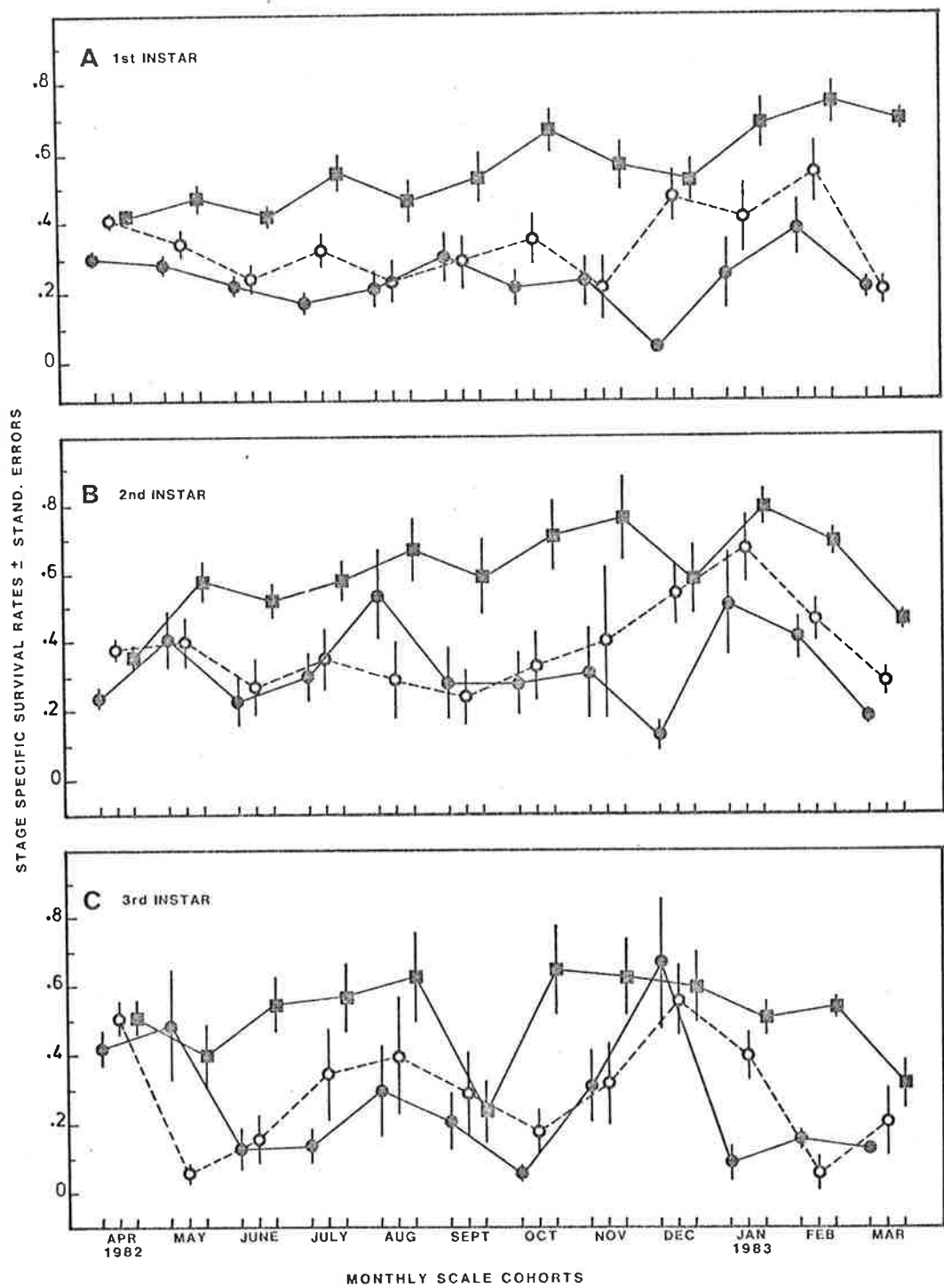
The computer program for Manly's model, obtained by Bishop and Maelzer (1982), produced estimates of stage-specific survival rates along with their standard errors, daily survival rate, durations of stages, and numbers entering different stages. It required data in a form such that at two points in time, the beginning and the end, there were no surviving insects. Since the design of the experiment entailed that each of the replicates in each of the treatments in each month, began at a single point in time, it was easy to set the initial time of "no insects" to a time interval (2 weeks) prior to the date of release. And because observations on the numbers of insects surviving were terminated when all scales had become adults, the end point with no insects was assumed to be the subsequent time interval (2 weeks) after observations on each cohort was terminated. Also, the program required whole numbers for the purposes of analysis, so data files were generated using the sums rather than the means of all the three replicates in the respective treatments.

The estimated stage-specific survival rates (SSSR) together with their standard errors for the 1st, 2nd, and 3rd instars in the three treatments for the 12 monthly cohort sets presented in Fig. 4.2.8 and Appendix Table 9 appeared to follow a definite trend under the influence of the treatments. The SSSR values for the caged treatment were generally higher than those of the open-caged treatment and the SSSR values of the open-caged treatment were generally higher than those of the uncaged treatment for each of the three instars.

In the following discussion, the standard error bars have been

Fig. 4.2.8

Estimates of stage-specific survival-rates (SSSRs) and their respective standard errors, from a fit of Manly's (1976) model, for each of the 1st instar (A), 2nd instar (B), and the 3rd instar (C) in each of the uncaged ( ● ), open-caged ( ○ ) and caged ( ■ ) treatments.



considered as an indication of statistically significant differences between treatments and only those instances have been considered in which the SSSR values for the caged treatment are significantly different from both the open-caged and the uncaged treatments. Figure 4.2.8 shows that the SSSR values are significantly different in all but the April and December (i.e. 10 out of 12) monthly cohort sets in the first instar (Fig. 4.2.8A), and all but the April, August, December and January (i.e. 8 out of 12) cohort sets in the 2nd instar (Fig. 4.2.8B). However, in the 3rd instar (Fig. 4.2.8C), the reverse is true; the SSSR values for the caged treatment are not significantly different from those of the other two treatments in any monthly cohort except those of June, October and February (i.e. 9 out of 12 not different).

The above analysis of SSSR values indicates that the survival rates of the scales in the uncaged and open-caged treatments are not significantly different. However, the survival rates of the scales from both the uncaged and open-caged treatments are significantly different from that of the caged treatment. One is, therefore, led to conclude that the sum total of mortality factors, especially the natural enemies, affecting the scales in the uncaged and open-caged treatments are similar and they are responsible for the significant difference in SSSR values when these treatments are compared with the caged treatment.

Manly's model provides estimates of SSSR values and their respective standard errors based on the assumption that the survival rates of all the stages of an insect are constant. It is very unlikely that this assumption would be true, and so the estimates may not be good in describing reality. The differences in SSSR values among treatments shown above would be true only if the estimated survival rates were good estimates. Manly does not provide any method of testing how good the estimates provided by his model are. Perhaps, the best test of the estimates in describing reality is by simulation studies using estimates of durations of developments and of survival rates to simulate the changing numbers of insects. The numbers of insects can then be compared with the numbers of insects from a real population. Until such a test is conducted, the estimates of SSSR values from Manly's model and the inferences drawn therefrom can only be accepted with caution. The apparent trends in the SSSR estimates in the three treatments in the 12 monthly cohort sets should also be accepted with caution.



### 4.3 SETTLING RATE OF CRAWLERS

#### 4.3.1 INTRODUCTION

Most scale insects which are sessile for a major part of their life time disperse by wind in their crawler stage and the wind dispersal of crawlers has been frequently studied (Willard, 1973, 1976; Moran et al., 1982). Due to their small size, low food reserves and high susceptibility to desiccation, only a tiny fraction of the crawlers produced are able to settle down and form new colonies. To compensate for the heavy loss, most species produce large numbers of crawlers.

The settling rate of crawlers is expected to play an important role in influencing the population dynamics of scale insects, and so the following experiment was conducted to estimate the settling rate of crawlers produced by Icerya purchasi.

#### 4.3.2 MATERIALS AND METHODS

The experiment consisted of two treatments comprising two locations -- one in a shade house and the other in the open. Potted plants of Acacia baileyana, which were about 100 cm high with a single main stem and no branches (Fig. 4.3.1A), were placed at each of the two locations. The stem of each plant supported two groups of 3 ovipositing scales. The first group of scales was enclosed in a clip-on-stem perspex cage (Fig. 4.3.1B) which confined the crawlers to the cage. The perspex cage had circular holes covered with polyester voile for aeration (Fig. 4.3.1B). In the cage both the living and the dead crawlers could be counted and so this group of scales provided estimates of the numbers of CRAWLERS PRODUCED. The second group of scales was enclosed in a net cage (Fig. 4.3.1B) to allow freedom of movement of crawlers in and out but to keep predators out, and this group of scales provided estimates of the numbers of CRAWLERS SETTLED.

Observations were taken at weekly intervals on the numbers of crawlers which SETTLED on the plant and those PRODUCED within the perspex-cages until the adults died. The experiment was replicated three times. Four such experiments were started in January, April, May and August, 1983.

Two similar experiments were also conducted in constant temperature rooms at 20° C and 25° C. These experiments lasted for one week only and produced a single observation of the numbers of crawlers produced and settled at the end of the week.

Fig. 4.3.1

Potted plant of Acacia baileyana with two types of cages that was used in the experiment to study the settling rate of crawlers.



### 4.3.3 RESULTS AND DISCUSSION

The numbers of crawlers produced in cages and the numbers of crawlers settled on the plants in Location-1 (shade house) and Location-2 (open) have been presented in Appendix Table 10 and Fig. 4.3.2. The results from the experiments conducted in constant temperature rooms have been presented in Table 4.3.1.

Figure 4.3.2A shows that the numbers of crawlers produced varied widely and followed no obvious trends, except that during the months of June and July the numbers of crawlers produced in Location 1 (shade house) were generally higher than those in Location 2 (open). This trend could perhaps be due to small variations in temperature in the cages between the two locations. The temperature in the cages in Location 1 could have remained relatively higher due to lower movement of wind in the shade house.

The data plotted in Fig. 4.3.2B, on the other hand, showed that the numbers of crawlers settled were very low in all the 4 experiments in both the locations except for two weeks in the last week of January and the first week of February at Location 1. Though the mean numbers of crawlers settled were generally slightly higher at Location 1 in all the experiments, the differences were not statistically significant, as shown by the standard errors (Appendix Table 10).

Figure 4.3.1C shows that the mean weekly maximum temperature remained below 20° C and the mean weekly minimum temperature remained below 15° C for major part of the experimental period except in January and February, when the maximum temperatures were 30° C and above and the minimum temperatures were above 15° C.

Both the numbers of crawlers produced and the numbers of crawlers settled were much higher in the experiments conducted in the constant temperature rooms (both 20° and 25° C) where there was negligible movement of air (Table 4.3.1). The data show that, in the constant temperature rooms, an extremely high percentage of crawlers that were produced, settled down.

The above results indicate that the settling rate of crawlers is influenced by temperature and wind disturbances. At higher temperatures not only was there a higher production of crawlers but the numbers of crawlers settled were also higher. It was expected that wind disturbances

Fig. 4.3.2

- (A) Mean numbers of crawlers produced by three adult scales in cages attached to plants kept at Location 1 (shade house) and Location 2 (open) at weekly intervals in four separate experiments.
  
- (B) Mean numbers of crawlers that settled from those produced by three adult scales on plants kept at Location 1 (shade house) and Location 2 (open) at weekly intervals in four separate experiments.
  
- (C) Weekly means of the daily maximum and minimum temperatures for the duration each of the above four experiments.

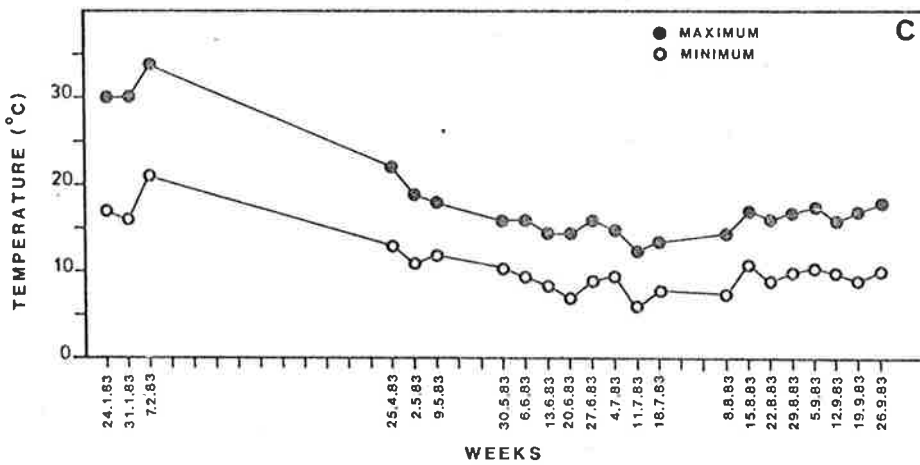
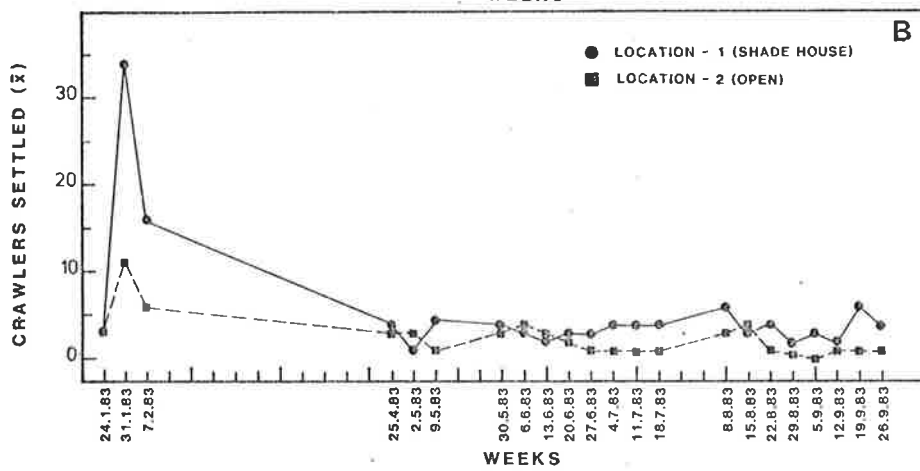
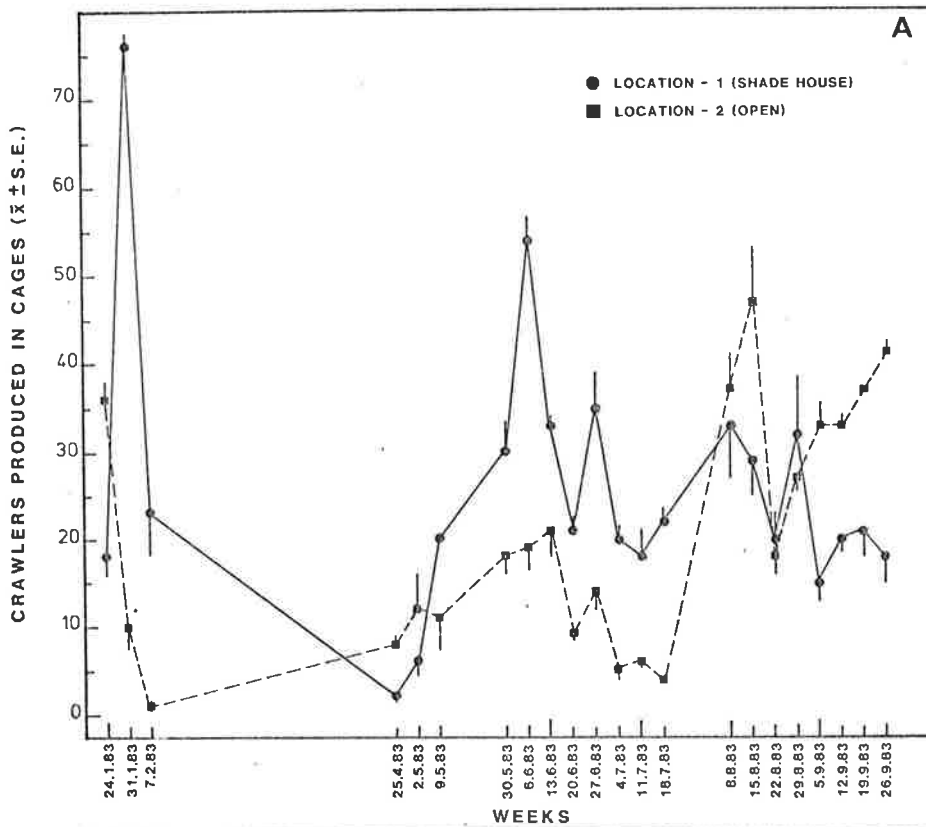


Table 4.3.1

MEAN NUMBERS OF CRAWLERS PRODUCED PER ADULT SCALE (N=3)  
IN CAGES AND MEAN NUMBERS OF CRAWLERS SETTLED PER ADULT  
(N=3) ON PLANTS IN CONSTANT TEMPERATURE ROOMS.

TEMPERATURE (° C)		R1	R2	R3	MEAN $\pm$ S.E.
20	CRAWL. PROD.	88.3	96.0	87.7	90.7 $\pm$ 2.7
	CRAWL. SETT.	56.0	78.7	82.7	72.5 $\pm$ 8.3
25	CRAWL. PROD.	95.3	91.7	136.7	107.9 $\pm$ 14.4
	CRAWL. SETT.	130.7	83.7	102.7	105.7 $\pm$ 13.7

would influence the settling rate of the crawlers because the dispersal of crawlers is known to take place by wind. However, the results also suggest that the wind disturbances at the two locations (shade house and the open) were not sufficiently different to produce significant differences in both the production and settling of crawlers. The consistently low settling rate of the crawlers, with relatively low fluctuations for a major part of the year at both the locations, further suggests that the influence of the settling rate of crawlers on the population dynamics of the scale would also be consistent through the year, and result in the lowering of the equilibrium level of the population. The dynamics of the population, can then be attributable to other factors such as the natural enemies. The results presented above, however, do not indicate how the settling rate of the crawlers influences the long term dynamics of the scale population.



#### 4.4 SEASONAL DYNAMICS OF THE SCALE AND ITS NATURAL ENEMIES : CONCLUSIONS

The data on the population dynamics of the scale and its natural enemies indicate that their numbers are extremely low for most of the year. The natural enemies, though present throughout the year in low numbers, became especially active in late spring and early summer, and were responsible for the crash in the scale population at that time. Heavy rainfall and wind disturbances in the winter months influenced the decline of the scale population after the peak in June/July.

The results from the natural enemy exclusion experiments substantiated the hypothesis that the natural enemies play a major role in keeping the scale population under control.

The settling rate of the crawlers was consistently low throughout the year. Low temperatures and wind disturbances were largely responsible for the low settling rate of the crawlers in the field.

Thus, three factors appear to be responsible for the low numbers of scales in Adelaide. The wind disturbances through the year lower the settling rate of the crawlers, thereby lowering the equilibrium level of the scale population. The rain and wind play an important role in reducing the scale population when the natural enemies are not active in the winter months. In spring and summer, when the scale population has the potential to build up rapidly, the natural enemies multiply faster and take over the scale population. Thus, the scale population never gets the opportunity to build up in large numbers throughout the year, and so the scales are so uncommon in South Australia.

**CHAPTER 5**

**NATURAL ENEMIES SEARCHING FOR ISOLATED PREY PATCHES IN NATURE**

## CHAPTER 5

### NATURAL ENEMIES SEARCHING FOR ISOLATED PREY PATCHES IN NATURE

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The idea with which we have to start is, therefore, that animal dispersal is on the whole a rather quiet, humdrum process, and that it is taking place all the time as a result of the normal life of animals.

-- Elton (1927, p. 148).

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#### 5.1 INTRODUCTION

##### 5.1.1 THE GENERAL SEARCHING PROCESS

The mechanisms by which predators search for patchily distributed prey in nature has intrigued biologists for a long time, but with the development of predator-prey models, the searching behaviour of predators is being studied more closely and in greater detail, in an attempt to unravel the intricate mechanisms involved, and thereby acquire a better understanding of the dynamics of such interacting populations. As Doult (1964a) states, "The manner by which hosts are actually found, and the many factors that determine the existence and maintenance of a particular host-parasite relationship are among the most challenging and fascinating research problems in the biology of parasites".

The foraging strategies of animals, and especially insects, are strongly influenced by the complex spatial structure of the environment. The natural distribution of prey will almost certainly be aggregated on a series of spatial scales, the problem of "clumps-within-clumps" (Heads and Lawton, 1983). Hassell and Southwood (1978) believe that a forager perceives the environment at three hierarchical levels : the habitat, the patch and finally the food. Very few biologists would have problems in defining what constitutes food. It obviously comprises prey for predators, hosts for parasitoids, foliage for herbivores, and so on. These food items are often aggregated in clumps or patches. However, the definition of what constitutes a patch is a major problem (Waage, 1979), and Hassell and Southwood (1978) warn that "we must beware of identifying a patch solely by what we perceive or consider reasonable. The forager itself defines the patch, and we should look to changes in the forager's behaviour to identify patch boundaries". Hassell and Southwood (1978) define a patch as an "area containing a stimulus or stimuli that at the proper intensity elicit a

characteristic foraging activity in a responsive forager". But the distribution of patches themselves is not homogeneous, thereby creating the need for a term for a cluster of patches. Again, patches can be clustered at different levels viz., leaves with prey on a plant, plants within a field, fields spread far apart and so on. For reasons of simplicity, Hassell and Southwood call a cluster of patches, a habitat. Such a classification of the environment in which the organism thrives is essential for the proper understanding of the foraging process. Thus, if prey are distributed in small clumps on the leaves of a trees within orchards within different localities, then a searching predator has to begin by first finding orchards within a locality, then trees within an orchard, and then leaves within a tree before it can find the prey on the leaves (a patch).

Insects use their great mobility to forage within a patch and also to move between patches or habitats that may be widely spaced. The behavioural responses of insects to different levels of food aggregates, viz., habitat, patch, and food, are very different; ranging from migratory behaviour, inter-patch dispersal, to various types of patch-specific behaviour.

In locating patches, foragers are influenced by various stimuli. The forager may either be attracted to the patch-specific stimulus, or to the stimuli emitted by the patch as a result of prey activity, or to the prey themselves. Thus, the parasitoids Alysia munducator and Nasonia vitripennis are known to be attracted to the odour of carrion, whether or not their hosts are present in the meat (Hassell and Southwood, 1978); and there are several examples of parasitoid females being attracted to the food plants of their phytophagous hosts rather than to the hosts themselves, e.g. the parasitoid, Diaeretiella rapae is attracted to the volatile mustard oils of the cruciferous plants upon which the aphid hosts feed (Read et al., 1970). On the other hand, the parasitoid Heydenia unica is attracted to the volatile terpene released as a result of feeding by the bark beetle (Camours and Payne, 1972); and the parasitoid Itoplectis conquisitor is attracted more to the red shoots of Pinus sylvestris than to green ones, the reddening being due to infestations of its host the moth, Rhyacionia buoliana (Arthur, 1966). Some parasitoids are attracted to the host's sex pheromones (Mitchell and Mau, 1971; Sternlicht, 1973), while

others are attracted to the sounds produced by their hosts (Cade, 1975; Soper et al., 1976).

Within a patch, a forager may search for its prey at random (Fleshner, 1950; Banks, 1954 for larval coccinellids) or be drawn to the prey organism itself as a result of stimuli emitted by the prey (e.g. sex pheromones or kairomones) (Wylie, 1958; Hassell, 1968; Waage, 1979). There are numerous examples of predators spending longer periods of time in those patches where the rate of encounter with food items is higher (Aggregative response) (see Chapters 6.1 and 8.1).

After their first encounter with prey the searching behaviour of many predators change so that there is a pronounced increase in turning rate (Klinokinesis) and a reduction in speed of movement (Orthokinesis) (see Chapter 8.2).

#### 5.1.2 FORAGING FOR VERY LOW NUMBERS OF PREY

Most ecologists would agree that animals that are relatively scarce are probably scarce because their natural enemies are very efficient. The corollary, that natural enemies which are able to find prey that are relatively scarce must be efficient searchers, should also be true. We also know that, in nature, spatial heterogeneity is common, as a result of which organisms are distributed in patches which are often far apart. Thus, as the number of an organism in a habitat declines, the number of individuals in a patch would also decline and the average distance between patches would increase. With such a prey distribution, the efficiency with which a predator finds its prey must also increase if it is to keep the prey population relatively scarce. The level at which a prey population exists is thus likely to be determined as a fine balance between the size of prey patch and the average distance between patches, on the one hand, and the efficiency with which the predator is able to first find these patches and then the prey within these patches, on the other.

#### 5.1.3 OBJECTIVES BEHIND MY EXPERIMENT

Data presented in Chapter 4.1 suggest that both Icerya purchasi and Rodolia cardinalis are relatively rare in South Australia. Considering the monophagous nature of Rodolia and almost sedentary nature of its larval stage, Rodolia adults must be fairly efficient in seeking out patches of prey on trees which are often far apart. To test such a hypothesis in the

limitless boundaries of nature is a difficult proposition. However, by the help of the following experiment, attempts were made to gather information on the patch finding abilities of the natural enemies of Icerya, especially Rodolia.

## 5.2 MATERIALS AND METHODS

Potted plants of Acacia baileyana and citrus were placed at two locations. Location 1 was under a large Acacia baileyana tree which harboured a natural scale and natural enemy population (Tree (A) used in sampling scale populations; Chapter 4.1). Location 2 was an isolated area about 500 m away from the nearest known host plant of the scale, and so presumably as far away from any natural population of the scale or its natural enemies. Patches of prey population were generated on four potted plants of each species in each of the two locations. Three patches of prey were generated on each of the plants present by releasing crawlers in clip-on-leaf cages. Thirty crawlers were released per patch in cohort set 1, 20 crawlers per patch in cohort set 2 and 3, and 10 crawlers per patch in cohort set 4. After four days the cages were removed and a record made of the numbers of crawlers settled. Four such releases (cohort sets) were made at fortnightly intervals starting from 20th November, 1981. Two randomly selected patches of prey on each host plant species at each location were caged in cohort sets 2, 3, and 4 with the aim of evaluating the impact of the natural enemies on the survival of the scales.

Data were collected at fortnightly intervals in each of the patches on the number of surviving scales and the presence of any natural enemies. Observations were terminated when all the surviving scales became ovipositing adults. Since the scales are sedentary in habit except for a brief period after each moult when they move a few cm, it was easy to keep track of individual scales throughout the experiment.

## 5.3 RESULTS

### (A) NUMBERS OF SCALES SURVIVING

The numbers of scales surviving and the natural enemies of the scales observed at fortnightly intervals on Acacia baileyana and citrus at Location 1 and Location 2 in cohort sets 1, 2, 3, and 4 have been tabulated

in Table 5.1, and plotted as proportions of the numbers of crawlers settled in Fig. 5.1.

Table 5.1A shows that in cohort set 1, over 60 % of the released crawlers settled down as first instar scales. However, the numbers of surviving scales dropped considerably in the first two fortnights thereafter, and most prey patches were completely destroyed after 10 weeks (F5). Only four scales on Acacia at Location 2 and three scales on citrus at Location 1 survived to the adult stage.

The only natural enemy observed feeding on the scales was Rodolia cardinalis. Eggs and larvae of the beetles were found at Location 2 on both Acacia and citrus after the first and second fortnight, and one adult beetle was found feeding on a scale on citrus at Location 1 after the first fortnight from the date of release of crawlers. The presence of eggs and larvae of Rodolia at Location 2 after the first fortnight suggests that adult beetles capable of laying eggs had discovered the patches of scales within a week of the release of the scales, and when all the scales were still first instars.

The numbers of scales surviving to adults increased in the successive cohort sets 2, 3, and 4, and neither Rodolia nor any other natural enemy of the scales were observed (Tables 5.1B, C, and D). In cohort sets 2, 3 and 4, a number of caged patches of prey were accidentally destroyed due to breaking of the leaves on which the patches were generated. Therefore, no inferences have been drawn from the numbers of scales surviving in the patches that were caged.

In order to test the influence of the cohort sets, host plant species, and location on the survival of the scales, the numbers of scales surviving as a proportion of the crawlers settled were subjected to an analysis of variance (Tables 5.2 and 5.3). The scales in the patches that were caged were left out of the analyses (Table 5.1). Two separate analyses of variance were conducted with data from the THIRD and SIXTH fortnight from the date of release of the crawlers and the data were transformed to arcsines prior to the analyses to homogenize the variances.

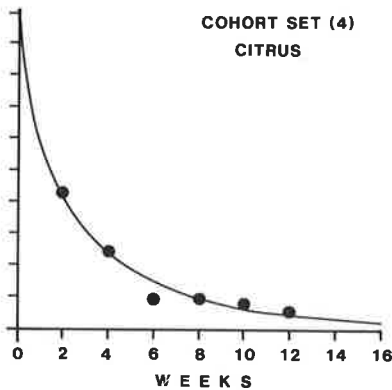
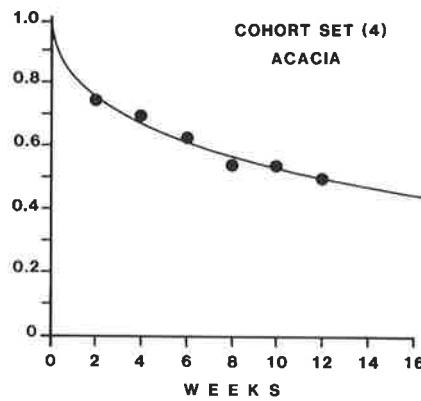
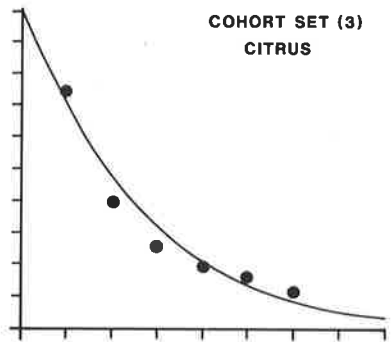
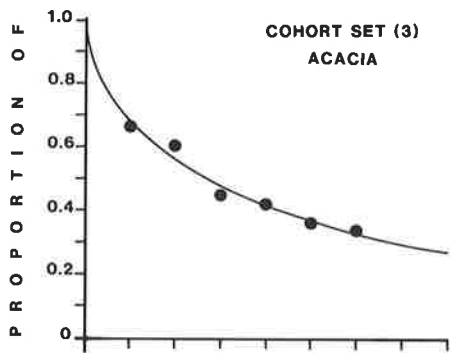
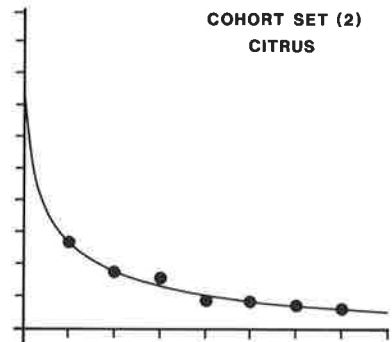
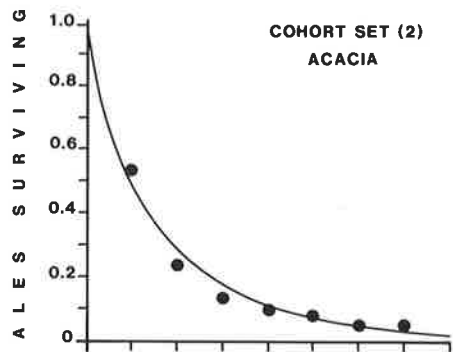
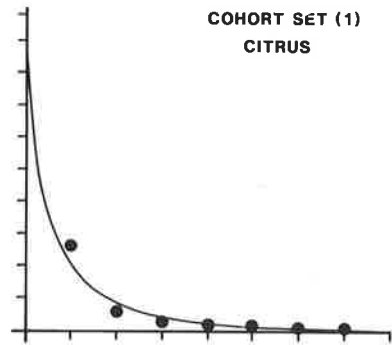
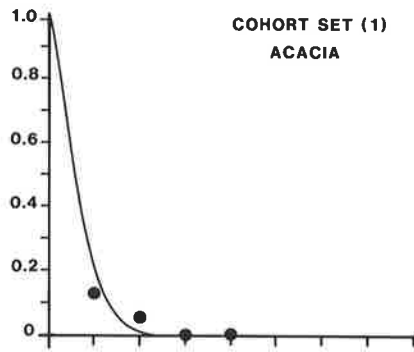
Each analysis of variance was conducted using the total numbers of scales surviving on all 4 plants. The plants were "PSEUDOREPLICATES" within each "plot" (location) (Hurlbert, 1984), and their effect may be determined from a sampling error M.S. (Steel And Torri, 1982) but it is of no interest because we are only concerned with main effects. Furthermore,

Fig. 5.1

The proportion of settled crawlers that survived over 16 weeks on Acacia baileyana and on citrus after each of four releases (cohort sets) at Location 1 (main figure) and Location 2 (overlay). The curved lines represent the fitted Weibull distribution.



● LOCATION-1



● LOCATION-1

LOCATION-2

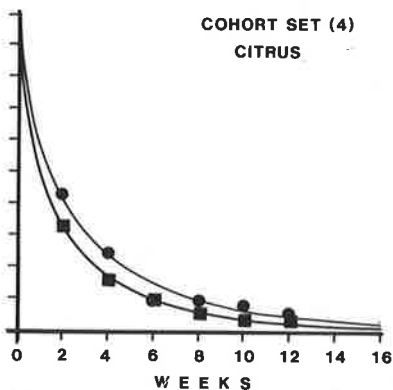
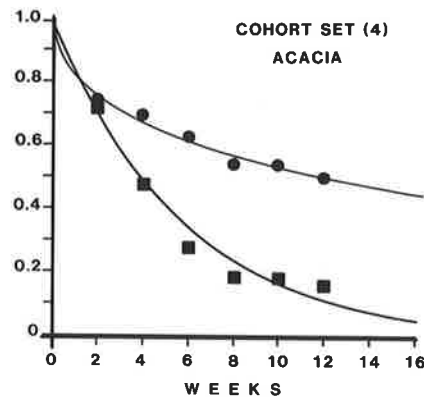
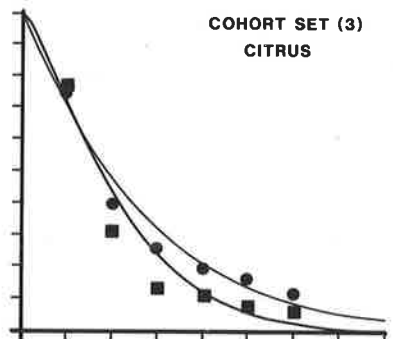
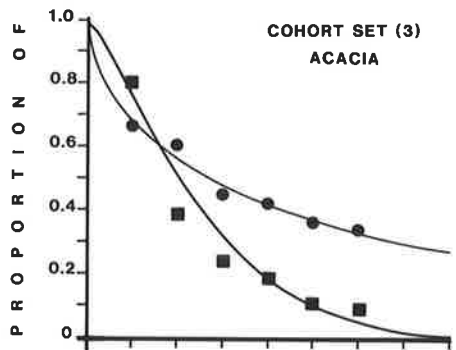
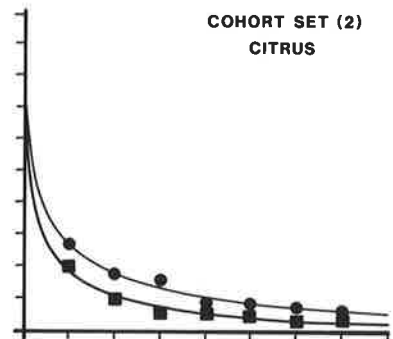
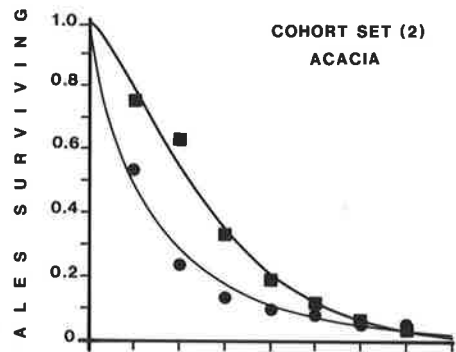
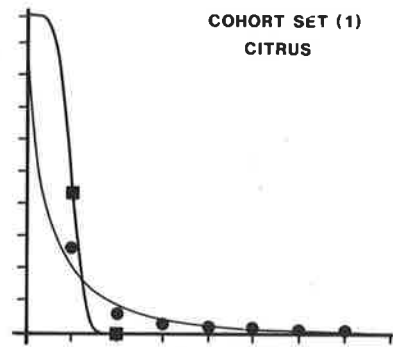
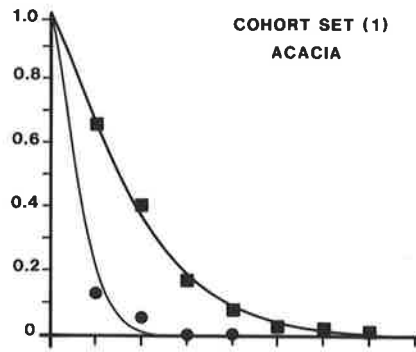


Table 5.1A

NUMBERS OF SURVIVING SCALES AND OF NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH PREY PATCH ON EACH OF 4 PLANTS IN EACH OF 2 LOCATIONS IN THE FIELD.

COHORT SET (1)

DATE OF INTRODUCTION : 20.11.1981

(*Rodolia cardinalis* was the only natural enemy observed; as larvae, at F1 and F2 at Location (2), and as adult at Location (1) only on Citrus)

HOST PLANT : <i>Acacia baileyana</i>																						
PLANT	PATCH	NREL	NSET	LOCATION (1)							NREL	NSET	LOCATION (2)							RODOLIA		
				F1	F2	F3	F4	F5	F6	F7			F1	F2	F3	F4	F5	F6	F7	F1	F2	
(1)	1	30	11	0	0	0	0	0	0	0	30	24	17	1	1	1	1	1	0	0	0	0
	2	30	13	0	0	0	0	0	0	0	30	24	23	15	0	0	0	0	0	0	0	1#
	3	30	16	0	0	0	0	0	0	0	30	25	25	22	7	2	2	1	0	0	0	0
(2)	1	30	20	1	0	0	0	0	0	0	30	23	4	3	3	3	0	0	0	0	1@	0
	2	30	20	0	0	0	0	0	0	0	30	22	19	15	6	2	1	1	1	0	0	0
	3	30	7	2	0	0	0	0	0	0	30	28	11	1	0	0	0	0	0	0	2@	0
(3)	1	30	28	11	2	0	0	0	0	0	30	27	17	14	9	3	0	0	0	0	0	0
	2	30	27	0	0	0	0	0	0	0	30	26	17	15	8	2	1	1	0	0	0	0
	3	30	27	18	12	1	0	0	0	0	30	22	15	12	9	5	1	1	1	0	0	0
(4)	1	30	12	0	0	0	0	0	0	0	30	8	5	2	2	1	1	1	1	0	0	0
	2	30	25	0	0	0	0	0	0	0	30	14	7	5	1	1	1	1	1	0	0	0
	3	30	30	0	0	0	0	0	0	0	30	14	10	0	0	0	0	0	0	0	1@	0
TOTALS		360	236	32	14	1	0	0	0	0	360	257	170	105	45	20	8	7	4	4	1	

HOST PLANT : CITRUS

(1)	1	30	26	0	0	0	0	0	0	0	30	22	13	0	0	0	0	0	0	0	0	0	1@	0	
	2	30	23	1	0	0	0	0	0	0	30	24	0	0	0	0	0	0	0	0	0	0	0	0	
	3	30	29	0	0	0	0	0	0	0	30	22	16	0	0	0	0	0	0	0	0	0	2@	0	
(2)	1	30	25	0	0	0	0	0	0	0	30	23	22	0	0	0	0	0	0	0	0	0	1@	0	
	2	30	20	20	0	0	0	0	0	0	30	15	5	0	0	0	0	0	0	0	0	0	0	0	
	3	30	13	4	0	0	0	0	0	0	30	15	0	0	0	0	0	0	0	0	0	0	0	0	
(3)	1	30	16	2	1	0	0	0	0	0	30	24	6	0	0	0	0	0	0	0	0	0	1@	0	
	2	30	4	4	2	2	2	2	2	2	30	16	7	0	0	0	0	0	0	0	0	0	2@	0	
	3	30	22	22	10	5	2	1	1	1	30	21	20	0	0	0	0	0	0	0	0	0	3\$	0	
(4)	1	30	9	0	0	0	0	0	0	0	30	27	4	0	0	0	0	0	0	0	0	0	0	0	
	2	30	17	0*	0	0	0	0	0	0	30	18	LEAF BROKEN							0	0	0	0	0	0
	3	30	19	7	1	0	0	0	0	0	30	20	16	0	0	0	0	0	0	0	0	0	1@	0	
TOTALS		360	223	60	14	7	4	3	3	3	360	247	109	0	0	0	0	0	0	0	0	0	11	0	

NREL = NUMBERS OF CRAWLERS RELEASED

NSET = NUMBERS OF CRAWLERS SETTLED

\$ = *Rodolia* eggs

@ = 1st instar larva

# = 2nd instar larva

\* = one *Rodolia* adult

F1 TO F7 ARE DATES OF OBSERVATIONS (FORTNIGHTLY APART)

F1 = 4.12.1981 F5 = 29.1.1982

F2 = 18.12.1981 F6 = 2.2.1982

F3 = 1.1.1982 F7 = 26.2.1982

F4 = 15.1.1982

Table 5.1B

NUMBERS OF SURVIVING SCALES AND OF NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH PREY PATCH ON EACH OF 4 PLANTS IN EACH OF 2 LOCATIONS IN THE FIELD.

COHORT SET (2)

DATE OF INTRODUCTION : 4.12.1981

(NO NATURAL ENEMIES OBSERVED. PATCHES OTHER THAN "CAG" -- UNCAGED)

HOST PLANT : <i>Acacia baileyana</i>																				
PLANT	PATCH	NREL	NSET	LOCATION (1)							NREL	NSET	LOCATION (2)							
				F1	F2	F3	F4	F5	F6	F7			F1	F2	F3	F4	F5	F6	F7	
(1)	1	20	20	17	13	8	7	6	6	6	CAG	20	14	14	13	11	11	4	2	2
	2	20	20	2	0	0	0	0	0	0	20	11	0	0	0	0	0	0	0	0
	3	20	14	4	4	3	3	2	0	0	20	12	9	4	2	1	1	1	1	0
(2)	1	CAG	20	7	7	6	5	5	3	3	20	15	15	13	7	6	5	3	1	
	2	20	11	8	0	0	0	0	0	0	20	13	11	9	4	3	2	2	2	2
	3	20	15	4	0	0	0	0	0	0	20	10	8	8	2	2	1	0	0	
(3)	1	CAG	20	18	17	16	14	11	9	9	20	16	16	14	11	5	3	1	1	
	2	20	16	16	16	11	6	6	3	3	20	18	18	14	10	4	1	0	0	
	3	20	20	17	0	0	0	0	0	0	20	14	14	14	4	3	2	1	1	
(4)	1	20	20	12	0	0	0	0	0	0	20	11	0	0	0	0	0	0	0	
	2	20	20	3	2	0	0	0	0	0	CAG	20	14	14	11	10	7	5	5	5
	3	20	4	4	4	1	0	0	0	0	20	0	0	0	0	0	0	0	0	
TOTALS (-CAG)		200	160	87	39	23	16	14	9	9	200	120	91	76	40	24	15	8	5	

HOST PLANT : CITRUS																				
PLANT	PATCH	NREL	NSET	LOCATION (1)							NREL	NSET	LOCATION (2)							
				F1	F2	F3	F4	F5	F6	F7			F1	F2	F3	F4	F5	F6	F7	
(1)	1	20	15	0	0	0	0	0	0	0	CAG	20	11	11	11	5	2	1	1	0
	2	20	13	0	0	0	0	0	0	0	20	11	0	0	0	0	0	0	0	0
	3	20	0	0	0	0	0	0	0	0	20	6	0	0	0	0	0	0	0	0
(2)	1	20	10	1	1	0	0	0	0	0	20	12	0	0	0	0	0	0	0	0
	2	20	11	9	0	0	0	0	0	0	CAG	20	5	5	5	5	2	2	1	1
	3	20	1	0	0	0	0	0	0	0	20	13	0	0	0	0	0	0	0	0
(3)	1	20	17	17	17	16	9	9	8	7	20	11	0	0	0	0	0	0	0	0
	2	20	0	0	0	0	0	0	0	0	20	15	14	11	5	5	5	3	3	
	3	CAG	20	12	12	12	4	4	2	0	20	20	0	0	0	0	0	0	0	0
(4)	1	20	15	0	0	0	0	0	0	0	20	17	13	3	3	3	2	2	2	
	2	CAG	20	19	15	10	LEAF BROKEN				20	19	0	0	0	0	0	0	0	0
	3	20	17	0	0	0	0	0	0	0	20	5	0	0	0	0	0	0	0	
TOTALS (-CAG)		200	99	27	18	16	9	9	8	7	200	129	27	14	8	8	7	5	5	

NREL = NUMBERS OF CRAWLERS RELEASED  
 NSET = NUMBERS OF CRAWLERS SETTLED  
 CAG = CAGED

F1 TO F7 ARE DATES OF OBSERVATIONS (FORTNIGHTLY APART)  
 F1 = 18.12.1981      F5 = 12.2.1982  
 F2 = 1.1.1982        F6 = 26.2.1982  
 F3 = 15.1.1982      F7 = 12.3.1982  
 F4 = 29.1.1982

Table 5.1C

NUMBERS OF SURVIVING SCALES AND OF NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH PREY PATCH ON EACH OF 4 PLANTS IN EACH OF 2 LOCATIONS IN THE FIELD.  
 COHORT SET (3) DATE OF INTRODUCTION : 18.12.1981  
 (NO NATURAL ENEMIES WERE OBSERVED. PATCHES OTHER THAN "CAG" -- UNCAGED).

HOST PLANT : <u>Acacia baileyana</u>																	
PLANT	PATCH	NREL	NSET	LOCATION (1)						NREL	NSET	LOCATION (2)					
				F1	F2	F3	F4	F5	F6			F1	F2	F3	F4	F5	F6
(1)	1	20	6	5	5	4	2	2	2	20	16	15	6	5	4	2	1
	2	20	16	15	14	12	12	8	8	20	16	8	7	5	3	0	0
	3	20	14	13	11	8	8	5	5	20	20	6	3	2	1	1	1
(2)	1	20	6	4	4	4	4	4	4	CAG	20	14	14	LEAF BROKEN			
	2	20	9	1	1	1	1	1	1	20	13	13	7	5	5	3	3
	3	20	16	10	10	9	9	9	9	20	14	14	8	6	6	5	4
(3)	1	20	15	9	9	8	8	8	5	20	11	10	3	1	1	0	0
	2	20	12	1	1	1	1	1	1	20	16	16	9	6	3	1	1
	3	CAG	20	18	16	16	9	7	7	CAG	20	14	14	14	14	14	12
(4)	1	20	9	7	7	0	0	0	0	20	14	13	8	2	2	2	2
	2	20	13	13	9	6	5	5	5	20	15	12	6	4	3	1	1
	3	CAG	20	17	15	15	12	10	10	20	18	18	5	3	3	3	3
TOTALS (-CAG)		200	116	78	71	53	50	43	40	200	153	125	62	39	31	18	16

HOST PLANT : <u>CITRUS</u>																		
(1)	1	CAG	20	11	11	11	1	0	0	0	20	14	13	4	0	0	0	
	2	20	15	10	3	0	0	0	0	20	11	7	4	0	0	0	0	
	3	20	8	8	0	0	0	0	0	20	14	14	8	3	3	3	3	
(2)	1	20	9	7	4	3	3	2	2	20	8	8	4	0	0	0	0	
	2	20	12	0	0	0	0	0	0	20	14	10	2	1	1	0	0	
	3	20	2	2	2	1	0	0	0	20	18	15	0	0	0	0	0	
(3)	1	20	8	8	4	3	3	3	3	20	10	10	7	6	5	4	4	
	2	20	10	10	9	8	6	6	4	20	7	7	4	3	3	0	0	
	3	20	6	2	1	0	0	0	0	CAG	20	14	11	10	8	LEAF BROKEN		
(4)	1	CAG	20	14	13	3	LEAF BROKEN			CAG	20	14	14	8	5	2	1	0
	2	20	15	15	7	5	5	4	2	20	17	5	3	1	1	1	0	
	3	20	9	9	8	6	2	1	1	20	6	4	3	3	1	1	1	
TOTALS (-CAG)		200	94	71	38	25	19	16	12	200	119	93	39	17	14	10	8	

NREL = NUMBERS OF CRAWLERS RELEASED  
 NSET = NUMBERS OF CRAWLERS SETTLED  
 CAG = CAGED

F1 TO F6 ARE DATES OF OBSERVATIONS (FORTNIGHTLY APART)  
 F1 = 1.1.1982      F4 = 12.2.1982  
 F2 = 15.1.1982    F5 = 26.2.1982  
 F3 = 29.1.1982    F6 = 12.3.1982

Table 5.1D

NUMBERS OF SURVIVING SCALES AND OF NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH PREY PATCH ON EACH OF 4 PLANTS IN EACH OF 2 LOCATIONS IN THE FIELD.  
 COHORT SET (4) DATE OF INTRODUCTION : 1.1.1982  
 (NO NATURAL ENEMIES WERE OBSERVED. PATCHES OTHER THAN "CAG" -- UNCAGED).

HOST PLANT : <i>Acacia baileyana</i>																	
PLANT	PATCH	NREL	NSET	LOCATION (1)						NREL	NSET	LOCATION (2)					
				F1	F2	F3	F4	F5	F6			F1	F2	F3	F4	F5	F6
(1)	1	10	3	3	3	3	0	0	0	10	2	2	1	1	1	1	1
	2	10	7	6	5	3	2	2	2	10	6	5	5	1	0	0	0
	3	10	3	3	3	2	2	2	2	CAG 10	3	3	3	3	3	3	3
(2)	1	10	4	2	2	2	2	2	2	10	6	3	1	1	1	1	1
	2	10	3	3	3	3	3	3	2	10	1	1	1	1	1	1	0
	3	CAG 10	8	6	5	5	5	5	5	10	1	0	0	0	0	0	0
(3)	1	10	8	7	7	7	7	7	6	10	5	5	3	2	0	0	0
	2	10	3	3	3	3	3	3	3	10	4	3	3	2	2	2	2
	3	10	1	1	1	1	1	1	1	CAG 10	7	5	LEAF BROKEN				
(4)	1	CAG 10	5	5	4	3	3	3	3	10	5	5	5	3	2	2	2
	2	10	8	3	2	2	2	2	2	10	5	4	0	0	0	0	0
	3	10	4	2	2	2	2	2	2	10	6	2	1	1	1	1	1
TOTALS (-CAG)		100	44	33	31	28	24	24	22	100	41	30	20	12	8	8	7

HOST PLANT : CITRUS																	
PLANT	PATCH	NREL	NSET	LOCATION (1)						NREL	NSET	LOCATION (2)					
				F1	F2	F3	F4	F5	F6			F1	F2	F3	F4	F5	F6
(1)	1	10	4	2	2	1	1	1	1	10	4	0	0	0	0	0	0
	2	CAG 10	3	2	2	2	2	2	2	10	3	0	0	0	0	0	0
	3	10	4	0	0	0	0	0	0	10	3	0	0	0	0	0	0
(2)	1	10	8	1	1	1	1	1	1	10	5	5	4	2	1	0	0
	2	10	7	6	2	2	2	1	1	10	9	3	2	1	1	1	1
	3	10	1	1	1	0	0	0	0	10	4	0	0	0	0	0	0
(3)	1	CAG 10	7	7	7	6	5	4	4	10	0	0	0	0	0	0	0
	2	10	3	0	0	0	0	0	0	CAG 10	5	2	2	2	2	2	2
	3	10	7	1	0	0	0	0	0	10	10	3	2	2	1	1	1
(4)	1	10	4	4	0	0	0	0	0	CAG 10	7	6	6	5	3	1	1
	2	10	5	2	2	0	0	0	0	10	4	4	0	0	0	0	0
	3	10	4	4	4	1	1	1	0	10	5	1	0	0	0	0	0
TOTALS (-CAG)		100	48	21	12	5	5	4	3	100	47	16	8	5	3	2	2

NREL = NUMBERS OF CRAWLERS RELEASED  
 NSET = NUMBERS OF CRAWLERS SETTLED  
 CAG = CAGED

F1 TO F6 ARE DATES OF OBSERVATIONS (FORTNIGHTLY APART)  
 F1 = 15.1.1982      F4 = 26.2.1982  
 F2 = 29.1.1982      F5 = 12.3.1982  
 F3 = 12.2.1982      F7 = 26.3.1982

Table 5.2A

ANOVA ON THE ARCSINE TRANSFORMATION OF PERCENTAGE OF THE SETTLED SCALES SURVIVING ON THE THIRD FORTNIGHT AFTER THEIR RELEASE IN THE PREY PATCH FINDING EXPERIMENT (4 COHORT SETS x 2 PLANT SPECIES x 2 LOCATIONS x 4 PLANTS (PSEUDOREPLICATES))

SOURCE	D.F.	S.S.	M.S.S.	F	P
COHORTS	3	5167.02	1722.34	3.25	>0.05
PLANT SPECIES	1	2907.23	2907.23	5.49	<0.05
LOCATION	1	16.39	16.39	0.03	>0.05
EXPERIMENTAL ERROR*	10	5296.64	529.66		
SAMPLING ERROR	48	17843.73	371.74		
TOTAL	63	31231.02	495.73		

\* EXPERIMENTAL ERROR USED IN THE ESTIMATION OF "F" STATISTIC (Cochran's Normality test statistic = 0.24; P>0.05)

Table 5.2B

ARCSINE TRANSFORMED DATA ON THE PERCENTAGE OF THE SETTLED SCALES SURVIVING ON THIRD FORTNIGHT ON ACACIA AND CITRUS PLANTS AT LOCATION 1 AND 2 IN THE FOUR COHORT SETS

COHORT SET	PLANT SPECIES	LOCATION (1)					LOCATION (2)				
		P1	P2	P3	P4	MEAN	P1	P2	P3	P4	MEAN
(1)	ACACIA	0	0	20.4	0	5.1	19.4	20.5	36.1	65.9	35.5
	CITRUS	0	0	24.1	0	6.0	0	0	0	0	0
(2)	ACACIA	26.8	0	33.6	28.5	22.2	68.9	35.8	46.2	0	37.7
	CITRUS	0	0	75.9	0	19.0	0	0	19.3	58.8	19.5
(3)	ACACIA	54.7	42.2	35.3	31.5	40.9	28.7	39.7	30.6	26.0	31.2
	CITRUS	0	24.7	42.6	42.6	27.5	61.3	30.0	46.7	24.7	40.7
(4)	ACACIA	51.7	57.7	73.2	35.3	54.5	30.0	30.0	41.8	30.0	33.0
	CITRUS	20.7	25.7	0	61.3	26.9	0	24.1	26.6	0	12.7

P1, P2, P3, and P4 represent the four plants

Table 5.3A

ANOVA ON THE ARCSINE TRANSFORMATION OF PERCENTAGE OF THE SETTLED SCALES SURVIVING ON THE SIXTH FORTNIGHT AFTER THEIR RELEASE IN THE PREY PATCH FINDING EXPERIMENT (4 COHORT SETS x 2 PLANT SPECIES x 2 LOCATIONS x 4 PLANTS (PSEUDOREPLICATES))

SOURCE	D.F.	S.S.	M.S.S.	F	P
COHORTS	3	3451.94	1150.65	2.14	<0.05
PLANT SPECIES	1	1464.69	1464.69	2.72	>0.05
LOCATION	1	105.96	105.96	0.20	>0.05
EXPERIMENTAL ERROR*	10	5390.06	539.01		
SAMPLING ERROR	48	18096.11	377.00		
TOTAL	63	28508.77	452.52		

\* EXPERIMENTAL ERROR USED IN THE ESTIMATION OF "F" STATISTIC (Cochran's Normality test statistic = 0.16; P = 0.76 (approx.))

Table 5.3B

ARCSINE TRANSFORMED DATA ON THE PERCENTAGE OF THE SETTLED SCALES SURVIVING ON SIXTH FORTNIGHT ON ACACIA AND CITRUS PLANTS AT LOCATION 1 AND 2 IN THE FOUR COHORT SETS

COHORT SET	PLANT SPECIES	LOCATION (1)					MEAN	LOCATION (2)					MEAN
		P1	P2	P3	P4	P1		P2	P3	P4			
(1)	ACACIA	0	0	0	0	0	31.6	21.7	31.1	48.2	33.2		
	CITRUS	0	0	56.7	0	14.2	0	0	0	0	0		
(2)	ACACIA	19.5	0	65.9	0	21.3	41.3	21.3	40.2	0	25.7		
	CITRUS	0	0	43.3	0	10.9	0	0	53.9	44.3	24.5		
(3)	ACACIA	40.2	42.2	28.1	28.5	34.8	38.4	30.6	37.5	20.9	31.8		
	CITRUS	0	68.9	32.7	20.7	30.6	61.3	0	29.0	41.3	32.9		
(4)	ACACIA	33.7	49.1	65.9	35.3	46.0	12.7	12.7	28.1	25.7	19.8		
	CITRUS	12.7	12.7	0	0	6.4	0	48.2	18.4	0	16.7		

P1, P2, P3, and P4 represent the four plants



the interactions between plant species, locations and cohorts were not significant, so their S.S. were pooled with the S.S. for plant species x locations x cohorts and the subsequent pooled error M.S. with 10 d.f. was used to test the main effects.

The analysis for the THIRD fortnight (Table 5.2) showed that the effect of host plant species was significant, and the effects of cohort sets and locations were not significant ( $P > 0.05$ ). However, the analysis of variance on data from the SIXTH fortnight (Table 5.3) showed that only the effect of cohort sets was significant and the effects of host plant species and locations were not significant ( $P > 0.05$ ). Thus, the effect of location was not significant in both the THIRD and SIXTH fortnight.

Therefore, the analyses of variance of the numbers of scales surviving on both the THIRD and SIXTH fortnight showed that the survival of the scales were not affected by the location of their host plants, i.e. close to (Location 1) or away (Location 2) from the source of natural enemies, which suggests that the sum of the mortality factors affecting the scales at both the locations were not different, which further suggests that the natural enemies of the scales were able to find the scales and attack them equally at both the locations. The numbers of Rodolia cardinalis observed (Table 5.1A) also support this hypothesis.

#### (B) DESCRIPTION OF THE SURVIVAL DATA USING THE WEIBULL MODEL

Attempts were made to describe the numbers of scales surviving at fortnightly intervals by the help of the Weibull model (see Chapter 4.2). The numbers of scales surviving were summed over all the uncaged patches and all the four plants of the same species to get as large numbers as possible for fitting the Weibull model. The numbers of scales surviving as a proportion of those initially settled over fortnightly intervals (as dots and squares), and the fitted Weibull curve have been plotted in Fig. 5.1 by the help of a main figure (Location 1) and an overlay (Location 2). Kolmogorov-Smirnov and Chisquare goodness of fit tests suggested that in most cases the Weibull model fitted the data satisfactorily (Table 5.4). The shape and scale parameters for the fitted Weibull curves, estimated by the Linear Regression Method (see Chapter 4.2), showed that the shape parameters for cohorts on Acacia at the two locations were not very similar, but the shape parameters for cohorts on citrus at the two locations were very similar (Table 5.5), which suggests that the

Table 5.4

CHISQUARE AND KOLMOGOROV--SMIRNOV GOODNESS OF FIT TESTS ON FITTED WEIBULL DISTRIBUTION TO DATA FROM PREY PATCH FINDING EXPERIMENT

COHORT SET	PLANT TYPE	LOCATION (1)					LOCATION (2)						
		N	KOL-SMIR TEST D(i)	TEST	$\chi^2$	D.F.	N	KOL-SMIR TEST D(i)	TEST	$\chi^2$	D.F.		
(1)	ACACIA	236	.077	NS	39.4	1	*	257	.035	NS	5.2	4	NS
	CITRUS	223	.062	NS	10.2	4	*						
(2)	ACACIA	160	.055	NS	5.9	4	NS	120	.088	NS	2.2	4	NS
	CITRUS	99	.021	NS	0.8	4	NS	129	.020	NS	1.2	4	NS
(3)	ACACIA	116	.044	NS	0.7	3	NS	153	.114	*	11.3	3	*
	CITRUS	94	.080	NS	4.3	3	NS	119	.109	NS	15.0	3	*
(4)	ACACIA	44	.030	NS	0.1	3	NS	41	.058	NS	1.8	3	NS
	CITRUS	48	.052	NS	1.1	3	NS	47	.013	NS	0.2	3	NS

NS = NOT SIGNIFICANT AT P<0.05 (GOOD FIT)  
 \* = SIGNIFICANT AT P<0.05 (NOT GOOD FIT)

Table 5.5

ESTIMATES OF THE SHAPE (c) AND SCALE (b) PARAMETERS FOR FITTED WEIBULL DISTRIBUTION TO DATA FROM PREY PATCH FINDING EXPERIMENT.

COHORT SET	DATE INTRODUCED	PLANT TYPE	LOCATION (1)		LOCATION (2)	
			SHPM	SCPM	SHPM	SCPM
(1)	20.11.1981	ACACIA	1.42	1.47	1.24	4.05
		CITRUS	0.60	0.94	**	
(2)	4.12.1981	ACACIA	0.79	3.06	1.33	5.83
		CITRUS	0.38	1.00	0.37	0.50
(3)	18.12.1981	ACACIA	0.59	10.55	1.31	5.51
		CITRUS	1.08	5.40	1.31	4.62
(4)	1.1.1982	ACACIA	0.52	25.32	1.00	5.73
		CITRUS	0.68	2.42	0.62	1.68

SHPM = shape parameter      SCPM = scale parameter  
 \*\* = No fit possible; only one data point.

survival-rates of the scales on citrus were not different at the two locations. The estimates of the parameters could not be subjected to statistical tests of significance because of the presence of single values only. Thus, the Weibull model serves nothing more than a description of the temporal distribution of the mortality in the scale cohorts.

### (C) PATCHES DESTROYED

The numbers of prey patches destroyed in time in all the four cohort sets followed a similar pattern when they were plotted as percentages of the total patches set up at the start (Fig. 5.2). In general, the percentages of the total patches destroyed gradually declined from cohort set 1 to cohort set 3, after which the percentages showed an increase in the cohort set 4. Such trends suggest that the effects of a group of mortality factors affecting the survival rate of the scales diminished with time through cohort set 1 to 3 and then it increased again. A plot of the period of the activity of the natural enemies of the scale in relation to the duration of the experiment (Fig. 5.3) showed that the overlapping of the period of activity of the natural enemies with the experiment also gradually declined through cohort set 1 to 4, and this trend was similar to the decline in the number of prey patches destroyed through cohort sets 1 to 3. The analyses of variance presented in Tables 5.2 and 5.3 also showed that the numbers of scales surviving in the different cohort sets were significantly different, and there was better survival of the scales in the subsequent cohort sets. Observations on the activity of the natural enemies on the prey patches at the two locations also showed that, within a fortnight of the start of the experiment (Table 5.1A), Rodolia adults capable of laying eggs were able to find the prey patches within a week even at the isolated Location 2; and the adults laid eggs, even when all the prey were first instars.

These results indicate that natural enemies did play an active role in reducing the scale population during the experimental period, and the increased survival of the scales in the subsequent cohort sets was, perhaps, due to the declining influence of the natural enemies as a result of a decline in their numbers in the field (Fig. 5.3).

Fig. 5.2

The percentage of patches of scales destroyed on Acacia baileyana and on citrus after each of four separate releases (cohort sets) at Location 1 and Location 2.

- (a) cohort set 1 : ●
- (b) cohort set 2 : ○
- (c) cohort set 3 : ■
- (d) cohort set 4 : □

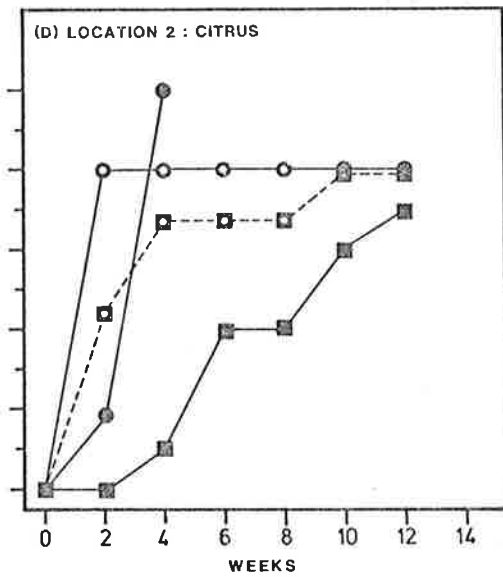
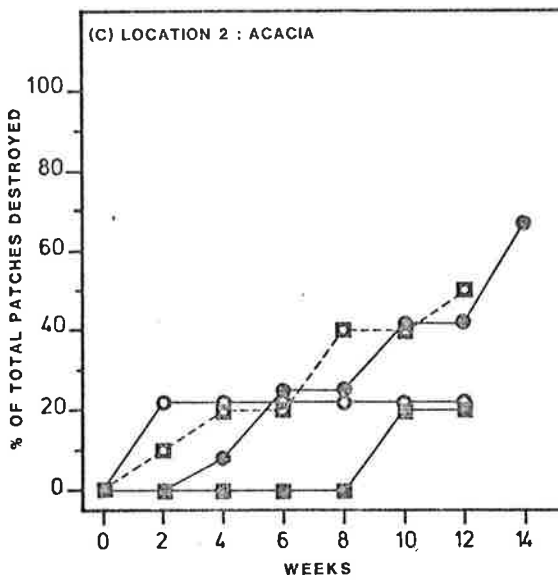
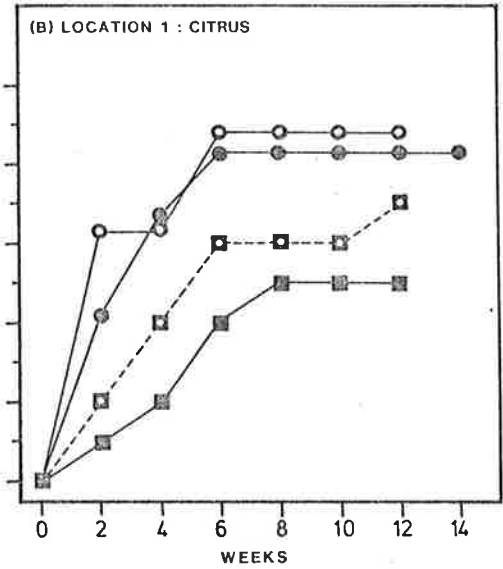
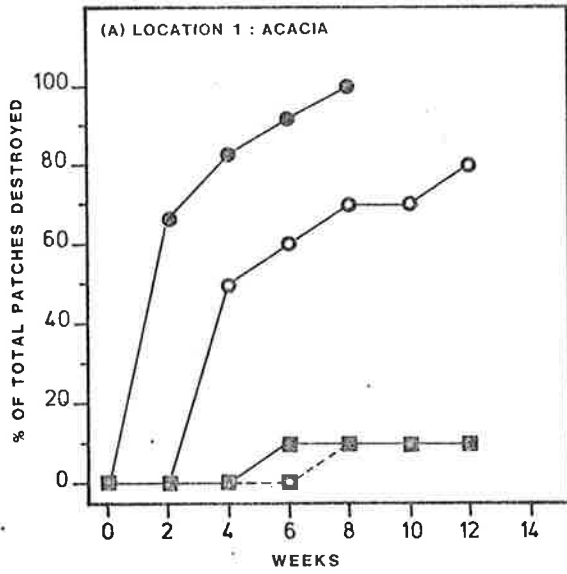
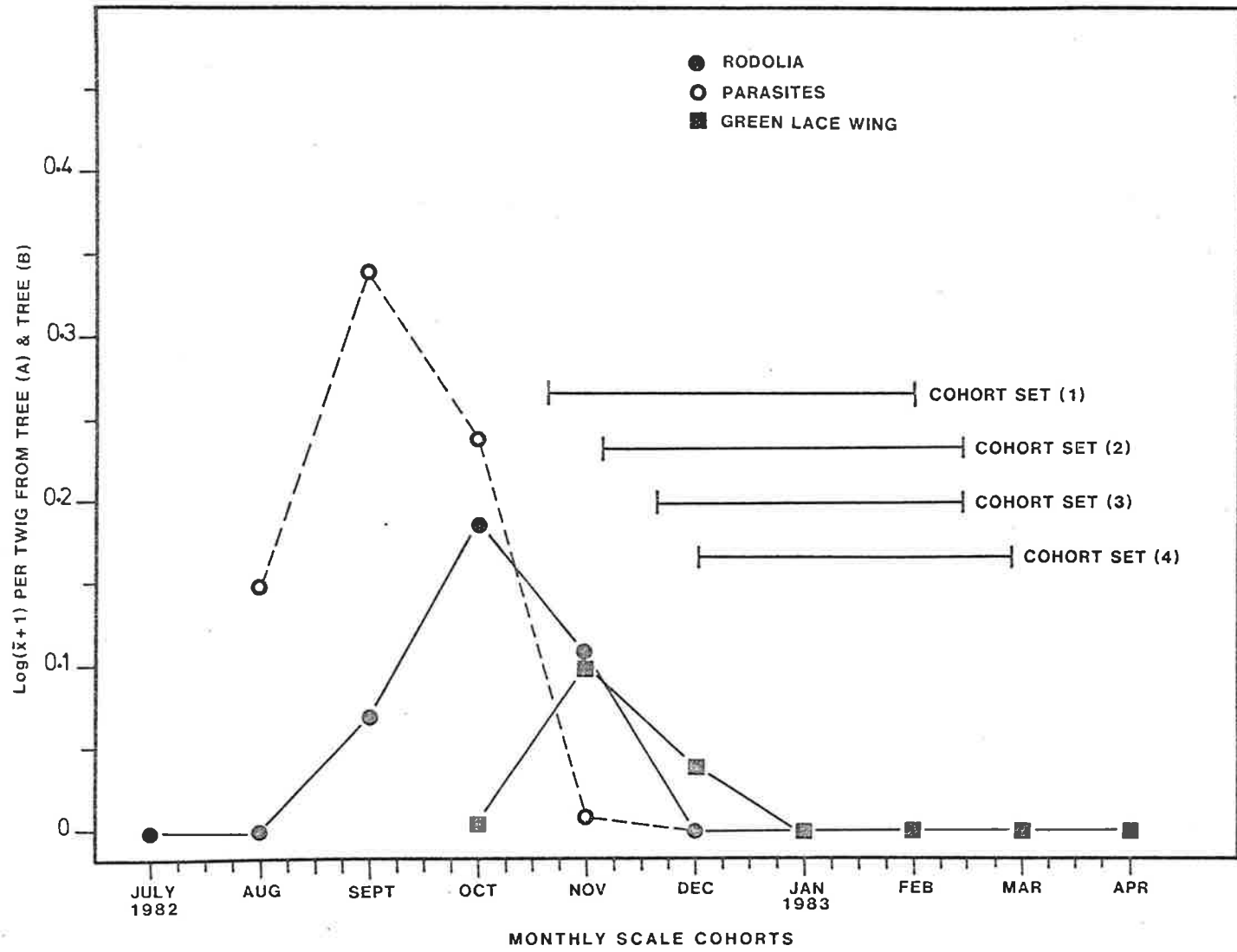


Fig. 5.3

The total numbers of natural enemies estimated from population samples taken at monthly intervals on Tree (A) and Tree (B) (Chapter 4.1), plotted in relation to the time taken by the scales released in cohort sets 1, 2, 3, and 4 to develop to adults.



#### 5.4 DISCUSSION

The data on the survival of the scales and the activities of Rodolia cardinalis on the patches at the two locations support the findings of earlier workers (Quezada and DeBach, 1973), that the beetle has the potential to find and destroy isolated patches of scales before the numbers of the latter get out of control. However, from the results gathered thus far, it is difficult to postulate exactly how the beetle goes about finding the patches of prey in the field, and whether it perceives the environment at the hierarchical levels (habitat, patch, and the food) suggested by Hassell and Southwood (1978). Most Coccinellids are believed to search for their prey at random (Fleshner, 1950; Banks, 1954) so much so that they have to bump onto their prey to notice them. If this is also true for Rodolia, then it would have to be extremely active and efficient to be able to find isolated patches of prey, especially when the prey numbers remain so very low (see Chapter 4.1), and often spread far apart on bushes and trees.

In the subsequent chapters, by the help of data gathered from laboratory experiments, attempts have been made to describe the mode of searching for prey by Rodolia cardinalis.



**CHAPTER 6**  
**RODOLIA SEARCHING FOR PREY PATCHES IN LABORATORY**

## CHAPTER 6

### RODOLIA SEARCHING FOR PREY PATCHES IN LABORATORY

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The experiment serves two purposes, often independent one from the other : it allows the observation of new facts, hitherto either unsuspected, or not yet well defined; and it determines whether a working hypothesis fits the world of observable facts.

-- Rene J. Dubos.

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#### 6.1 DIFFERENTIAL RESPONSE TO PREY DENSITY

##### 6.1.1 INTRODUCTION

If the whole of predation biology was to be summed up in a single line, it would surely be -- "predators respond to prey density". Biologists have studied this phenomenon from every conceivable angle. The functional, the ovipositional, the numerical, the behavioural, the individual, the aggregative, and the developmental responses; the area of discovery, the searching efficiency, even the optimal foraging studies all, in one way or another, deal with the predator's response to prey density. Though some of the aforementioned terms are often used synonymously, viz. functional response with ovipositional response, area of discovery with searching efficiency, others deal with different aspects of the predator's response to prey density. One can well imagine the impact that the predator's response to prey density has on the dynamics of animal populations.

The term "functional response" was introduced by Solomon (1949) as a primary feeding response for changes in the number of prey killed per predator in relation to prey density. In contrast, the numerical response is reproductive in nature and refers to the changes in the predator population in response to prey density (Hassell, 1978a). Thus, the functional response is immediate because given more food the predator immediately eats more, but the numerical response has a delayed effect which may lead to cyclic fluctuations in the population of both the predator and prey (Hassell, 1978b). The behavioural response is the result of behavioural changes on the part of each parasite or predator in response to spatial differences in host or prey density (Hassell, 1966). The behavioural response can either be (a) an individual response when the

behavioural response of a single parasitoid is under consideration, or (b) an aggregative response which results from a non-random distribution of parasitoids corresponding with spatial differences in host density (Hassell, 1966). As a result of the behavioural response, predators aggregate at dense prey patches, and spend more time there. Studies on the searching behaviour of predators have led to much speculation of the influence of this response on the dynamics of interacting predator/prey populations. The developmental response can be caused by the predator eating more prey at higher prey densities, growing more as a consequence, and then killing more prey because of its larger size (Murdoch, 1971; Murdoch, 1973). This has been the least studied response (Murdoch and Oaten, 1975).

The area of discovery/searching efficiency is a parameter estimated from a study of the predator's response to prey density. Optimal Foraging Theories deal with all those factors that influence the predator's decision to emigrate from a prey patch; apparently, prey density plays a vital role in this decision, too. These two aspects of the predator's response to prey density viz. searching efficiency and optimal foraging behaviour have been considered at considerable length in Chapters 7 and 8 respectively.

There are two contrasting ways of investigating how a predator (parasite) responds to different prey (host) densities. Firstly, one or more parasites can be exposed to each of a number of different host densities for the same period of time (Functional response) (Holling, 1959). This method does not allow the parasites a choice of spending more time at certain host densities in preference to others, but the method is used to assess the importance of factors such as "handling time" and egg limitation. Alternatively, parasites can be presented with a range of different host densities at the same time, thus providing them with a choice and permitting them to spend different periods of time searching at different host densities (Behavioural response) (Hassell, 1966; Hassell, 1971). This second experimental procedure is closer to realism because spatial heterogeneity is common in nature and most parasites probably respond to concentrations of hosts by spending a longer time searching in areas of high host density than in areas of low host density.

(A) FUNCTIONAL RESPONSE

Predation biologists now recognize three different forms of functional responses and all three responses level off at high prey densities because the predator becomes satiated and/or runs out of time in which to eat more prey (Holling, 1959; Hassell, 1978a). In the Type-I response, the curve rises linearly to a plateau and produces density-independent mortality up to satiation; the Type-II curve rises at a continually decreasing rate to an upper asymptote producing inversely (or negatively) density-dependent mortality over the entire range. The Type-III response has a curve with a sigmoid form and is the only response which produces density-dependent mortality (Hassell, 1978b; Begon and Mortimer, 1981).

Most arthropod predators show a Type-II response and almost all predators show Type-II response when given only one prey species (Murdoch and Oaten, 1975). However, Hassell et al. (1977) produce evidence which suggests that sigmoid functional responses may be more common in arthropod predators than was once thought; and van Lenteren and Bakker (1976) have shown that a sigmoid response may appear as a Type-II response in the absence of behavioural observations, especially at lower prey densities.

The Type-II arthropod functional responses were reviewed for a variety of predators and parasitoids (Hassell et al., 1976), and all the three responses have been modelled considering their effect on the outcome of the interaction of predator and prey populations (Hassell, 1978b). Several factors, are known to influence the functional response of invertebrate predators, 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, 1975; Gresens et al., 1982).

Models of predator-prey interactions have shown that the most common type of functional response (Type-II) has a destabilizing effect on populations of interacting species while the sigmoid response has a stabilizing effect. Theoretical biologists have tried to recognize those complications in the real world that affect the predator's behaviour and thus might alter the response so that it becomes stabilizing. Murdoch and Oaten (1975) have shown that "patchiness" in the distribution of prey, "switching" between a number of prey species and the presence of "refuges" for prey can impart stabilizing properties to two interacting populations

by altering a Type-II response into a sigmoid form.

Experimental techniques used for the study of the functional response have varied, but usually each predator is presented with a fixed number of prey; the prey are replaced as they are eaten or the number presented is large enough so that predation removes only a small fraction (say 10 %) of the prey.

(B) BEHAVIOURAL RESPONSE (AGGREGATIVE RESPONSE)

In functional response studies, it is assumed that the predator is searching within a patch of prey or that the prey's distribution in space does not influence the predation rate. However, in nature, a prey population is often distributed in discrete patches and spatial heterogeneity is common. Furthermore, it has been known for a long time that at least some predators behave in such a way that they concentrate their attack upon denser patches of prey. Laing (1937) studying Trichogramma evanescens Westw. and Wylie (1958) working on Nasonia vitripennis (Walk.) noticed changes in parasitoid behaviour following the discovery of their hosts. These changes resulted in more time being spent in higher host density areas. In such cases, one would expect a higher percentage of hosts to be parasitized where host density is greatest and vice versa (i.e. a density dependent behavioural response) (Hassell, 1966). Such a differential response towards patches of different prey densities is a behavioural response more commonly referred to as the "aggregative" response in the literature. Waage (1983) points out that the term "aggregation" in searching behaviour has been rather loosely used for "concentration of total foraging time in most profitable patches, the concentration of searching time there, or positive density dependent parasitism itself". Aggregation of total foraging time may generate patterns of parasitism ranging from positive to negative density-dependence, as the proportionate contribution of handling time is increased (Hassell, 1982b).

Laboratory studies indicate that many parasitoids spend more time searching in patches of high host density (Hassell, 1971; Akinlosotu, 1973 & Noyes, 1974, both in Hassell, 1978b; van Lenteren and Bakker, 1978; Waage, 1979; van Alphen and Galis, 1982). In field studies, the outcome of parasitoid searching is largely based on inferences drawn from patterns of

parasitism (Morrison and Strong; 1980, 1981; Morrison et al., 1981; Hassell, 1980; Heads and Lawton, 1983). Inferences drawn from patterns of parasitism obviously have their limitation because (a) an absence of parasitism in a patch does not necessarily indicate absence of searching parasitoids (Chesson, 1982), and (b) parasitoids allocating searching time in different ways may generate identical patterns of parasitism (Hassell, 1982b). Alternatively, estimates may be made of the numbers of adult parasitoids at different host densities, along with estimates of parasitism (Waseleh, 1973; Stamp, 1982; Bryan and Wratten, 1984). However, these estimates still allow only an indirect estimation of parasitism and so the inferences drawn therefrom may be ambiguous (Waage, 1983). Waage's (1983) study of Diadegma sp., a larval parasite of Plutella xylostella is the first field study indicating aggregation of foraging time from direct observations. This study also confirms Morrison and Strong's (1980) hypothesis that in the field most parasitoids do not generate density-dependent patterns of parasitism.

It can be argued that a predator which spends more time in dense patches than in sparse patches would be at a greater selective advantage. However, if a predator demonstrates a Type-II response, then a prey individual in a dense patch has a lower probability of being eaten per unit of time that the predator spends in that patch. Only if the predator spends enough extra time in the dense patch will the probability of attack for the average prey there exceed that in a sparse patch.

The prime objective of this project was an attempt to identify those factors that contribute to the better effectiveness of Rodolia as a predator. Therefore, rather than testing the beetle's functional response in the conventional manner (section 6.1.1A), it was considered more appropriate to test the beetle's differential response to prey density as one of the attributes possessed by an efficient biological control agent (Hassell, 1978b), by providing it with a range of prey densities simultaneously. The following experiment was carried out with the above idea in mind.

### 6.1.2 MATERIALS AND METHODS

Prey patches were generated on 5.08 cm dia citrus leaf-discs. Twenty four such discs were placed in two prey culture units (Chapter 3), which together with a lid served as the searching arena for the predator (Fig. 6.1.1). The size of the searching arena that resulted was 270x410x120 mm. Four replicates of each of six prey densities 0, 1, 2, 4, 8, and 16 third instar scales per leaf-disc were set up in the arena in random positions. The experiment was started by releasing into the arena, a single female beetle which was two days old and had been mated and satiated. The experiment was replicated three times.

Data were collected every 24 h over 5 days on the number of prey eaten and eggs laid. After each 24 h, the prey that had been eaten were replaced and the eggs laid were removed.

Video equipment was set up on one of the replicates on the fourth day to record the time spent by the beetle at different prey patches. This recording was done over a period of 8 h in two sessions of 4 h each. Similar data were also collected by direct observation on the fourth day on two of the replicates.

The experiment was conducted in a constant temperature room at  $25 \pm 1^{\circ}$  C. Light was provided by a bank of ten 40 W fluorescent tubes and a 14L:10D photoperiod was maintained.

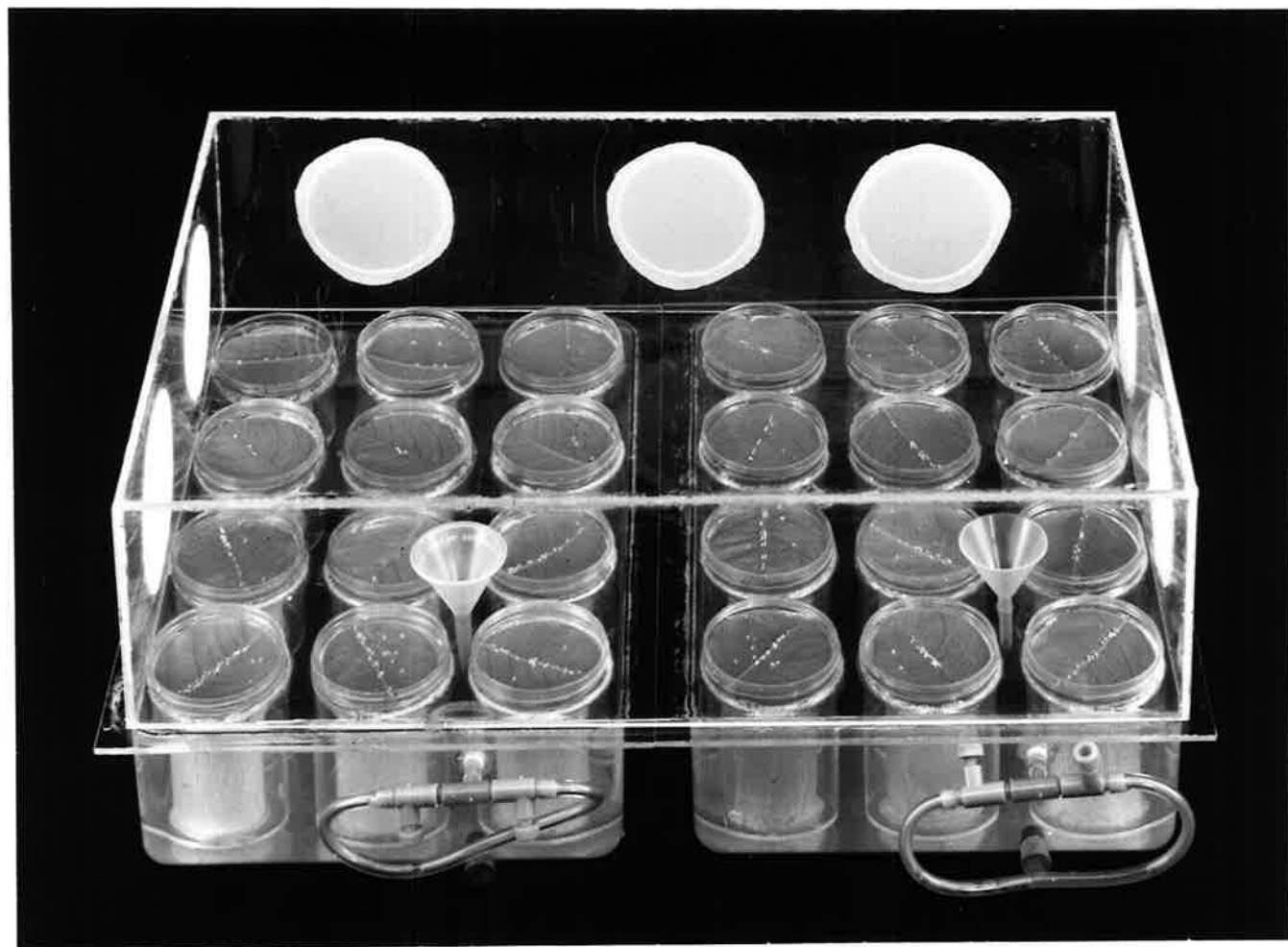
### 6.1.3 RESULTS

At the outset, I must state that some of the graphs presented in the following are very similar in shape to Holling's Type-II functional response curve, and though the nature of the relationship is the same (predator's response to prey density), a basic difference in the design of the experiment remains. Also, the results have been presented under two separate headings (a) predator's response BETWEEN patches (patch selection), and (b) predator's response WITHIN patches, since they are two separate components of the predator's behaviour, as will become evident later. Each data point plotted in the figures is a mean estimated over 5 days x 3 replicates (15) (see Appendix Table 11).

Fig. 6.1.1

Photograph of the experimental set-up for the experiment described in Chapter 6.1.





### 6.1.3.1 PREDATOR'S RESPONSE BETWEEN PATCHES - PATCH SELECTION

If we consider each leaf-disc in the searching arena as representing a patch then, because of the small size of the searching arena (270x410x120 mm), a searching predator may well be expected to have discovered all the 24 patches present in any experimental time period of 24 h. However, the results indicate that the beetle did not eat prey or lay eggs on all the patches present (Appendix Table 11), so that the number of patches present were much higher than the beetle's requirements for eating prey and laying eggs. The following two definitions relating to patches discovered can, therefore, be used to test the beetle's response to patches of different prey densities.

- (i) PATCHES VISITED : patches discovered by the beetle but at which NO prey were eaten and NO eggs were laid.
- (ii) PATCHES ATTENDED : patches discovered by the beetle and at which prey were eaten and/or eggs were laid.

Because of the smallness of the arena, all the 24 patches would have been VISITED by the beetle and so the beetle's response to patches of different prey densities (patch type) in terms of their being VISITED would be the same. However, when the patches ATTENDED (Appendix Table 12) were expressed as a percentage of the total patches ATTENDED per day and plotted against prey density per patch (Fig. 6.1.2A), there was a significant linear regression ( $Y = 1.03X + 12.32$ ;  $t=2.24$ ;  $P<0.05$ ), indicating an increase in the number of patches ATTENDED with an increase in prey density per patch. On the other hand, the slope of the similar regression of the number of patches attended as a percentage of the total present (4) was not significantly different from zero ( $t=1.55$ ;  $P>0.05$ ) (Fig. 6.1.2B). These results demonstrate that the beetle possesses the power of discrimination between patch types and exercises preference by attending a larger proportion of patches of relatively higher prey densities.

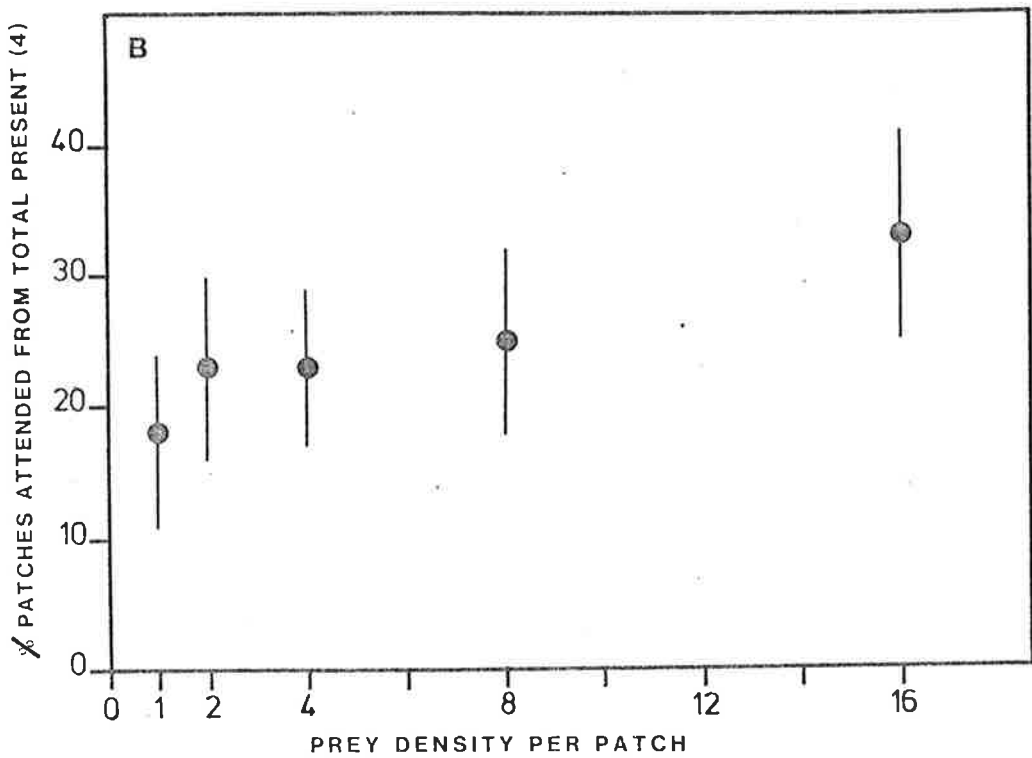
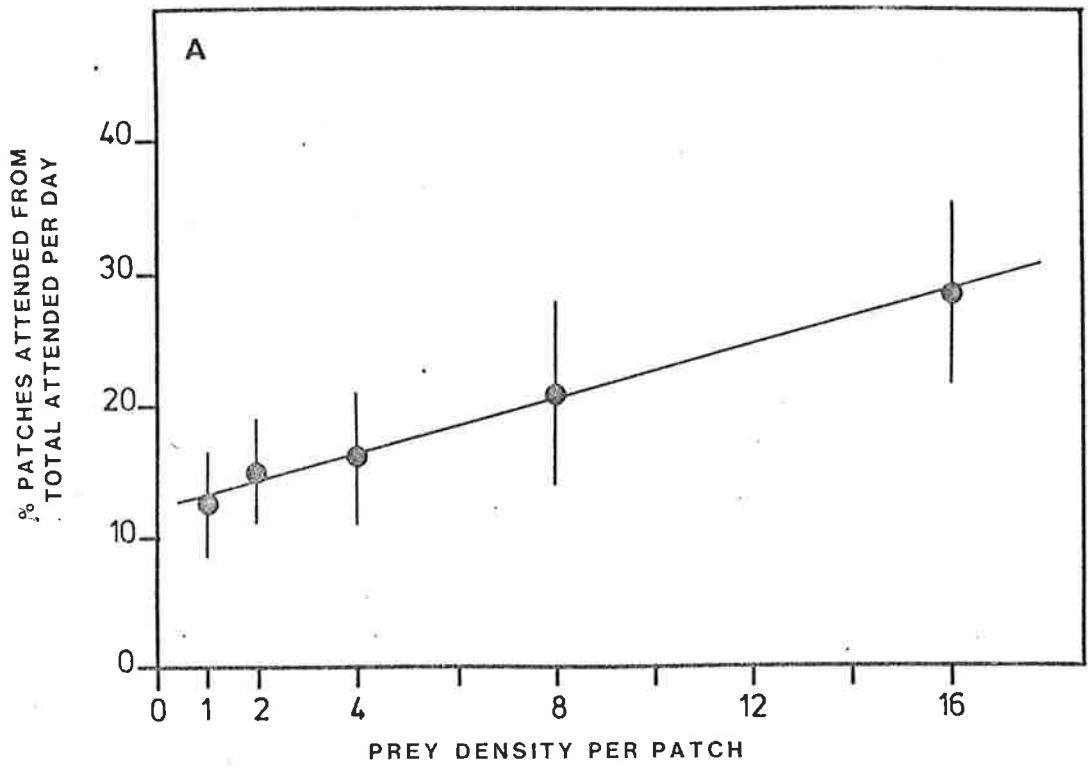
### 6.1.3.2 PREDATOR'S RESPONSE WITHIN PATCHES

#### (i) OVIPOSITIONAL BEHAVIOUR

In Chapter 2, it was pointed out that the beetle behaves more like a parasitoid in its egg laying behaviour, because it lays its eggs only above, under or close to the prey, an adaptation that probably ensures a certain degree of survival of its progeny. The location of the eggs laid away from the prey was also restricted to the leaf-disc only, and no eggs

Fig. 6.1.2

- (A) The number of patches ATTENDED as a percentage of the total patches ATTENDED per day plotted against prey density per patch. Line ( $Y = 1.03X + 12.32$ ;  $t=2.24$ ,  $P<0.05$ ) fitted by linear regression.
- (B) The number of patches ATTENDED as a percentage of the total patches of a particular prey density that was PRESENT (which was 4). The fitted linear regression was  $Y = 0.83X + 19.5$ ;  $t=1.55$ ,  $P>0.05$ .



were laid on leaf-discs with no prey. Thus, it was easy to keep track of all the eggs laid by the beetle.

The plot of the number of eggs laid against prey density per patch shows a curve similar in shape to Holling's Type-II functional response curve (Fig. 6.1.3A). Since the number of eggs laid increased with an increase in prey density per patch, it was of interest to know the frequency distribution of eggs per scale at patches of different prey densities. The total number of scales above or under which eggs were laid (Fig. 6.1.3B) also showed a decelerating rise to an upper asymptote, similar to that of the curve of the total eggs laid (Fig. 6.1.3A). Such trends demonstrate that the higher number of eggs laid at patches of higher prey density are spread over larger number of prey and are not clustered on a few. This trend is further substantiated by the numbers of prey with 1, 2, 3, and >3 eggs presented below.

The newly hatched larvae begin to feed on the prey where they are born, and so the number of eggs laid per prey is of great significance in the survival of the progeny, especially since cannibalism is a common phenomenon in Rodolia, as in other Coccinellids. The numbers of scales with 1, 2, 3, and >3 eggs per scale have been plotted against prey density per patch in Fig. 6.1.3B. All the four graphs seem to show a positive trend with prey density up to patch type 8 after which the trends either level off or decline to patch type 16. To test these apparent trends, an analysis of variance (all factors fixed) was conducted on the number of scales with 1, 2, 3, and >3 eggs at patches of different prey densities, using a natural logarithmic transformation ( $\ln(x+1)$ ) (Table 6.1.1A). It was found that the numbers of scales with different number of eggs per scale were significantly different ( $F=14.94$ ;  $P<0.0005$ ). The effect of patch type was also significant ( $F=8.86$ ;  $P<0.0005$ ) whilst the interaction of scales with eggs and patch type was not significant ( $F=0.87$ ;  $P>0.05$ ).

The table of means (Table 6.1.1B) shows that the number of scales with 1 and 2 eggs were not significantly different from one another, and the number of scales with 3 and >3 eggs were not significantly different from one another. However, the number of scales with 1 and 2 eggs were significantly different from those with 3 and >3 eggs. Table 6.1.1B also shows that there was a significant difference between patches with prey density 1 and 2 but not between patches with prey density 4, 8, and 16. It is also interesting to note that the numbers of scales with 1 and 2 eggs

Fig. 6.1.3

- (A) Means  $\pm$  S.E. of the numbers of eggs laid by beetles at patches of different prey densities. The curve was fitted by eye.
- (B) Means  $\pm$  S.E. of the total numbers of scales with eggs of Rodolia (●); and means of the numbers of scales with 1 (○), 2 (□), 3 (■), and >3 (▲) eggs of Rodolia per scale at patches of different prey densities.
- (C) Mean numbers of eggs laid by Rodolia either ABOVE (▲), UNDER (○) or AWAY (□) from scales at patches of different prey densities.

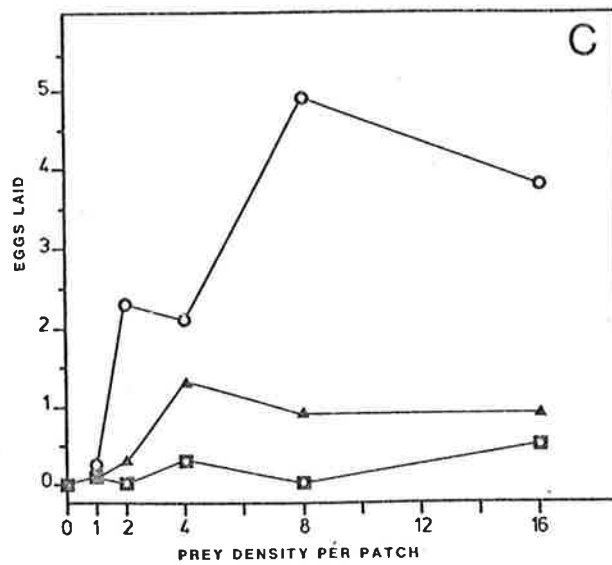
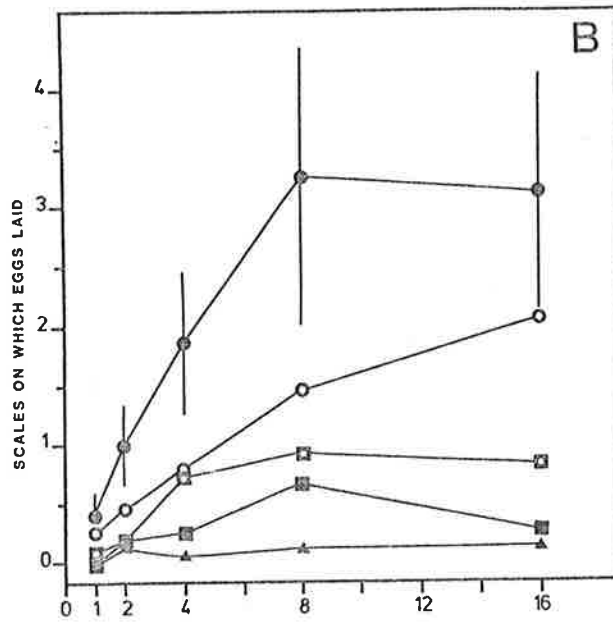
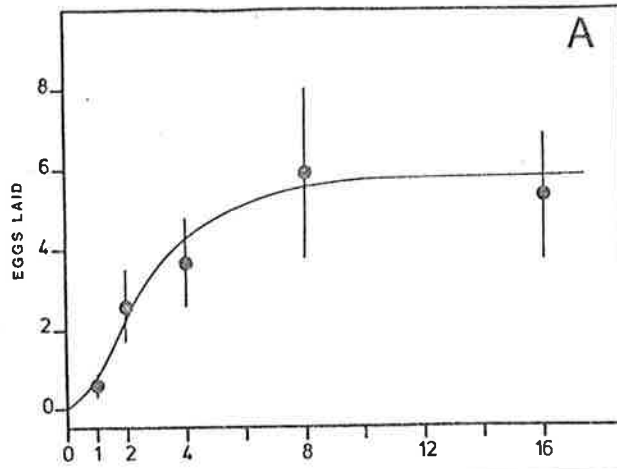


Table 6.1.1A

ANOVA OF THE NUMBERS OF PREY WITH DIFFERENT NUMBERS OF EGGS PER SCALE AT PATCHES OF DIFFERENT PREY DENSITIES. DATA TRANSFORMED TO  $(\ln(x+1))$ .

SOURCE	DF	SS	MSS	F	P
EGGS PER SCALE	3	12.38	4.13	14.94	<0.0005
PATCH TYPE	4	9.80	2.45	8.86	<0.0005
INTERACTION	12	2.88	0.24	0.87	>0.05
ERROR	40	11.05	0.28		
TOTAL	59	36.11			

Table 6.1.1B

TABLE OF MEAN NUMBERS OF SCALES WITH DIFFERENT NUMBERS OF EGGS PER SCALE (SIGNIFICANT DIFFERENCES BETWEEN MEANS BASED ON ANOVA Table (6.1.1A)).

EGGS PER SCALE	PREY DENSITY PER PATCH															MEANS (N=15)*
	(1) R1	(1) R2	(1) R3	(2) R1	(2) R2	(2) R3	(4) R1	(4) R2	(4) R3	(8) R1	(8) R2	(8) R3	(16) R1	(16) R2	(16) R3	
1	0.00	1.61	0.00	1.10	1.61	0.69	1.61	1.95	1.10	1.95	2.64	1.39	1.39	3.00	2.30	1.488a
2	0.00	0.69	0.69	0.69	1.10	0.00	1.79	1.61	1.10	1.39	2.08	1.61	1.10	1.95	1.39	1.146a
3	0.00	0.00	0.00	0.00	1.10	0.69	0.00	1.39	0.69	1.69	1.79	1.61	0.69	0.69	1.10	0.697b
>3	0.00	0.00	0.00	0.00	0.00	1.10	0.00	0.00	0.69	0.00	0.69	0.69	0.00	1.10	0.00	0.285b
MEANS (N=12)#		0.250x			0.674y			0.994yz			1.377z			1.225z		

\* Means followed by the same letters NOT significantly different at  $P < 0.05$  ( $F_{3,40} = 2.84$ ) ; L.S.D. = 0.437.  
 # Means followed by the same letters NOT significantly different at  $P < 0.05$  ( $F_{4,40} = 2.61$ ) ; L.S.D. = 0.391.



are higher than those with 3 and  $>3$  eggs at patches of any prey density.

The number of eggs laid either above, under or away from scales for patches of different prey densities are shown in Fig. 6.1.3C. On patches of any one prey density, most of the eggs were laid under the scales, which was followed by the eggs laid on top of the scales. An analysis of variance (Table 6.1.2A) conducted with the natural logarithms of the number of eggs laid ( $\ln(x+1)$ ) showed significant differences between locations of eggs ( $F=27.07$ ;  $P<0.0005$ ) and also between patches of different prey densities ( $F=3.83$ ;  $P<0.025$ ); but the interaction of location and patch type was not significant ( $F=1.45$ ;  $P>0.05$ ). The treatment means in Table 6.1.2B show that the number of eggs laid above, under, and away from scales were all significantly different from one another ( $P<0.05$ ). These differences suggest that the pattern of eggs laid above, under, or away from scales are sufficiently homogeneous to be considered to be consistent over patches of different prey densities.

(ii) PREY EATEN

In Figure 6.1.4 are given (a) the numbers of prey eaten, and (b) the percentage of prey eaten in relation to patches of different prey densities. The numbers of prey eaten can be represented by the hand drawn curve, with the response at patch with prey density four again being somewhat different from the general trend. With the exception of the beetle's unusual response to patch type 4, the general trend shows a decelerating rise to an upper asymptote. Also, as expected, the reverse of this was true for the percentage of prey eaten from any patch type, i.e. only a very small proportion of the total prey are eaten at higher prey densities. Functional response studies produce similar trends. Thus, not only do the beetles exercise discrimination among patch types in laying eggs, they also eat a larger number of prey from patches of higher prey densities

(iii) TIME SPENT

The time spent by the beetle in searching patches of different prey densities and the percentage of the total time spent on patches of different prey densities (Appendix Table 13), both showed a sigmoid relationship with patch type (Figs. 6.1.5A & B). This is explicable if the searching behaviour of the predator is altered after an encounter with the first prey, and if the predator keeps searching for some time before giving up and leaving the patch, even though at lower prey densities there are not

Fig. 6.1.4

Means  $\pm$  S.E. of the numbers of prey eaten (●) and of the percentages of prey eaten (⊙) from patches of different prey densities by Rodolia.

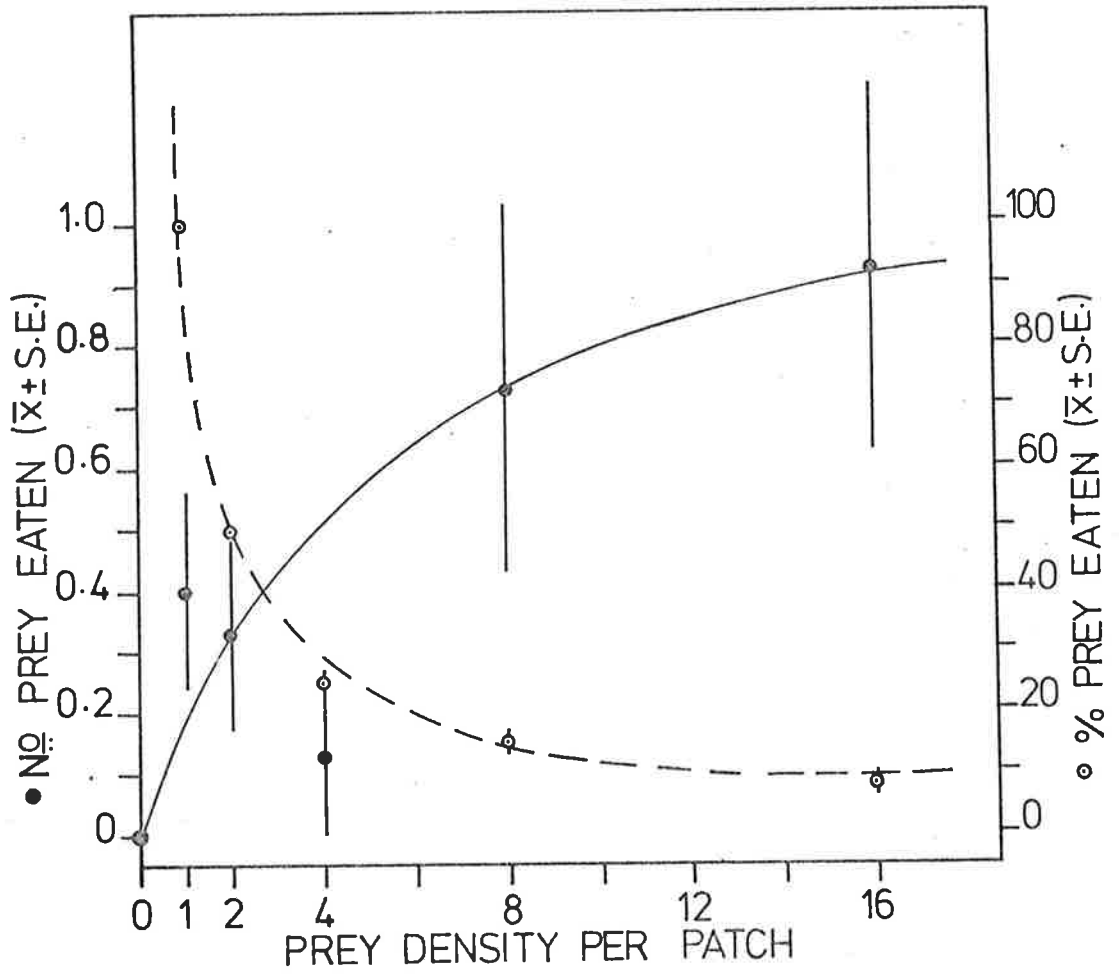


Table 6.1.2A

ANOVA OF THE NUMBERS OF EGGS RELATION TO (a) THEIR LOCATION (LAID UNDER, ABOVE OR AWAY FROM SCALES), AND (b) PATCH OF DIFFERENT PREY DENSITIES. DATA TRANSFORMED TO  $(\ln(x+1))$ .

SOURCE	DF	SS	MSS	F	P
LOCATION	2	31.23	15.62	27.07	<0.0005
PATCH TYPE	4	8.86	2.22	3.84	<0.025
INTERACTION	8	6.70	0.84	1.45	>0.05
ERROR	30	17.31	0.58		
TOTAL	44	64.10			

Table 6.1.2B

TABLE OF MEAN NUMBERS OF EGGS LAID AT DIFFERENT LOCATIONS (SIGNIFICANT DIFFERENCES BETWEEN MEANS BASED ON ANOVA Table (6.1.2)).

LOCATION OF EGGS	PREY DENSITY PER PATCH															MEANS (N=15)*
	(1) R1	(1) R2	(1) R3	(2) R1	(2) R2	(2) R3	(4) R1	(4) R2	(4) R3	(8) R1	(8) R2	(8) R3	(16) R1	(16) R2	(16) R3	
ABOVE	0.00	0.69	0.00	0.00	1.39	1.10	1.39	2.64	1.61	0.00	2.57	1.10	0.00	2.71	0.00	1.012A
UNDER	0.00	1.79	1.10	1.61	2.49	3.00	2.49	2.40	2.40	2.77	3.47	3.37	2.40	3.37	3.00	2.375A
AWAY	0.00	0.00	0.69	0.00	0.00	0.00	0.00	1.10	1.10	0.00	0.00	0.00	0.69	2.08	0.00	0.378A
MEANS (N=12)#		0.475B			1.064BC			1.679C			1.474C			1.582C		

\* Means followed by the same letters significantly different at  $P < 0.05$  ( $F_{2,30} = 3.32$ ) ; L.S.D. = 0.0568.

# Means followed by the same letters NOT significantly different at  $P < 0.05$  ( $F_{4,30} = 2.69$ ) ; L.S.D. = 0.733.

many prey present. If the beetle lays more eggs and eats more prey from patches of higher prey densities, then it may be expected to spend a larger amount of time at patches of higher prey densities (see Chapter 8.1., where similar data have been discussed at length).

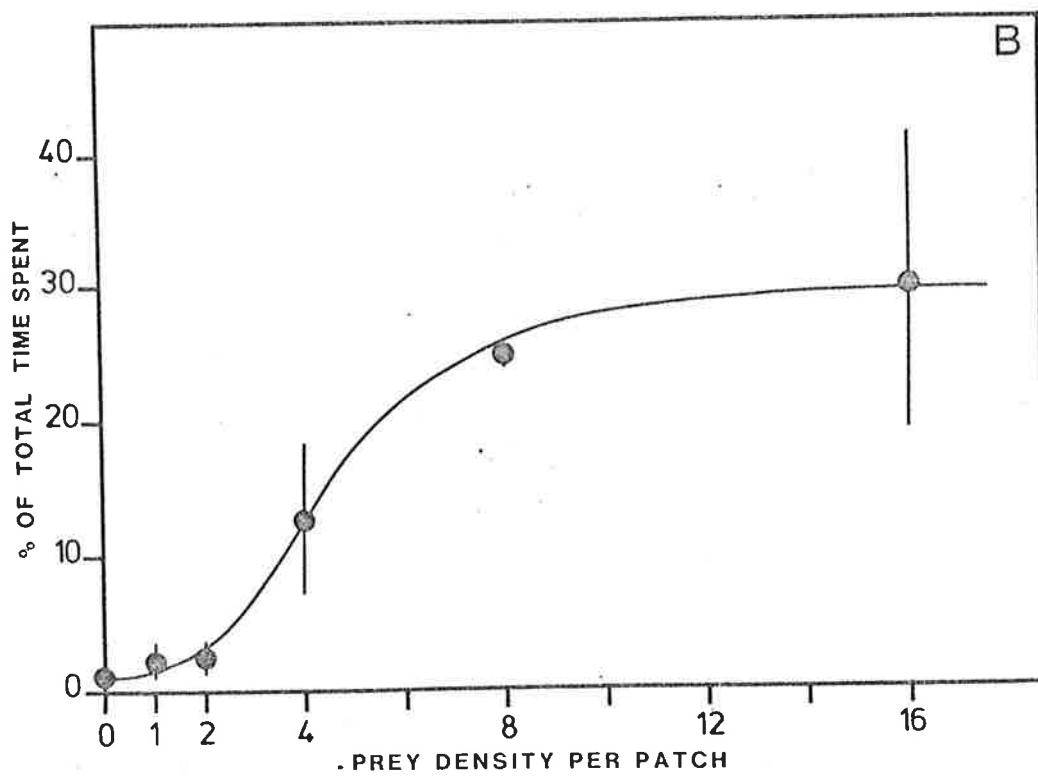
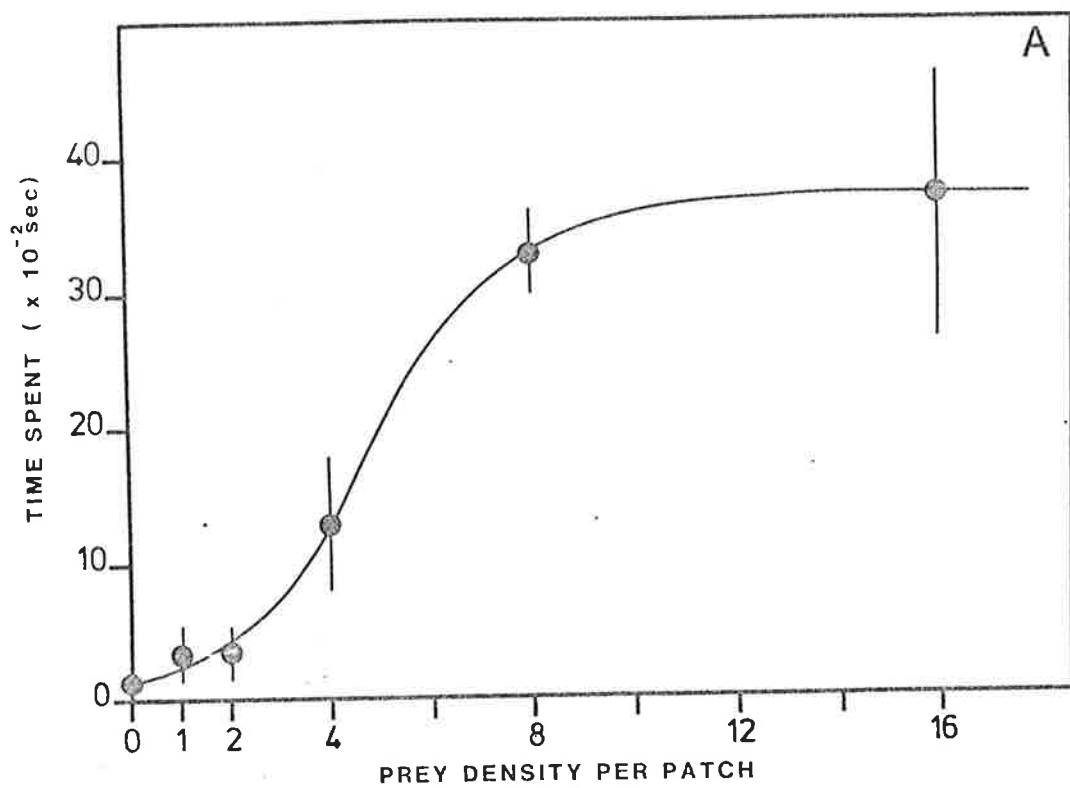
#### 6.1.4 DISCUSSION

The observations on the behavioural response of Rodolia reported above fall into the category of the individual response (Hassell, 1966) because only the response of a single individual has been considered, but in the literature such responses are also considered under the heading of "aggregative" responses. The response of individual Rodolia adults were tested especially because they are so scarce in the field that the chance of the activities of one adult being interfered with by another is negligible. And furthermore, the response of a single individual must be understood before attempts are made at studying the response of a group of them.

In studies dealing with the response of predators to patchily distributed prey, the response is more realistically considered to comprise two separate components (i) between patches - referring to the differential selection of patches of different prey density, and (ii) within patches - referring to how the predator responds to a patch once it has been selected. The former would be of considerable importance, especially when dealing with parasitoids that are attracted from a distance to host kairomones, the concentrations of which depend on the host density at the patch. Nemeritis and many other parasitoids fall into this category (e.g. Wylie, 1958; Hassell, 1968; Waage, 1979), and for them, patches with higher prey density may be discovered more quickly and revisited more often than those with lower prey density (Waage, 1983). This component of behaviour is obviously different from what the predator does once it finds itself in a patch. For the period between its entry and leaving the patch, the predator's response to prey density is akin to the functional response; the only difference is that in the former the predator is not confined to one prey density at a time for a fixed period. The decision to leave the patch lies with the predator itself and not with the experimenter. Therefore, it is not surprising that the results for responses within patches (Figs. 6.1.3 & 6.1.4) follow trends similar to those obtained from functional response studies.

Fig. 6.1.5

Means  $\pm$  S.E. of the time spent (Fig. A), and the percentages of the TOTAL time spent (Fig. B) by Rodolia at patches of different prey densities.



For reasons that are made obvious in the following chapter, the method of evaluating a predator's response to prey density by providing it with a choice of a number of patches of different prey densities has more merit than the conventional functional response procedures. One of the important features of such a method is that it provides data on the differential response of the predator to a range of different prey densities. In order to test the differential response of a parasitoid, Hassell (1971) conducted a laboratory experiment in which he presented the parasitoids "with the choice of a range of different host densities at the same time". Similar experiments were also conducted by Yeargan and Lateef (1976) to study the differential response of Bathyplectes curculionis (Thompson), a larval parasitoid of Hypera postica (Gyllenhal). However, in both these studies, a range of parasite densities was tested with the aim of studying mutual interference between searching parasites. Therefore, only the results of one of the treatments discussed by Hassell (1971) and Yeargan and Lateef (1976) are relevant to the present study, namely that in which a single parasitoid was used. Neither Hassell nor Yeargan and Lateef present results on the proportion of patches of any host density that were "ATTENDED". If the results presented for Rodolia are an indication, in the treatment with a single parasitoid, all the patches are unlikely to have been "attended". By ignoring the number of patches ATTENDED, a vital piece of information about the parasite's behaviour relating to patch selection, is lost.

Hassell (1971) found a significant relationship between host density per container and the k-values for parasitism even when a single parasite was searching. Yeargan and Lateef, on the other hand, did not find any significant relationship. In Hassell's experiment, the parasite in the smaller cage (28 x 18 x 11 cm) spent almost all of its searching time at the highest host density, and the relation between prey density per patch and the proportion of total time spent appeared to follow a positive exponential form. Later studies have shown that the form of such relationships range from convex to concave to sigmoid. And indeed a plot of the data for Rodolia took a sigmoid form (Fig. 6.1.5). Hassell (1980) suggests that "the idealized response to prey distribution will tend to be sigmoid" as a result of the predator's lower discriminatory abilities between patches at lower and higher prey densities (Hassell and May, 1974; Hassell, 1980). The sigmoid response is an outcome of the predator's



optimal foraging behaviour (this topic has been considered at considerable length in chapter 8.1.). Since the searching arena and the distance between patches were very small in Hassell's and my own experiment, the parasitoid/predator would have needed very little time to "sample" the patches and so was actually making a choice among simultaneously available host/prey densities. Thus, in such an arena, the time lost in transit between patches would have been negligible.

Both laboratory and field studies provide evidence that parasitoids and predators spend a larger proportion of their searching time in areas of high prey density (see Hassell, 1978b for review). Hassell (1968) using Varley's field data on the predators of the winter moth, showed that the parasitic tachinid fly Cyzenis aggregated at dense prey patches, spending more time at such patches. Clarke (1963) while studying the distribution of Syrphus eggs in relation to numbers of tests of the psyllid, Cardiaspina albitextura per leaf surface, also found a positive relationship between the number of predator eggs and prey density.

A number of workers have looked at searching behaviour of predators more closely in an attempt to understand the mechanisms involved in the production of an aggregative response. Fleshner (1950) working with mites and Banks (1957) and Dixon (1959) using ladybirds, showed that the predators tended to remain for some time in the immediate vicinity of their last feeding. There was an increase in turning rates immediately after feeding, and the rates stayed high for a short period before random search was resumed (for details, see Chapter 8.2). Thus, a number of successive feeds would probably take place at dense patches. As a result, each predator will stay longer in patches with many prey than in patches with few, and if all the predators behave in the same way, more predation will occur at the denser patches. Other workers have shown that some predators are actually attracted to areas of high prey density (Hassell and May, 1973; Hassell, 1978b).

In summary, the results discussed above indicate that, within the confines of the test arena, the beetle showed the ability to differentially exploit patches of prey in relation to prey density such that it killed more prey, laid more eggs, and spent more time at patches of higher prey densities.

## 6.2 INDEX OF ACTIVITY

### 6.2.1 INTRODUCTION

The activities of organisms are undoubtedly influenced by temperature and quantity and quality of their food (Andrewartha and Birch, 1954). Temperature is known to alter the behaviour of female parasites by affecting their ability to locate and attack hosts (Burnett, 1951; Biever, 1971; Bolt, 1974). The rate of travel (Bolt, 1974; Dreisig, 1981), the capture rate (Dreisig, 1981), the area of discovery (Podoler, 1981) and the rate of parasitization (Burnett, 1956; Ables and Shepard, 1976; Podoler and Mendel, 1979), have all been found to increase with an increase in temperature.

A considerable proportion of the study of predation deals with the influence of food supply (in the form of prey density) on the outcome of predator search (section 6.1). Different levels of starvation of the predator have also been found to influence the numbers of prey killed, with the numbers increasing with an increase in starvation levels (Holling, 1966). Murdoch and Oaten (1975) have argued that ".... the predator's efficiency of search and/or capture may increase with the number of meals eaten per unit time; or he may hunt faster as he receives increasing amounts of stimulus from the prey or the prey may behave differently as their density increases....".

The following inferences can be drawn from the above findings. If a starved predator also has to search for prey prior to feeding, the level of starvation should also influence its search effort. The search effort should also increase with starvation up to a point at which the stored energy starts becoming a limiting factor, and the intensity of search then declines. Since search is an energy depleting process, both the intensity and duration of search should depend on the amount of stored energy. And the rate at which energy is depleted depends on the rate of metabolism, which is a temperature dependent process. Thus, both the intensity and duration of search must depend on the level of stored energy and on temperature. Also there can only be a fixed amount of energy that can be stored in an organism (the satiation level). Therefore, temperature and the level of starvation must interact to influence the search activity of a predator.

Fig. 6.2.1

Photograph of the experimental set-up for the Index of Activity experiment described in Chapter 6.2.

The following experiment was designed to test the influence of temperature and starvation on the flight activity of a predator. An index of activity (IA) was defined as the number of flights per unit time (5 min) within a test arena and was estimated for the predator.

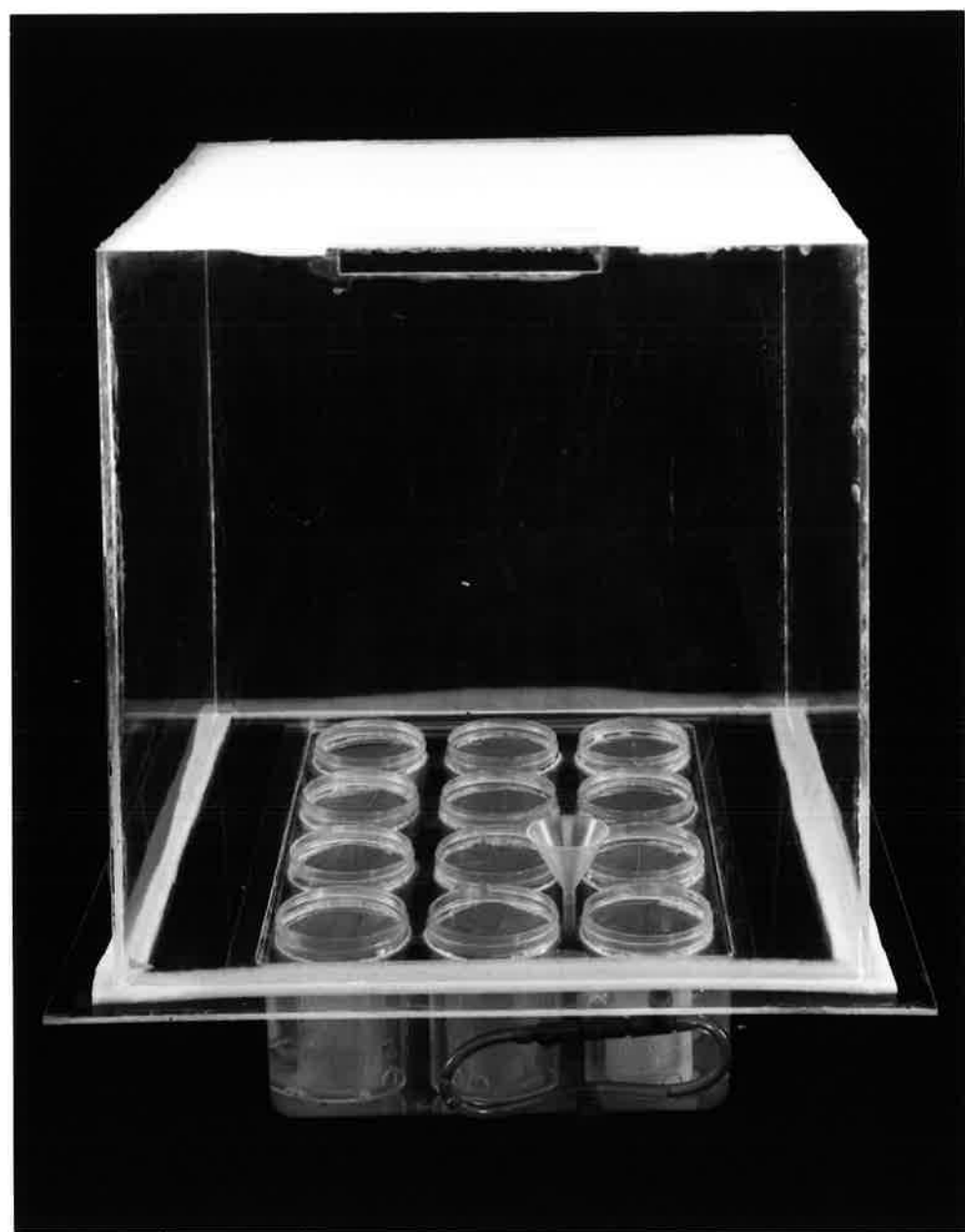
### 6.2.2 MATERIALS AND METHODS

The experiment was conducted in 2 constant temperature rooms, and it consisted of four treatments comprising two constant temperatures (25° and 30° C) and starvated or unstarvated initial states. The experiment was replicated three times.

The body of the testing arena consisted of a cubical cage (30 cm), the top of which was made of polyester voile. One of the culture units (see Chapter 3) served as the base (Fig. 6.2.1). For the unstarved beetles, prey were provided on citrus leaf-discs, but for the starved beetles the leaf-discs were kept free of prey. The searching beetles (predators) had access to water through the water-film trapped between the leaf-discs and the walls of the individual vials of the culture units. The provision of water to the beetles eliminated the confounding effect of dehydration and starvation.

The beetles used in the study were obtained from the stock culture. Prior to its use in the experiment, each beetle was well fed and acclimatized at the test temperature for a 24 h period. At the start of the experiment, a single female beetle, which was mated and 5 days old, was introduced into the test arena and allowed to search for prey. Data were collected twice daily, in the morning (1000 h) and the afternoon (1600 h) until the beetle died. During each observation session, four recordings of IAs were made, at quarter hourly intervals. Three replicates in a treatment were observed simultaneously. In the analysis, the data from the unstarvation treatment were considered only up to a time comparative to that of the starvation treatment at the same temperature; the rest were ignored.

The constant temperature rooms had a temperature variation of  $\pm 1^{\circ}$  C and were illuminated by a light bank made up of ten 40W daylight fluorescent tubes. Photoperiod was maintained at 14L:10D.



### 6.2.3 RESULTS AND DISCUSSION

There was an enormous variability in individual IA values among replicates in any treatment, with values ranging from 0 to near 200 (Appendix Table 14). However, their means and respective standard errors were adequate to demonstrate trends and draw conclusions therefrom.

#### (A) Temperature - 25° C

At 25° C, the IA values (Fig. 6.2.2A) for the unstarved beetle in the mornings fluctuated within a narrow range of 0 and 4.6, and in general an increasing trend in IA values with time could be noticed. In the same sort of arena, the IA values in the afternoon showed wider fluctuations between 0 and 18.8. So there was no common trend of morning and afternoon estimates of IA values at 25° C.

For the starved beetle (Fig. 6.2.2B), the IA values in the mornings increased steeply after 24 h and they remained high upto 96 h; the beetle finally died of starvation at 120 h. In the same sort of arena in the afternoon, the IA values of the beetle showed a general decline, with a peak IA value of 10.4 at only 6 h after the start of the experiment.

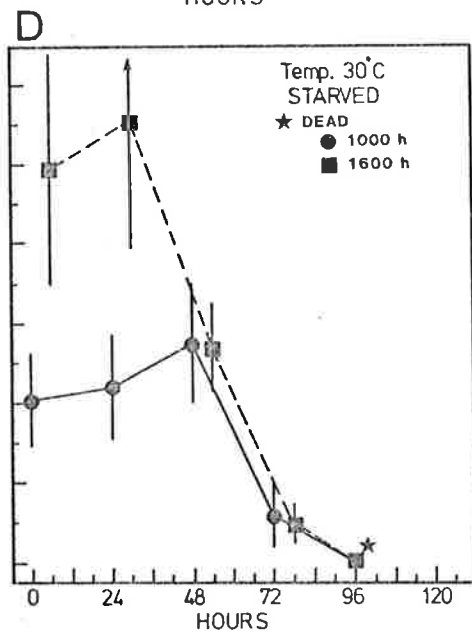
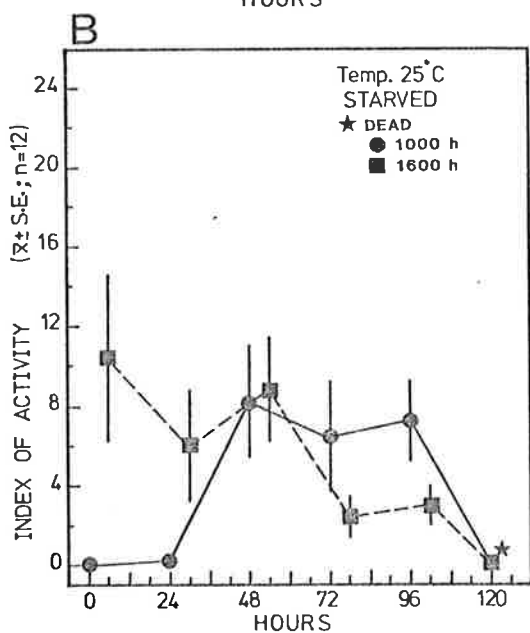
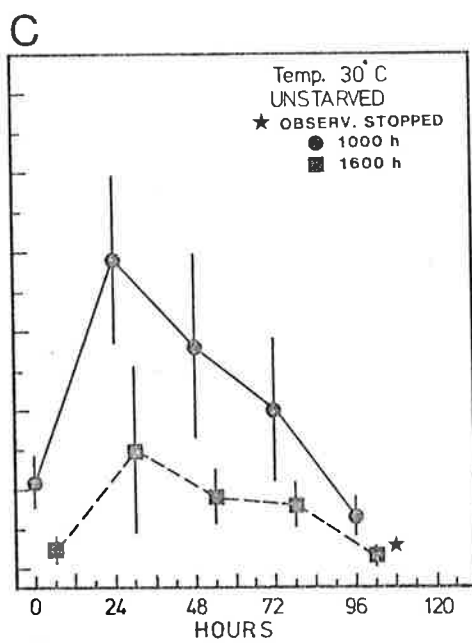
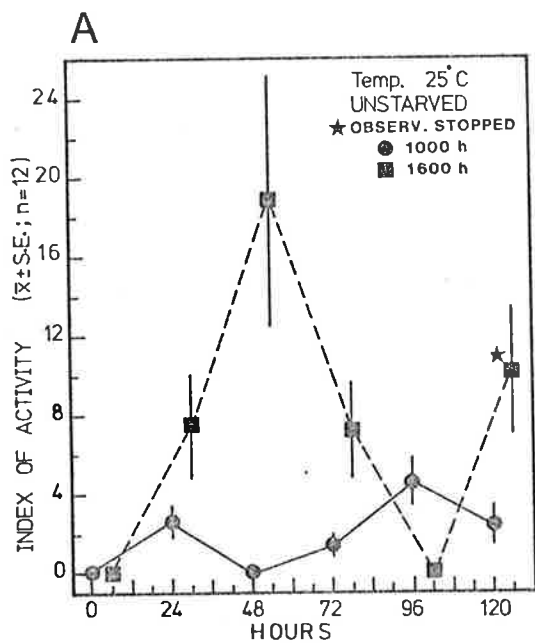
#### (B) Temperature - 30° C

At 30° C, on the other hand, the IA values followed a common pattern in both morning and afternoon (Figs. 6.2.2C & D). As hypothesized, there was an initial increase in IA values over a 24 h period, after which there was a decline for both the starved and unstarved beetles in both the mornings and afternoons. For the starved beetles, the initial IA values were considerably higher than those for the unstarved beetles, namely 8.33 and 4.42 respectively. This difference could be because the unstarved beetle found prey soon after the start of the experiment and its activities were then reduced. The increasing trend in IA values in the first 24 h period, for the unstarved beetle could be a result of a general urge of the predator to leave the patch in search of another after having fed and laid eggs, as part of its phasic behaviour (Chapter 8.1). Alternatively, this increase in IA values for the unstarved beetle could be a genuine increase in search effort stimulated by an increase in starvation. The gradual decline in IA values after 24 h, for the unstarved beetle, could be attributed to the beetle's getting acclimatized to the experimental set up. The presence of more than enough prey may also be responsible for the decline in the search intensity of the beetle. A steeper decline in the IA values for the starved beetles after 24 h could be due to the decrease in

Fig. 6.2.2

Means  $\pm$  S.E. of the numbers of flights per 5 min (Index of Activity) made by beetles at 1000 and 1600 h each day for 5 days for :

- (A) an unstarved beetle at 25° C,
- (B) a starved beetle at 25° C,
- (C) an unstarved beetles at 30° C,
- (D) a starved beetles at 30° C.





the level of stored energy resulting in increased sluggishness until the beetle totally exhausted its energy reserves and died.

Another remarkable feature of the IA values at 30° C was a reversal in the trend of morning and afternoon values for the starved and unstarved beetles. The IA values in the morning for the starved beetles were consistently higher than those in the afternoon. However, the reverse of this was true for the unstarved beetles. This reversal in trend between morning and afternoon activity could be a result of a diurnal influence on search effort. It appears that, in the morning, both starved and unstarved beetles resume activities at nearly the same rate, and so show comparable IA values, but then the unstarved beetles encounter and feed on prey during the day, which reduces their activities so that they have much lower IA values in the afternoons. Contrary to this, the starved beetles do not find any prey, in spite of constant searching, and they increase their search effort during the day thereby showing high values of IA in the afternoon.

The results discussed above indicate that the index of activity shows a better common trend at 30° C than at 25° C for both the starved and the unstarved beetles (Fig. 6.2.2). There is also evidence that Rodolia, in general, searches more actively for prey at 30° C than at 25° C, similar to Trichogramma spp. in which the rate of search also increased with an increase in temperature (Biever, 1971; Bolt, 1974). The results also support the hypothesis that, at least at a higher temperature (30° C), the unstarved beetles show an initial increase in search intensity which later declines till the beetle's death under the influence of depleting energy reserves.

**CHAPTER 7**  
**ESTIMATION OF SEARCHING EFFICIENCY OF RODOLIA**

## CHAPTER 7

### ESTIMATION OF SEARCHING EFFICIENCY OF Rodolia cardinalis

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If we respect truth we must search for it by persistently searching for our errors by indefatigable rational criticism and self criticism.

-- Karl Popper, of scientific attitude.

Error is all round us and creeps in at the least opportunity. Every method is imperfect.

-- Charles Nocole.

To do a great right, do a little wrong.

-- William Shakespeare.

---

#### 7.1 INTRODUCTION

In almost every field of science, a tension constantly exists between the theorists and the experimentalists. The theorists always march ahead with their conjectures of what is to come, though the experimentalists often reject some of these conjectures for lack of adequate evidence, and they reject others for their lack of realism. In addition, good quantitative data are difficult to obtain whilst conjectures are relatively easy to propound. Undaunted by the criticisms of the experimentalists, the theorists, however, march on propounding more conjectures, and the gap between theory and experimental evidence from the real world grows. In predation biology, this gap has grown so wide that the experimentalists find themselves in a curious dilemma. The theory, they know, is too far from realism, yet they cannot refrain from using it to help explain complex natural phenomena on the assumption that some of it may be true. Some theories appear to be true because they are often based on isolated instances of occurrences of a particular phenomenon, more commonly from artificial laboratory conditions.

There is another reason for the tension between theorists and experimentalists in biology. Contemporary biologists are indulging more and more in mathematical modelling of natural phenomena in the belief that vague ecological questions can be posed more succinctly in mathematical

terms. The modellers, often recruited from such diverse fields as physics and mathematics, have plunged into some of the most difficult biological problems with a seemingly impressive array of mathematical skills and an equally impressive innocence of biological principles (Way, 1973). The experimentalists, on the other hand, are often innocent of the mathematical techniques involved in model building. So the gap between theoretical and experimental biology widens, with little worthwhile synthesis (Way, 1973; Gilbert et al., 1976; Morrison and Strong, 1981), and in most decisions of an applied nature, theory as yet plays no significant role. In biological control, for example, trial-and-error or hit-and-miss techniques are still adopted (Gilbert et al., 1976; van Lenteren, 1980).

With the vast amount of literature on predator-prey interactions, one would have hoped that biological control by the importation of natural enemies would have by now emerged as a standardized scientific venture, and not remain the "try-it-and-see" form of technique that it was during the early part of this century. It is true that theoretical predation biology has enormously enhanced our understanding of the dynamics of predator-prey interactions in certain artificial environments, but as yet its predictions serve little use in the selection of biological control agents. Thus, though the literature tells us what characteristics to look for in prospective biocontrol agents, it fails to tell us how to compare those characteristics in a number of candidate species in order to select the "best" species.

Both theoretical and applied entomologists agree that an efficient natural enemy must possess a high "searching efficiency" (Flanders, 1947; Douth, 1964a; DeBach, 1974; Beddington et al., 1978; Hassell, 1978b; van Lenteren, 1980). But in spite of its importance, this term has remained ill defined in the literature, and there is much confusion about its use because it has been used to denote a number of related concepts, perhaps because all these concepts have evolved from the same idea. Thus, "searching efficiency" has been used to denote all of the following :-

- (a) NICHOLSON'S AREA OF DISCOVERY :- Most probably the term had its origin in this context. Nicholson's Area of Discovery has been defined as :  
 "the probability of encountering any particular host in the searching lifetime of the parasitoid." In more physical terms, it is the proportion of the total area that is searched by a single

parasitoid (Hassell, 1978a). It is usually denoted by the letter "a".

- (b) ATTACK RATE :- Denoted by  $a'$ , it is a parameter estimated from functional response experiments.
- (c) SEARCH RATE :- This term is also used synonymously with ATTACK RATE.

In 1982 Hassell published a paper entitled, "What is searching efficiency? ", in which he tried to define the term and clear some of the confusion, but the matter is far from resolved, as will be evident from section 7.1.2.

#### 7.1.1 HISTORICAL DEVELOPMENT OF THE SEARCHING EFFICIENCY CONCEPT

The first theoretical models of predator-prey interaction were developed over half a century ago by Lotka (1925), Volterra (1926), Thompson (1924), and Nicholson and Bailey (1935). These early attempts were purely deductive; there was no attempt to verify assumptions from field or laboratory data.

The Lotka-Volterra model, produced independently by Lotka (1925) and Volterra (1926), is a differential equation model characterized by a particular pattern of population change over time in which the predator and prey populations oscillate out of phase with each other; the successive oscillations being of the same amplitude. This model is based on assumptions similar to that of the Nicholson-Bailey model discussed below.

The Nicholson-Bailey model, based on Nicholson's (1933) general theory for the interaction of parasitoids and their hosts, is essentially a difference equation model implying completely discrete generations. This model has played a significant role in the evolution of the searching efficiency concept in predation biology and, therefore, has been considered here at length.

There are four basic assumptions upon which Nicholson's (1933) theory rests --

- (1) Parasitoids search for their hosts at random.
- (2) Parasitoids are not limited by their egg supply, or predators never become satiated.
- (3) Parasitoids of given species have a characteristic searching efficiency, which he called the AREA OF DISCOVERY.

(4) The number of hosts encountered per parasitoid (assuming no exploitation) is a linear function of host density.

On the basis of these assumptions, Nicholson produced a "competition curve" which relates the percentage parasitism of the host population to the number of parasitoids searching, and the following models are based on this competition curve.

Thus the population model for the host :

$$N_{t+1} = \lambda N_s = \lambda N_t \exp(-aP_t) \quad \dots\dots\dots (1a)$$

and, the population model for the parasitoid :

$$P_{t+1} = N_{HA} = N_t(1 - \exp(-aP_t)) \quad \dots\dots\dots (1b)$$

where :  $a$  = area of discovery

$N_t$  = number of hosts at generation  $t$

$N_s$  = number of hosts surviving parasitism

$N_{HA}$  = number of hosts parasitized

$N_{t+1}$  = host population in the next generation

$\lambda$  = host's rate of increase

$P_t$  = parasitoid population at generation  $t$

$P_{t+1}$  = parasitoid population in the next generation

The above equations are based on the first term of the Poisson distribution (Parker, 1973), which serves to distribute the encounters with hosts randomly, and yields the ( $N_{HA}$ ) hosts actually parasitized (some will have been encountered more than once).

Thus, given an initial parasitoid population ( $P_t$ ) and the area of discovery ( $a$ ), the percentage parasitism may be predicted. The number of hosts so parasitized ( $N_{HA}$ ) becomes the parasitoid population that searches in the next generation ( $P_{t+1}$ ). This assumes that only a single parasitoid larva can develop within each host attacked and that there is no mortality of the parasitoid progeny. The surviving hosts reproduce with a fixed rate of increase ( $\lambda$ ) to give the hosts of the next generation ( $N_{t+1}$ ).

Nicholson's area of discovery ( $a$ ) is easily calculated from the following expression for any set of data, provided that the number of

parasitoids ( $P_t$ ), the initial density of hosts ( $N_t$ ), and the number of surviving hosts ( $N_s$ ) are known. Thus we have --

$$a = (1/P_t) \cdot \text{Log}_e (N_t/N_s) \quad \dots\dots\dots (2)$$

where :     a = area of discovery  
 $P_t$  = number of parasitoids searching  
 $N_t$  = number of hosts present  
 $N_s$  = number of hosts surviving parasitism.

It was later found that all of Nicholson's assumptions were too far from realism. Parasitoids did not necessarily search for their prey at random, as was assumed by Nicholson, but were often attracted to the host's sex pheromones or kairomones (see Chapter 6.1). Neither is it true that parasitoids never run out of eggs, nor that predators never become satiated. So, too, the searching efficiency was found not to be constant and characteristic of a species but to vary with numerous factors, such as prey density, spatial heterogeneity in the distribution of hosts and parasitoids, and predator density (mutual interference between searching parasitoids) (Hassell, 1978b). Therefore, the first three assumptions of Nicholson were unrealistic. However, Holling's (1959) pioneering study of predation showed that there was some justification for Nicholson's fourth assumption of a linear relationship between the number of hosts encountered and host density, and that study produced what is now called Holling's Type-I functional response which is linear over a limited range of prey density but unlike Nicholson's linear response, also includes an upper limit so that a predator is no longer assumed to have an infinite appetite (or unlimited egg supply in parasitoids). Nicholson's fourth assumption also denies the importance of "handling time", which was found to be of vital significance in prey exploitation by arthropod predators (see below).

To obtain a Type-I functional response, we need merely assume a constant rate of encountering prey (the attack rate  $a'$ ) and a threshold prey density ( $N_x$ ) above which there is no further feeding by the predator. This response corresponds to the behaviour of filter-feeders; prey intake is proportional to prey density until the predator is satiated when it

abruptly ceases feeding. Thus, the relationship —

$$N_A = a'T_S N \quad \text{when } N < N_x \quad \dots\dots\dots(3a)$$

$$N_A = a'T_S N_x \quad \text{when } N > N_x \quad \dots\dots\dots(3b)$$

where :  $N_A$  = number of prey attacked per predator,  
 $N_x$  = threshold prey density above which there is  
 no further feeding by the predator,  
 $T_S$  = time available for searching (a constant here)  
 $N$  = the number of prey available,  
 $a'$  = the attack rate, which is a constant

For the sake of simplicity, the basic model assumes that prey is constantly replenished as eaten so that the value of  $N$  does not decline during the time period  $T_S$ . The constant ( $a'$ ) is an instantaneous rate of discovery of prey by one predator — the  $N_A/N$  per unit of searching time obtained by rearranging equation (3). Its value depends to a large extent on the predator's activity and ability to perceive. Equation (3) therefore predicts a linear relationship (with slope  $a'T_S$ ) between the number of prey encountered ( $N_A$ ) and the prey density ( $N$ ) for each predator, up to a certain prey density,  $N_x$ , after which the relationship abruptly levels off due to satiation (Fig. 7.1A).

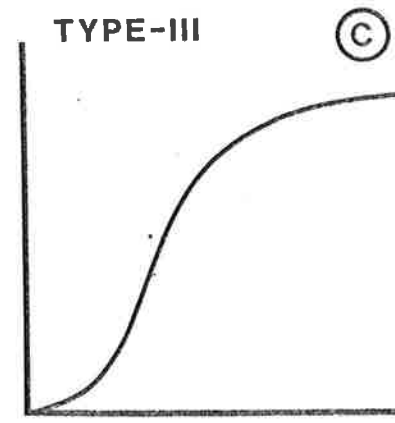
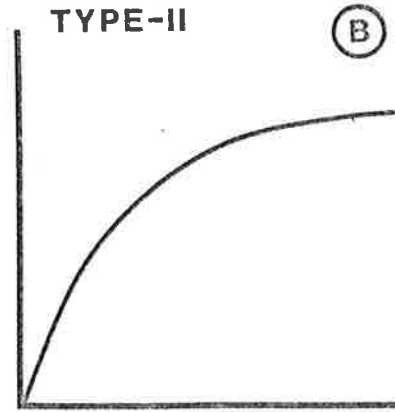
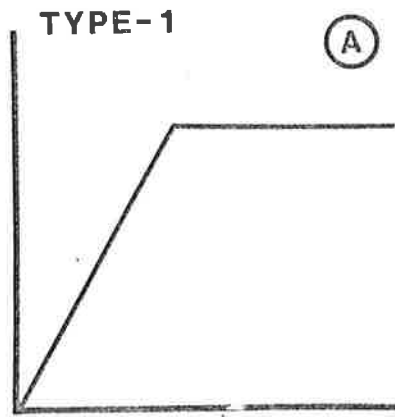
The Type-I functional response has been found to be unrepresentative of insect parasitoids and invertebrate predators in which the number of attacks per predator shows a decelerating rise to an upper asymptote (Fig. 7.1B). Such a response was predicted by Holling from a simple model developed by deductive reasoning. He disputed that searching time ( $T_S$ ) in equation (2) could be a constant. The acts of quelling, killing, eating, and digesting a prey are time consuming activities, which he collectively called the "Handling Time", and it reduces the time available for further



Fig. 7.1

Three types of functional responses identified by Holling.

NUMBER OF PREY ATTACKED PER PREDATOR



PREY DENSITY

search. Thus,

$$T_s = T - T_h N_A \quad \dots \dots \dots (4)$$

where :  $T_s$  = searching time  
 $T$  = the total time available for search,  
 $T_h$  = the handling time.

Holling, therefore, modified Nicholson's expression of area of discovery to take into account handling time and he produced the famous DISC EQUATION, which is obtained by substituting equation (4) in equation (3a) :

$$N_A = a'(T - T_h N_A)N \quad \dots \dots \dots (5)$$

Or,

$$N_A = a'NT / (1 + a'T_h N) \quad \dots \dots \dots (6)$$

(Disc Equation)

The "disc equation" is so called because it was supported by experiments in which a blindfolded subject (representing the predator) searched for sandpaper discs (representing the prey) on a flat surface. The form of the functional response predicted from this model depends upon two parameters, the attack coefficient, ( $a'$ ), and the handling time, ( $T_h$ ). The value of ( $T_h$ ) determines the maximum number of prey that can be attacked within the time ( $T$ ) (i.e.  $T/T_h$ ), and ( $a'$ ) defines how rapidly the response rises to the maximum level. The manner in which these are obtained from the data is fully described by Rogers (1972) and takes into account the depletion of available prey (or unparasitized hosts) as the experiment proceeds.

Any changes in this searching time,  $T_s$ , are directly related to changes in the area of discovery ( $a$ ) from the equation :

$$a = a'T_s = N_A/N = a'T / (1 + a'T_h N) \quad \dots \dots \dots (7)$$

where the term  $aP_t$  has been replaced by the more complex expression for a Type-II functional response. The Nicholson-Bailey model is now only a special case achieved when (i) handling time becomes zero, i.e. TYPE-I response, and (ii) the time period is equal to one generation. In that special case, the Attack Rate ( $a'$ ) becomes synonymous to Nicholson's Area of Discovery ( $a$ ).

Equation (7) when substituted in equation (1) gives the population model for predators showing a type-II response in the following form,

For the host population :

$$N_{t+1} = \lambda N_t \cdot \exp[-a' TP_t / (1 + a' T_h N_t)] \quad \dots \dots \dots (8a)$$

and for the parasitoid population,

$$P_{t+1} = N_t \{1 - \exp[-a' TP_t / (1 + a' T_h N_t)]\} \quad \dots \dots \dots (8b)$$

where the term ( $aP_t$ ) from equation (1) has been replaced by the more complex expression for the Type-II functional response.

The above equations (Type-II) have been further modified and referred to as "ATTACK EQUATIONS". These were first given by Royama (1971) and later by Rogers (1972) and are as follows :

(i) For parasitoids :

$$N_a = N_t [1 - \exp(-a' TP_t / (1 + a' T_h N_t))] \quad \dots \dots \dots (9a)$$

(ii) For predators :

$$N_a = N_t [1 - \exp\{-a' P_t (T - T_h \cdot N_a / P_t)\}] \quad \dots \dots \dots (9b)$$

The estimates of ( $a'$ ) and ( $T_h$ ) are acquired from a standard non-linear least-squares technique applied directly to the untransformed data. The much simpler alternative proposed by Rogers (1972), of a linear regression applied to the transformed data, is unfortunately fraught with statistical problems and hence prone to yield biased estimates of the parameters, as fully discussed by Cook (1977).

### 7.1.2. WHAT IS SEARCHING EFFICIENCY ?

In a paper entitled "What is searching efficiency? ", Hassell (1982a) attempted a review of the concept of searching efficiency and defined it in the following manner :

*"The term 'searching efficiency' has been used by both applied and theoretical ecologists in roughly the same sense-- a more efficient predator ATTACKS a larger proportion of the prey over a given period of time than does a less efficient one. A universal rigorous definition, however, of use both in population models and in assessing the performance of natural populations in the field, is still lacking." ( my capitals for attacks).*

Even here Hassell uses the term ATTACKS rather than "finds" or "discovers" or some other similar term related to SEARCHING. The dictionary meaning of "search" is "an attempt to find", but the phenomenon which the term searching efficiency is used to denote has nothing to do explicitly with the act of finding. Thus, if we consider a prey population distributed in discrete patches, the act of attacking prey in any patch can only follow the act of first FINDING a patch of prey. But the patch finding process has never been included in any earlier definition of searching efficiency. Therefore, the term is a misnomer in the manner in which it has been used in the literature on predation.

Predation biologists have realized the importance of evaluating searching efficiency taking into account the patchy distribution of prey, but they have not specifically included the patch finding process. Thus, Hassell (1982a) deals with the problem of searching efficiency in a patchy environment and says that "... in such a heterogeneous situation we must distinguish between two types of searching efficiency : that within a single patch and that over all patches.". He also presents equations for evaluating the two processes :

$$a_i' = (1/P_i T_{si}) \cdot \text{Log}_e (N_i/N_i - N_{ai}) \dots\dots\dots (10)$$

(for within patch)

$$a' = (1/n) \cdot (1/(P_i T_{si})) \cdot \text{Log}_e (N_i/(N_i - N_{ai})) \dots\dots (11)$$

(for over all patches)

Equation (10) is an expression of the searching efficiency within a single patch, based on the assumption that exploitation within a patch,  $i$ , is random. Equation (11), on the other hand, is an expression for the overall searching efficiency over a number,  $n$ , of patches. Searching efficiency in a patchy environment, Hassell argues, is sensitive to two factors :

- (1) the patch-specific, intrinsic searching ability of the predators, and
- (2) the extent to which the distribution of the predators relative to the prey is non-random.

He also points out that, to some extent, the overall searching efficiency is misleading in that it is the value (eg. in  $m^2$  per unit time, if the populations are expressed in  $m$ ) that would have been necessary to cause the observed mortality had the searching been at random (Free et al., 1977). This arises from the structure of Eq. (10) which assumes the total prey  $N$  to have been randomly exploited by  $P$  predators.

Equation (11) therefore, is an average of the patch specific searching efficiencies for the  $n$ , number of patches, based on the assumption that information is available about the distribution of prey and predators, searching time and prey attacked over a number,  $n$ , of individual patches. Hassell further points out that "By taking full account of the actual searching time per patch and the resulting number of prey eaten, Eq.10 provides the best measure so far of the real searching efficiency in a patchy environment. It is however, labour intensive!". (Eq. 10 of Hassell is the same as Eq.(10) here). Hassell's method is not only "labour intensive" but also cumbersome. Besides, in the above form, the outcome is essentially only an AVERAGE of the individual attack rates over  $n$  prey patches. Thus, though Hassell's method recognizes the importance of evaluating searching efficiency as a function of the patchy distribution of prey, it fails to evaluate the Patch Finding Process.

### 7.1.3 A NEW CONCEPT OF SEARCHING EFFICIENCY

I think that searching efficiency ought to be evaluated as an overall response which is dependent on two distinct processes -- (a) the PATCH FINDING, followed by, (b) the ATTACK of prey at the discovered patch. Furthermore, the process of the predator's EMIGRATION from a prey patch cannot be ignored, because without such a departure from a prey patch the concept of searching efficiency would still remain incomplete and

biologically unrealistic (see the flow diagram in Fig. 7.21). Most of Optimal Foraging theory, for example, deals with the factors that influence the predator's decision to emigrate from a prey patch (see Chapter 8.1). While I have not come across an expression that deals with the first process i.e. finding of a prey patch, the attack rate estimated from FUNCTIONAL RESPONSE experiments comes close to the second process (attack of prey at patches), though there are criticisms as to the manner in which functional response experiments are conducted (see Section 7.1.4 below). I have attempted to develop an expression for the first process, which I have referred to as PATCH FINDING EFFICIENCY (PFE) and discuss in section (7.1.5) below.

However, what is needed is not a separate evaluation of each of the different processes involved, but a single evaluation of all the component processes. Such an evaluation would produce a more realistic estimate of the searching efficiency of predators, and searching efficiency could then be defined as --

"the RATE at which patches of prey are discovered and prey attacked, in a patchily distributed prey population."

A concept of searching efficiency based on such a definition is not only simple but also free from the constraints of the earlier concepts as will become evident from the discussion of the data gathered for Rodolia cardinalis (section 7.3. & 7.4.).

Using data gathered from field experiments on the response of natural populations of Trichogramma spp. to artificially generated patches of different densities of Heliothis zea eggs, Morrison et al. (1980) were able to integrate the patch finding process and the attack rate by plotting the mean number of eggs parasitized per discovered patch (leaf). However, they did not discuss their results in the context of searching efficiency. The rates at which eggs were parasitized per discovered patch in relation to patches of different prey densities are the estimates of searching efficiency of Trichogramma. Morrison et al.'s estimates of the rates do not take into account the number of parasitoids searching.

Chesson (1982) criticized the method in which Morrison et al. (1980) handled their data on statistical grounds. Chesson used a model based on the binomial distribution and showed that Morrison et al.'s analysis could

produce misleading conclusions about the searching behaviour of parasitoids.

Morrison and Lewis (1984), while accepting the "naivety" in the statistical handling of their data, have warned against the dangers in drawing conclusions on the searching behaviour of parasitoids using Chesson's binomial model. Morrison and Lewis have produced an elegant case against the use of binomial distribution as an analytical tool in the analysis of data on the response of parasitoids to patches of prey, and they argue that Chesson's attempt is an oversimplification of a rather complex behavioural response of parasitoids to patches of different host densities. They point out that conclusions drawn from an application of Chesson's model must invariably be substantiated by a detailed study of the searching behaviour of the parasitoid.

#### 7.1.4 CRITICISMS OF FUNCTIONAL RESPONSE EXPERIMENTS

Solomon (1949) defined the Functional Response as a change in the numbers of prey attacked in a period of time by a single predator when the initial prey density is changed. The general method of conducting a Functional Response experiment is to confine a predator with each of different numbers of prey in relatively small containers and leave it there for some time. This time is fixed by the experimenter and is the same for all densities of prey. However, such an experiment can be criticised on the following grounds :-

- (1) By confining a predator in a relatively small cage with one prey density, the experimenter forces the predator to stay at "sites" with very low densities of prey for a longer period than it would probably do in nature. As a consequence, the number of prey eaten at these low densities might be considerably higher than if the experiment was terminated as soon as the predator stopped searching for prey.

Due to the small space and the often relatively long time a predator is left together with prey, even at the lowest densities, there is a high probability that another prey will be found when the predator resumes searching after its rest. That is, the predator in the cage has no alternative; it can only return to the site which it has already searched. Emigration would be an obvious alternative, and the effects of such emigration are important.

These criticisms have also been forwarded by van Lenteren and



Bakker (1976), who felt that for a proper analysis of functional response, behavioural observations on the predation process are indispensable. They have shown that, in the absence of such observations, what could have been a TYPE-III SIGMOID FUNCTIONAL RESPONSE could appear to be a TYPE-II Functional Response, which is supposed to be typical of invertebrate predators.

- (2) Where larger cages are used in such predation experiments, generally more than one predator is used, and the attack rate is estimated per predator by averaging over the numbers of predators. This averaging may lead to an overestimation of attack rate because of the inherent assumption that all of the predators in the cage were searching for the full duration of the experiment. However, that might not necessarily be true. One or more individuals may not search all the time but may, for example, simply sit on the roof or walls of the cage. I have noticed such behaviour in the cage experiments that I have conducted. Ideally such individuals ought to be left out of the analyses of results. It is therefore extremely important to know the response of each individual before we attempt to describe the response of a group of them.

#### 7.1.5 PATCH FINDING EFFICIENCY

Consider an experiment in which a searching arena of volume,  $V$ , has  $X$  patches of prey at  $d$  distances apart. And suppose that each patch supports  $Y$  sub-patches with different densities of prey, so there are a total of  $X.Y = N$  sub-patches present. Then if  $P$  predators searching for time,  $T$ , ATTEND\*  $n$  sub-patches, the PATCH FINDING EFFICIENCY (PFE) can be defined by :

$$PFE = (1/PTV).(n/N) \dots\dots\dots(12)$$

\* sub-patches ATTENDED are those sub-patches which are discovered by the predator and at which prey are eaten and/or eggs are laid.

Thus, Patch Finding Efficiency (PFE) is a measure of the sub-patches ATTENDED per predator per unit time per unit volume of the searching arena, and PFE simply becomes the proportion of the total sub-patches ATTENDED when  $T, P$  and  $V$  are reduced to unity. PFE is thus a measure of the inherent

potentiality of the predator to find sub-patches of prey and ATTEND them. Estimates of PFE would depend on a number of factors, such as prey density per sub-patch, distance between sub-patches, distance between patches, temperature, etc.

Equation (12) is an attempt to quantify the first process in the newly defined searching efficiency of a predator, i.e. The Patch Finding Process. As mentioned earlier, what happens after a sub-patch has been discovered, is the second step and falls in the category of ATTACK RATE.

#### 7.1.6 OBJECTIVES BEHIND MY EXPERIMENTS

Having gathered data in support of Rodolia's ability to find isolated patches of prey in the field, the next step was to quantify its searching efficiency. However, as explained above, previous methods of estimating the searching efficiency of a predator were considered to be unsatisfactory.

In the following experiment, an attempt was made to get closer to biological realism and evaluate the searching efficiency of Rodolia by :

- (a) Providing varying densities of prey in discrete patches at the same time thus allowing the predator the freedom to arrive at or leave a prey patch whenever it wanted to.
- (b) Using a single searching predator but using a large cage and allowing the predator to fly among patches of different prey densities.
- (c) Measuring the Patch Finding Efficiency and the Attack Rate.

The long term aim of this experiment was to develop, experimentally, a more realistic concept of searching efficiency which would allow comparison of two or more biological control candidates.

## 7.2 MATERIALS AND METHODS

### 7.2.1 INITIAL EXPERIMENTS

Initially the experiment was planned to be conducted in a large searching arena in which were to be placed a number of prey patches. Each patch was to comprise of four sub-patches of prey. A single ovipositing beetle was to be introduced as the searching predator, and data were to be

collected every 24 h on (a) the number of prey eaten, and (b) the number of eggs laid at each sub-patch.

The experiment was to be repeated in different sizes of searching arena, and the effect of altering the distances between patches of prey was also to be measured. Different sizes of glasshouses were to be the searching arenas, potted plants of Acacia baileyana were to be the patches, and circular citrus leaf-discs with prey were to be the sub-patches on each patch. The leaf-discs with prey were to be placed on plastic containers fixed to dowelling rods used for staking the plants (see Fig. 7.3 and description of Expt. 3 below). However, serious practical problems were encountered in preliminary experiments, and although these experiment failed, I would like to briefly discuss them in order to illustrate the problems that can be encountered when attempting to conduct a predator/prey experiment in a large cage.

(i) THE ROCKPILE

The "Rockpile" is a glass and concrete structure with a corrugated metal roof. It was designed to conserve and recycle natural heat for maintaining temperature regimes. Though each cubicle of the Rockpile has four walls of glass, natural light enters through only one of them, which therefore is the brightest. The first experiment was conducted in a Rockpile cubicle.

Seven prey patches (potted plants with sub-patches of prey as described above) were positioned at the corners of an equilateral hexagon; the remaining patch occupied the central position. The direction and intensity of light in the cubicle played a significant role in influencing the searching behaviour of the beetle. The beetle spent most of its time fluttering on the glass wall which had the highest light intensity. A few modifications of the cubicle were made to reduce the light gradient, e.g. whitewashing the glasswalls, but none made the beetle search for prey among the patches that were provided. This behaviour of the beetle raised a suspicion that the experiment would also fail in a large glasshouse and alternate methods were, therefore, considered.

(ii) CAGE IN THE OPEN WITH POTTED PLANTS

To overcome the problem with the light gradient, an experiment was next set up in the open, in a 2x2x2 m cage made of white polyester voile. Again, potted plants constituted prey patches with sub-patches of prey on citrus leaf-discs, as previously described. The plants were about 100 cm high, and the roof of the cage was about 200 cm high. In this cage, the beetle sat on the roof and walls of the cage doing nothing. Occasionally, it would wander around, but it never got to the patches of prey below. This was a typical example of what I later came to know as the CAGE EFFECT. The behaviour of the beetle was attributed to the large empty space in the cage above the plants.

(iii) CAGE IN THE OPEN WITH A LARGE *Acacia iteaphylla* BUSH

In this attempt, a cage similar to the above was set up over a large *Acacia iteaphylla* bush, which is also a good host plant for the scale. The canopy of the bush filled almost the entire volume of the cage. Sub-patches of prey were provided on citrus leaf-discs which were supported by plastic containers fixed to 1.27 cm dia dowelling (wooden rods). The dowelling rods were fixed into the ground and they stood up through the canopy.

In this arena too, the beetle spent most of its time in the corner of the roof and walls of the cage. It was again seemingly drawn to the light because its position changed with the position of the sun during the day.

(iv) CAGED EXPERIMENT IN AN INSECTARY ROOM

An experiment was next set up in one of the rooms of an insectary with artificial light provided by twelve 80 watts Daylight Fluorescent tubes from a light bank suspended from the roof. A cage 150x150x200 cm was set up in the room and the experiment repeated. The experiment again failed for apparently the same reason, i.e. the beetle mainly fluttered within a distance of 10-20 cm from the roof of the cage, apparently attracted to the light source.

I then decided to lower the roof of the cage to a height of about 10 cm above the tips of the prey patches, and surprisingly the experiment seemed to work in the sense that the beetle started flying between patches, feeding on prey and laying eggs.

### 7.2.2 DETAILED DESCRIPTION OF THE FINAL EXPERIMENTAL ARENA

The final experimental arena consisted of a cage 150x150x110 cm made of white polyester voile (Fig. 7.2). The lower end of the cage was glued to the floor of the cubicle. The roof of the cage was kept extended by the help of a square frame made of 1.27 cm dia dowelling rods and aluminium clamps. The frame was suspended from the roof of the cubicle by means of a rope and pulley (Fig. 7.2B). Such a mechanism allowed the roof of the cage to be positioned at varying heights, and enabled entry into the cage for observation. A slit in one side of the cage served as a door and was otherwise closed by a VELCROW nylon fastener. During the experiment, the roof of the cage was suspended at a height of 110 cm from the ground so that it remained only 10 cm above the top most sub-patch of prey.

In the arena, seven PATCHES of prey were positioned at the corners of an equilateral hexagon (65 cm); the remaining patch occupied the central position (Fig. 7.2C). The patches were placed at positions such that each one was equidistant from the next around. Each PREY PATCH consisted of a 20 cm dia plastic pot filled with soil, on top of which was placed a circular wooden disc with a hole in the centre. A 1.27 cm dia dowelling rod was pushed vertically through the central hole in the wooden disc into the soil such that the tip of the exposed rod was 100 cm from the base of the pot.

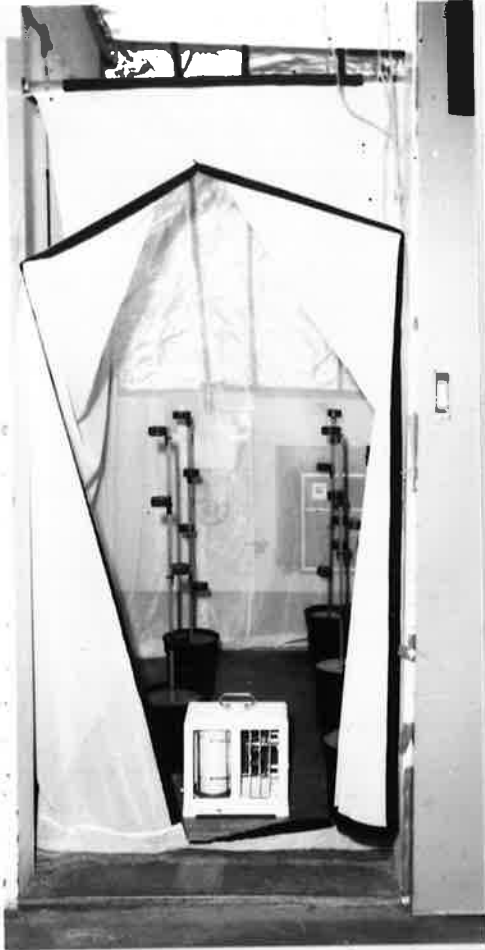
Each such patch supported four SUB-PATCHES, each of which comprised a 2x5.08 cm dia plastic container (Fig. 7.2C) supporting a citrus leaf-disc with scales. The leaf-disc rested on a foam-plastic disc which was immersed in water, and the whole container was fixed to the dowelling rod by plastic-coated wire. Each patch contained four different prey densities (2, 4, 8, and 16 prey or 1, 3, 12, and 20 depending on the experiment; see below) which were randomly distributed to the four sub-patches. The top most sub-patch on a patch was 100 cm from the ground and the distance between the sub-patches was 20 cm.

Predators and prey used in the experiments were reared in the insectary at temperatures of  $28 \pm 5^{\circ}$  C. Newly emerged female beetles were confined with males to facilitate mating on the first day. When the females were five days and had fed and were capable of laying eggs, they were used in an experiment. Second instar scales which were one week old and reared on 5.08 cm dia citrus leaf-discs in the insectary (Chapter 3),

Fig. 7.2

Photograph of the experimental set-up showing polyester voile cage (A), the roof of which was suspended by means of rope and pulley to allow alteration of height (B). The inside of the cage shows seven patches each with four sub-patches of prey (C).

A



B



C



were used.

Each experiment was conducted at a constant temperature of  $27 \pm 2^{\circ}$  C. Light was provided by a bank of twelve 40 W Daylight Fluorescent tubes and a 14L:10D photoperiod was maintained.

Data were collected every 24 h for four days on the number of prey eaten and the number of eggs laid for each beetle tested. The prey eaten were replaced and the eggs that were laid were removed after the data were recorded each day. Each experiment was replicated three times in the sense that three different Rodolia beetles were used as the three replicates of each experiment and the responses of each beetle were recorded separately. Since there was only one searching arena, the experiments had to be replicated in time.

### 7.2.3 THE EXPERIMENTS CONDUCTED

The following five experiments were conducted. Experiments 1, 2, 3, and 5 were conducted in the arena within the insectary room as described above, but Expt. 4 was conducted in a glasshouse (see below).

- (a) EXPERIMENT (1) : four prey densities of 2, 4, 8, and 16 prey per sub-patch (leaf-disc) were used, and each patch contained all four prey densities.
- (b) EXPERIMENT (2) : four prey densities of 1, 3, 12, and 20 prey per sub-patch were used, and each patch contained all four prey densities. These prey densities were complementary to those in Expt. 1, and were chosen to extend the range of densities after pooling.
- (c) EXPERIMENT (3) : same as Expt. 1 but potted plants of Acacia baileyana were also used (Fig. 7.3). The sub-patches for each patch were fixed to the dowelling rod which staked a plant.
- (d) EXPERIMENT (4) : This experiment was also similar in design to Expt. 1 (i.e. prey densities 2, 4, 8, and 16 used), except that the size of the searching arena was increased and the distance between nearest patches doubled to 130 cm. In this experiment, the arena consisted of a cage of 300x300x110 cm which was set up in a glasshouse. The walls of the



Fig. 7.3

Potted plant of Acacia baileyana used as a patch, with four sub-patches attached to the dowelling rod.



glasshouse were whitewashed to permit entry of diffused light only. Light was also provided from the top by a bank of twelve 40 W Daylight Fluorescent tubes, and the photoperiod was about 14L:10D. The temperature was maintained at  $27 \pm 3^{\circ}$  C.

(e) EXPERIMENT (5) : This experiment was also conducted in the insectary room with 2, 4, 8, or 16 prey per sub-patch. However, in contrast to Expt. 1, all four sub-patches in all the seven patches had the same prey density at one time (i.e. either 2 or 4 or 8 or 16 prey). Thus, Expt. 5 had to be conducted in four parts, and in each part a different prey density was used. Each part of the experiment, in which either prey density 2, 4, 8 or 16 were used, was replicated three times.

### 7.3 RESULTS AND DISCUSSION

As pointed out in Chapter 2, Rodolia cardinalis is an unusual predator which behaves more like a parasitoid in that it lays its eggs on, under or close to its prey. Thus, the beetle's response to prey density can be studied both in terms of the numbers of prey that it kills, and also the number of eggs that it lays. Consequently, attempts were made to evaluate the searching efficiency of the beetle on the basis of (a) its killing power (ATTACKING POTENTIAL), and (b) its egg laying power (OVIPOSITIONAL POTENTIAL).

Before presenting the results, a few terms that are used in the course of the discussion need to be defined :

- (a) SUB-PATCHES VISITED : A sub-patch discovered by the beetle but at which NO prey eaten and NO eggs laid.
- (b) SUB-PATCHES ATTENDED : A sub-patch discovered by the beetle and at which prey eaten and/or eggs laid.

#### 7.3.1 EXPERIMENTS (1) TO (4)

Because the basic design of experiments 1, 2, 3, and 4 was similar, their results have been discussed simultaneously and in a comparative manner. The raw data gathered from these experiments have been tabulated in Appendix Tables (15A to 15D), and a summary of the results has been presented in Table 7.1. Summarized data from the experiment in Chapter 6.1 have also been presented in Table 7.1, to illustrate the influence of the

Table 7.1

SUMMARY OF RESULTS (MEANS ± S.E.) FROM EXPERIMENTS DESCRIBED IN CHAPTER (6.1) AND CHAPTER (7). MEANS CALCULATED PER BEETLE PER DAY HAVE BEEN DRAWN FROM THE LAST COLUMN IN APPENDIX TABLES 11 AND 15, AND REARRANGED FOR EACH VARIABLE (e.g. ET, EU, TOT, etc.) AT EACH PREY DENSITY.  
(For description of abbreviations see end of Table)

RESP ONSE	PREY DENS.	CHAP.(6.1)	EXPT.(1)	CHAPTER (7) EXPT.(3)	EXPT.(4)	PREY DENS.	CHAP.(7) EXPT.(2)
	0	0	NA	NA	NA		
	1	0.07 ± 0.07	NA	NA	NA		
ET	2	0.33 ± 0.23	0	0.17 ± 0.17	0	1	0
	4	1.33 ± 0.65	0.25 ± 0.13	0	0	3	0
	8	0.93 ± 0.56	1.17 ± 0.66	0	0	12	0
	16	0.93 ± 0.75	3.92 ± 1.14	0	0	20	0
	0	0	NA	NA	NA		
	1	0.47 ± 0.22	NA	NA	NA		
EU	2	2.27 ± 0.76	3.08 ± 0.54	1.50 ± 0.58	1.25 ± 0.51	1	1.67 ± 0.70
	4	2.07 ± 0.83	6.58 ± 1.46	4.50 ± 0.44	2.92 ± 0.68	3	5.67 ± 1.01
	8	4.93 ± 1.78	8.67 ± 1.25	9.08 ± 1.63	10.33 ± 0.70	12	16.67 ± 1.82
	16	3.80 ± 1.11	11.58 ± 1.32	11.58 ± 1.28	12.33 ± 1.25	20	16.58 ± 2.31
	0	0	NA	NA	NA		
	1	0.07 ± 0.07	NA	NA	NA		
EA	2	0	0	0	0	1	0.25 ± 0.25
	4	0.77 ± 0.18	0.08 ± 0.08	0	0	3	0
	8	0	0.17 ± 0.11	0	0	12	0
	16	0.53 ± 0.24	0.25 ± 0.13	0	0	20	0
	0	0	NA	NA	NA		
	1	0.60 ± 0.29	NA	NA	NA		
TOT	2	2.60 ± 0.90	3.08 ± 0.54	1.67 ± 0.67	1.25 ± 0.50	1	1.92 ± 0.78
	4	3.67 ± 1.11	6.92 ± 1.57	4.50 ± 0.44	2.92 ± 0.68	3	5.67 ± 1.01
	8	5.87 ± 2.14	10.00 ± 1.38	9.08 ± 1.63	10.33 ± 0.70	12	16.67 ± 1.82
	16	5.27 ± 1.60	15.75 ± 1.78	11.58 ± 1.28	12.33 ± 1.25	20	16.58 ± 2.31
	0	0	NA	NA	NA		
	1	0.40 ± 0.19	NA	NA	NA		
SED	2	1.00 ± 0.34	1.83 ± 0.30	0.92 ± 0.31	1.00 ± 0.39	1	0.83 ± 0.35
	4	1.87 ± 0.60	4.17 ± 0.79	3.08 ± 0.34	2.67 ± 0.53	3	3.25 ± 0.41
	8	3.27 ± 1.12	6.92 ± 0.69	5.92 ± 0.91	7.92 ± 0.50	12	11.33 ± 1.34
	16	3.13 ± 0.96	11.67 ± 1.23	9.58 ± 1.13	10.17 ± 1.03	20	12.25 ± 1.48
	0	0	NA	NA	NA		
	1	0.27 ± 0.15	NA	NA	NA		
1E	2	0.47 ± 0.19	1.00 ± 0.25	0.50 ± 0.20	0.75 ± 0.28	1	0.33 ± 0.19
	4	0.80 ± 0.28	2.08 ± 0.43	1.83 ± 0.47	2.42 ± 0.40	3	1.83 ± 0.24
	8	1.47 ± 0.56	5.00 ± 0.60	3.33 ± 0.56	5.83 ± 0.72	12	7.33 ± 1.13
	16	2.07 ± 0.70	8.33 ± 0.96	7.83 ± 1.10	8.25 ± 1.00	20	8.58 ± 0.99
	0	0	NA	NA	NA		
	1	0.13 ± 0.09	NA	NA	NA		
2E	2	0.20 ± 0.15	0.50 ± 0.20	0.17 ± 0.11	0.25 ± 0.13	1	0.25 ± 0.18
	4	0.73 ± 0.25	1.83 ± 0.55	0.92 ± 0.23	0.25 ± 0.18	3	0.67 ± 0.23
	8	0.93 ± 0.33	1.33 ± 0.38	2.08 ± 0.56	1.75 ± 0.37	12	2.83 ± 0.39
	16	0.67 ± 0.19	3.00 ± 0.70	1.50 ± 0.34	1.67 ± 0.31	20	2.92 ± 0.56
	0	0	NA	NA	NA		
	1	0	NA	NA	NA		
3E	2	0.20 ± 0.11	0.25 ± 0.13	0.17 ± 0.11	0	1	0.17 ± 0.11
	4	0.27 ± 0.15	0.17 ± 0.11	0.17 ± 0.11	0	3	0.58 ± 0.34
	8	0.67 ± 0.30	0.33 ± 0.19	0.42 ± 0.19	0.33 ± 0.19	12	1.00 ± 0.48
	16	0.27 ± 0.12	0.08 ± 0.08	0.25 ± 0.13	0.25 ± 0.18	20	0.58 ± 0.34
	0	0	NA	NA	NA		
	1	0	NA	NA	NA		
>3E	2	0.13 ± 0.09	0.08 ± 0.08	0.08 ± 0.08	0	1	0.08 ± 0.08
	4	0.07 ± 0.07	0.08 ± 0.08	0.08 ± 0.08	0	3	0.17 ± 0.11
	8	0.13 ± 0.09	0.25 ± 0.13	0	0	12	0.17 ± 0.11
	16	0.13 ± 0.09	0.25 ± 0.18	0	0	20	0.08 ± 0.08
	0	0	NA	NA	NA		
	1	0.40 ± 0.16	NA	NA	NA		
NET	2	0.33 ± 0.16	1.33 ± 0.31	0.50 ± 0.23	1.67 ± 0.47	1	1.00 ± 0.25
	4	0.13 ± 0.13	2.08 ± 0.60	1.83 ± 0.35	2.08 ± 0.38	3	1.50 ± 0.52
	8	0.73 ± 0.30	2.58 ± 0.48	2.58 ± 0.36	2.25 ± 0.48	12	3.17 ± 0.39
	16	0.93 ± 0.30	2.83 ± 0.74	3.75 ± 0.37	2.83 ± 0.42	20	3.50 ± 0.63

EA = EGGS LAID ABOVE SCALES  
 EU = EGGS LAID UNDER SCALES  
 EA = EGGS LAID AWAY FROM SCLAES  
 TOT = TOTAL EGGS LAID  
 SED = SCALES WITH EGGS  
 NA = NOT APPLICABLE

1E = SCALES WITH 1 EGG  
 2E = SCALES WITH 2 EGGS  
 3E = SCALES WITH 3 EGGS  
 >3E = SCALES WITH >3 EGGS  
 NET = PREY EATEN

size of the searching arena on the ovipositional behaviour of the beetle. The searching arena used in the experiment in Chapter 6.1 was 270x410x120 mm (Fig. 6.1), which is much smaller than those used in the experiments described here.

### 7.3.1.1 OVIPOSITIONAL BEHAVIOUR

The data on the ovipositional behaviour of the beetle (Table 7.1 & Fig. 7.4) show that the proportions of eggs laid either above, under or away from the scales were only similar in the experiment from Chapter 6.1 and Expt. (1) in this Chapter (7). In both these experiments, over 75 % of the total eggs laid were deposited under the scales, 14 to 20 % of the eggs were laid above the scales, and the eggs laid away from the scales were negligible (<5 %). In contrast, the eggs laid above and under the scales were negligible in Expts. (2), (3), and (4). The data, therefore, indicate that almost all the eggs laid were deposited under the scales as the complexity of the searching arena (Expt. 3), and its size (Expt. 4) increased.

Though the numbers of scales with 1, 2, and 3 eggs were similar across experiments, the numbers of scales with >3 eggs were negligible in Expts. (3) and (4), indicating that the beetle distributed its eggs more evenly (i.e. there was less clustering of eggs on individual scales) as the complexity and size of the searching arena increased.

On the basis of these results, one may perhaps expect that in nature, where the size of the searching arena is infinite, almost all the eggs would be laid under the scales and the number of eggs laid per scale would be three or less if all the scales were 2nd instar scales. But the number of eggs laid per scale in nature may also be a function of the age (size) of the scale.

### 7.3.1.2 EVALUATION OF SEARCHING EFFICIENCY

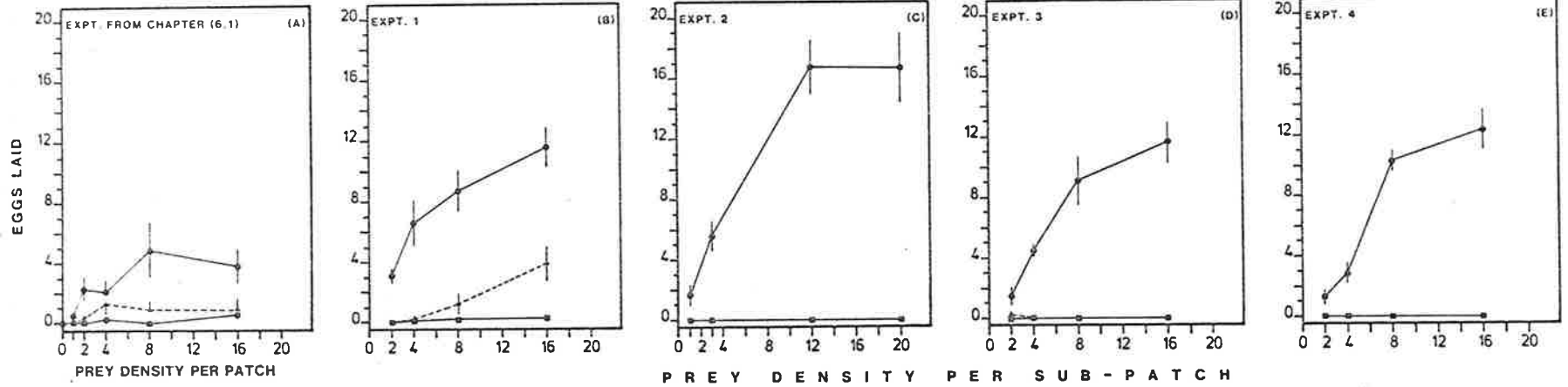
Initially, the data for the first two components of searching efficiency, viz. (a) the Patch Finding Process, and (b) the Attack Rate, have been presented separately. Then, the data for the two processes have been integrated to evaluate the overall response of the two processes in order to obtain the searching efficiency of the beetle, in accordance to the arguments presented in section 7.1.

The results from Expts. (1) and (2) have been plotted together as a

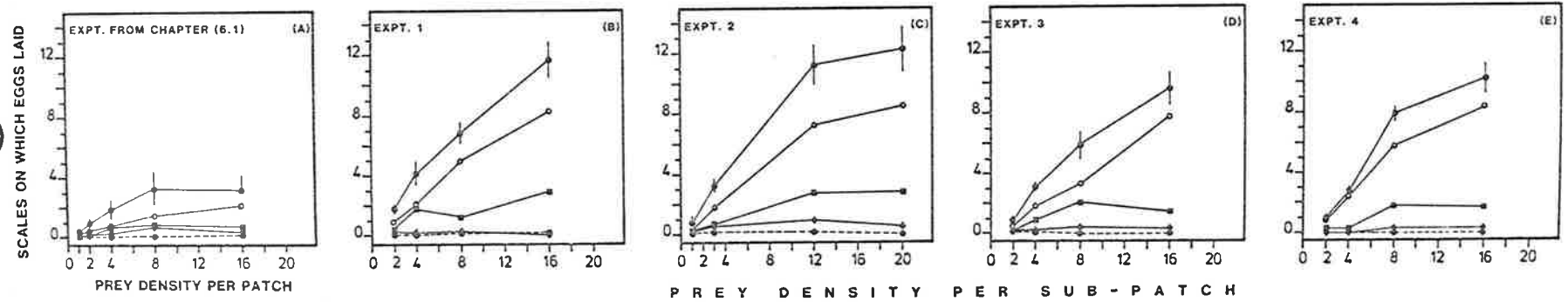
Fig. 7.4

The ovipositional behaviour of Rodolia from one experiment described in Chapter 6.1 and four experiments described in Chapter 7. The top five figures (1) show the means  $\pm$  S.E. of the numbers of eggs laid either ABOVE (●), UNDER (▲), or AWAY (■) from the scales at patches of different prey densities. The bottom five figures (2) show the means  $\pm$  S.E. of the total scales (●) with Rodolia eggs and the means of the numbers of scales with 1 (○), 2 (■), 3 (◆), and >3 (-●-) Rodolia eggs per scale at patches of different prey densities.

(1)



(2)



series of "A" figures wherever practicable, because the prey densities per sub-patch were complementary. Such a method of presenting the data allowed a better representation of the trends in the relationships, based on a larger number of data points. The results from Expt. (3) and Expt. (4) have been plotted as a series of "B" and "C" figures respectively.

### 7.3.1.2.1 THE PATCH FINDING COMPONENT OF SEARCHING EFFICIENCY

#### (A) HEIGHT OF SUB-PATCHES AND THEIR NUMBERS ATTENDED

In the preliminary experiments, before the roof of the cage was lowered to be just above the highest sub-patch of prey, the beetle had a tendency to spend most of the time on the roof of the cage, probably because it was attracted to the source of light above. Therefore, in these later experiments in which the beetle seemed to behave naturally, the first hypothesis to be tested was whether the beetle ATTENDED the top-most patches more frequently, possibly because of a continued attraction to the light source above the cage. Only if this hypothesis was rejected could the beetle's response to different prey densities be evaluated on the reasonable assumption that every sub-patch on a particular patch had an equal chance of being ATTENDED.

The numbers of sub-patches at any height ATTENDED per day have been presented in Appendix Table 16, and their totals per replicate have been plotted in Fig. 7.5. L1 represents the topmost position on a patch; L2, L3 represent the subsequent lower positions respectively, while L4 is the bottom position. A statistical test of correlation between the position of the sub-patch and their numbers ATTENDED was found to be NOT significant in each of the four experiments (Fig. 7.5), indicating that the height of the sub-patch did not influence its probability of its being ATTENDED by the beetle.

#### (B) PREY EATEN AND EGGS LAID

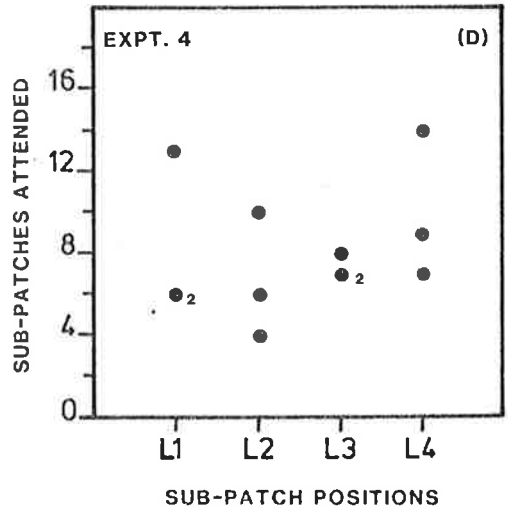
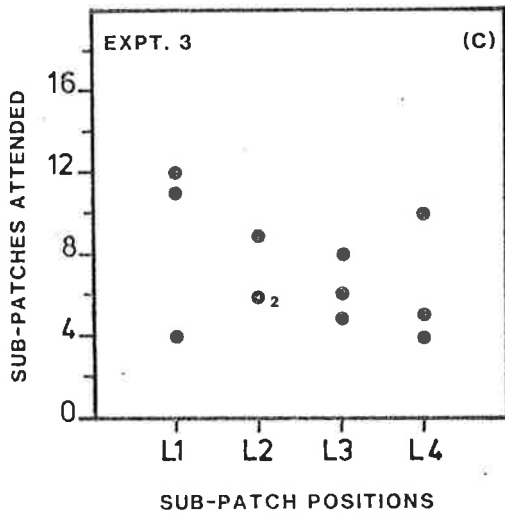
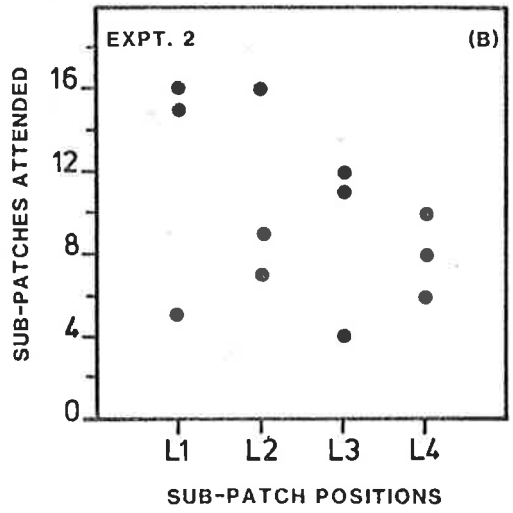
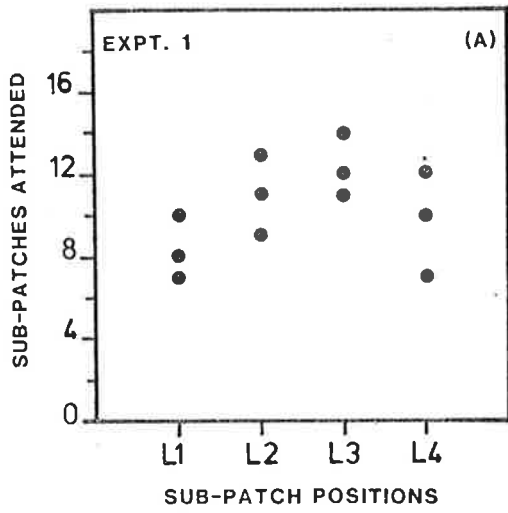
The numbers of prey eaten, eggs laid, the sub-patches ATTENDED for eating prey, the sub-patches ATTENDED for laying eggs, and the total sub-patches ATTENDED have been presented in Appendix Table (17A to 17D). Pooled analyses of variance were conducted on the numbers of prey eaten and the numbers of eggs laid per day from Expts. (1), (3), and (4) in order to test the influence of different types of searching arenas used in the



Fig. 7.5

Numbers of sub-patches ATTENDED at different positions by each of the three beetles (replicates) in each of the four searching efficiency experiments.

- (a) L1 : Top sub-patch,
- (b) L2 : Second from top sub-patch,
- (c) L3 : Third from top sub-patch,
- (d) L4 : Bottom Sub-patch.



different experiments (Tables 7.2 and 7.3). Experiment (2) was left out of these analyses because the prey densities per sub-patch were not comparable. The analyses of variance showed that, across experiments : (a) the numbers of prey eaten per day were not significantly different (Table 7.2A;  $F=0.007$ ;  $P>0.25$ ); but (b) the numbers of eggs laid were significantly different (Table 7.3A;  $F=7.48$ ;  $P<0.005$ ). The mean number of eggs laid in Expt. (1) was significantly smaller than those in both Expts. (3) & (4) (Table 7.3B). However, the mean number of eggs laid were not significantly different between Expts. (3) & (4).

The results, therefore, indicate that the conditions of the experiment (probably the complexity or the size of the searching arena) did not influence the numbers of prey eaten per day but they did influence the numbers of eggs laid per day. There was a significant decline in the number of eggs laid as a result of either making the searching arena more complex (Expt. 3), or increasing the size of the searching arena (Expt. 4). This decline in the numbers of eggs laid could be a result of a significant decline in the total number of sub-patches ATTENDED in Expts. (3) and (4) (see the following section C).

### (C) NUMBERS OF SUB-PATCHES ATTENDED

The sub-patches ATTENDED for eating prey and the sub-patches ATTENDED for laying eggs were not mutually exclusive, i.e. at any single sub-patch ATTENDED, both the acts of eating prey and laying eggs could take place. Therefore, the total numbers of sub-patches ATTENDED was not equal to the sum of the sub-patches ATTENDED for eating prey and the sub-patches ATTENDED for laying eggs.

The total numbers of sub-patches ATTENDED per beetle per day are given in Appendix Table (17A to 17D), and rearranged in Table 7.4B for Expts. (1), (3), and (4). The ANOVA of these data is given in Table 7.4A. It indicated that the mean numbers of sub-patches ATTENDED per day were significantly different across experiments ( $F=9.8$ ;  $P<0.01$ ). The mean number in Expt. (1) was significantly higher than that in either Expt. (3) or Expt. (4) (Table 7.4B). However, the mean number of sub-patches ATTENDED was not significantly different between Expts. (3) and (4). The results, therefore, indicate that there was a significant decline in the total numbers of sub-patches ATTENDED either as the searching arena became more complex (Expt. 3) or as its size increased (Expt. 4). Such a trend

Table 7.2A

POOLED ANALYSIS OF VARIANCE OF THE NUMBERS OF PREY EATEN PER DAY  
IN EXPERIMENTS (1), (3), & (4).

SOURCE	D.F.	S.S	M.S.S.	F	P
BETWEEN EXPTS.	2	0.06	0.03	0.007	>0.25
BETWEEN DAYS	3	39.64	13.21	3.374	<0.05
EXPTS. x DAYS	6	17.94	2.99	0.764	>0.25
ERROR	24	94.00	3.92		
TOTAL	35	151.64	4.33		

Table 7.2B

NUMBERS OF PREY EATEN PER DAY BY EACH BEETLE (=REP)

DAYS	REP.	EXPT.(1)	EXPT.(3)	EXPT.(4)	MEAN
(1)	1	6	8	7	7.67
	2	9	12	6	
	3	7	6	8	
(2)	1	7	9	9	10.11
	2	14	10	10	
	3	13	9	10	
(3)	1	9	10	10	7.89
	2	7	8	8	
	3	5	5	9	
(4)	1	8	8	11	9.56
	2	12	10	8	
	3	9	10	10	
MEAN PREY EATEN/DAY		8.83a	8.75a	8.83a	

Means with same letter not significantly different at  $P < 0.05$ .

Table 7.3A

POOLED ANALYSIS OF VARIANCE OF THE NUMBERS OF EGGS LAID PER DAY  
IN EXPERIMENTS (1), (3), & (4).

SOURCE	D.F.	S.S	M.S.S.	F	P
BETWEEN EXPTS.	2	696.89	348.44	7.47	<0.005
BETWEEN DAYS	3	165.00	55.00	1.18	<0.05
EXPTS. x DAYS	6	231.33	38.56	0.83	<0.05
ERROR	24	1118.67	46.61		
TOTAL	35	2211.89	63.20		

Table 7.3B

NUMBERS OF EGGS LAID PER DAY BY EACH BEETLE (=REP)

DAYS	REPS.	EXPT.(1)	EXPT.(3)	EXPT.(4)	MEANS
(1)	1	25	23	20	26.78
	2	48	26	18	
	3	26	34	21	
(2)	1	26	25	27	29.22
	2	45	28	26	
	3	33	25	28	
(3)	1	40	32	29	32.22
	2	33	26	24	
	3	45	31	30	
(4)	1	30	28	32	31.56
	2	51	27	39	
	3	32	17	28	
MEAN EGGS LAID/DAY		36.17a	26.83b	26.83b	

Means with same letter not significantly different  
at P<0.05 (L.S.D.= 4.77; N=12).

Table 7.4A

POOLED ANALYSIS OF VARIANCE OF THE TOTAL NUMBERS OF SUB-PATCHES ATTENDED PER DAY IN EXPERIMENTS (1), (3), & (4).

SOURCE	D.F.	S.S	M.S.S.	F	P
BETWEEN EXPTS.	2	63.72	31.86	9.80	<0.01
BETWEEN DAYS	3	28.97	9.66	2.97	>0.05
EXPTS. x DAYS	6	30.28	5.05	1.55	>0.05
ERROR	24	78.00	3.25		
TOTAL	35	200.97	5.74		

Table 7.4B

TOTAL NUMBER OF SUB-PATCHES ATTENDED PER DAY BY EACH BEETLE (=REP)

DAYS	REPS.	EXPT.(1)	EXPT.(3)	EXPT.(4)	MEANS
(1)	1	9	6	8	7.00
	2	8	7	5	
	3	6	8	6	
(2)	1	9	7	7	8.78
	2	12	7	11	
	3	10	8	8	
(3)	1	11	9	9	9.11
	2	11	6	10	
	3	9	8	9	
(4)	1	13	6	9	9.22
	2	16	7	11	
	3	10	7	4	
MEAN S/PATCHES ATTENDED/DAY		10.33a	7.17b	8.08b	

Means with same letter not significantly different at  $P < 0.05$  (L.S.D. = 1.26; N=12).

may be expected because an increase in either the complexity or the size of the searching arena would increase the transit time between patches and sub-patches, thereby reducing the total numbers of sub-patches ATTENDED within a fixed period of time.

Another question of interest was whether the number of prey eaten was a function of the number sub-patches ATTENDED for this purpose? And similarly, was the number of eggs laid a function of the number of sub-patches ATTENDED for that purpose? The numbers of sub-patches ATTENDED for eating prey were plotted against the numbers of prey eaten (Fig. 7.6), and the slope of the regression lines were found to be significant in Expts. (1) and (2) but not significant in Expts. (3) and (4). There is some indication, therefore, that the number of sub-patches ATTENDED for eating prey increased with an increase in the number of prey eaten. The numbers of sub-patches ATTENDED for laying eggs were plotted against the numbers of eggs laid (Fig. 7.7); the slopes of the regression lines were significant in all the four experiments, which indicated that the number of sub-patches ATTENDED for laying eggs also increased with an increase in the number of eggs laid.

From the above relationships, it can be inferred that when the beetle lays more eggs, it does not dump them on a few sub-patches but finds more sub-patches and distributes them more evenly; and if enough sub-patches are not found, the numbers of eggs that are laid decline. Such a behaviour would increase the chances of survival of its progeny by lowering intra-species competition in the form of cannibalism, which is a common occurrence in predatory Coccinellids.

#### (D) DIFFERENTIAL RESPONSE IN SUB-PATCHES ATTENDED

Appendix Table (18A to 18D) gives the numbers of sub-patches of different prey densities that were ATTENDED for eating prey (SPPE), those that were ATTENDED for laying eggs (SPEL), and the total sub-patches ATTENDED (TSPA) in each of the four experiments. To test the beetle's differential response in the selection of sub-patches of different prey densities, the numbers of sub-patches of any prey density ATTENDED as a proportion of the total sub-patches ATTENDED was plotted against prey density per sub-patch (Figs. 7.8, 7.9, and 7.10). The estimated proportions were obtained from the totals over four days (Appendix Table 18A to 18D) in the manner described below for beetle 1 in Expt. (1):

Fig. 7.6

Numbers of sub-patches ATTENDED by each of the three beetles (replicates) for eating prey, plotted against the numbers of prey eaten, for each of the four searching efficiency experiments. The lines were fitted by linear regression with the following results :

- (A) Experiment 1 :  $Y = 0.46X + 1.54$ ;  $t=5.32$ ,  $P<0.0001$ .
- (B) Experiment 2 :  $Y = 0.71X - 0.65$ ;  $t=4.88$ ,  $P<0.001$ .
- (C) Experiment 3 :  $Y = 0.12X + 3.88$ ;  $t=0.94$ ,  $P>0.05$ .
- (D) Experiment 4 :  $Y = 0.21X + 3.13$ ;  $t=0.90$ ,  $P>0.05$ .

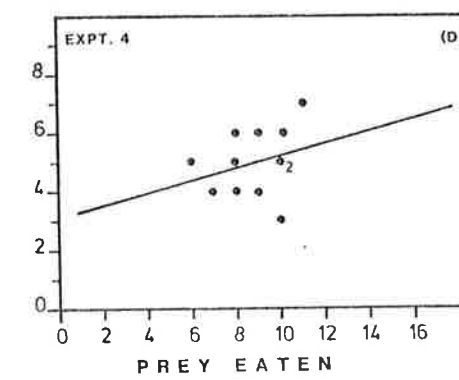
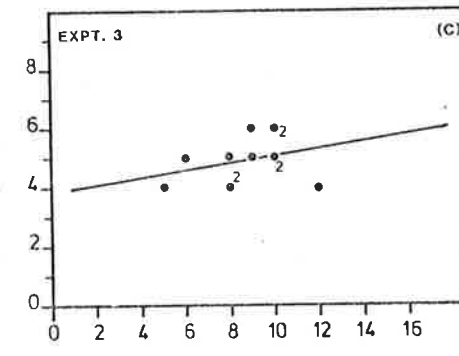
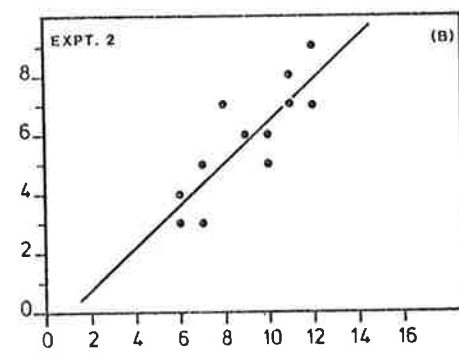
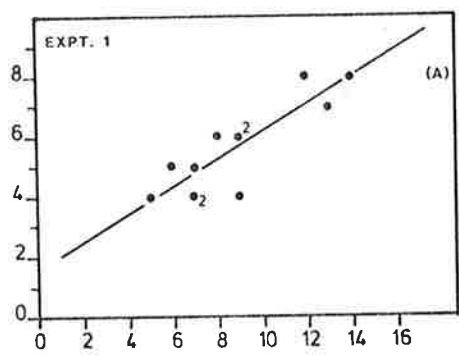
Fig. 7.7

Numbers of sub-patches ATTENDED by each of the three beetles (replicates) for laying eggs, plotted against the numbers of eggs laid, for each of the four searching efficiency experiments. The lines were fitted by linear regressions with the following results :

- (A) Experiment 1 :  $Y = 0.18X + 2.82$ ;  $t=2.54$ ,  $P<0.05$ .
- (B) Experiment 2 :  $Y = 0.20X - 0.37$ ;  $t=2.31$ ,  $P<0.05$ .
- (C) Experiment 3 :  $Y = 0.16X + 2.19$ ;  $t=2.45$ ,  $P<0.05$ .
- (D) Experiment 4 :  $Y = 0.19X + 1.86$ ;  $t=2.05$ ,  $P>0.05$ .

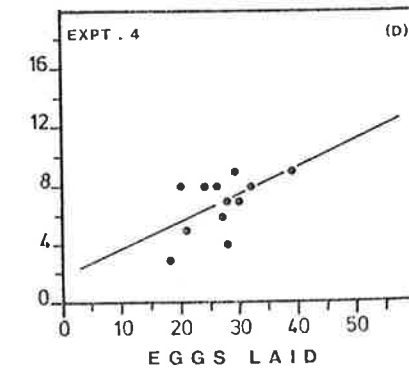
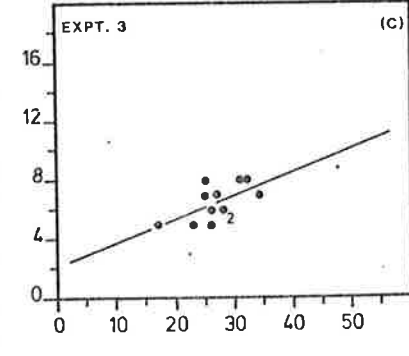
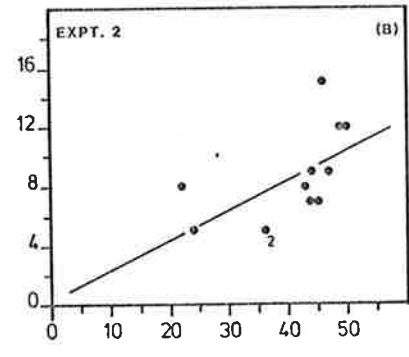
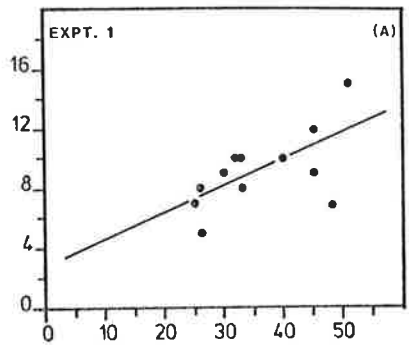


SUB-PATCHES ATTENDED FOR EATING PREY



PREY EATEN

SUB-PATCHES ATTENDED FOR LAYING EGGS



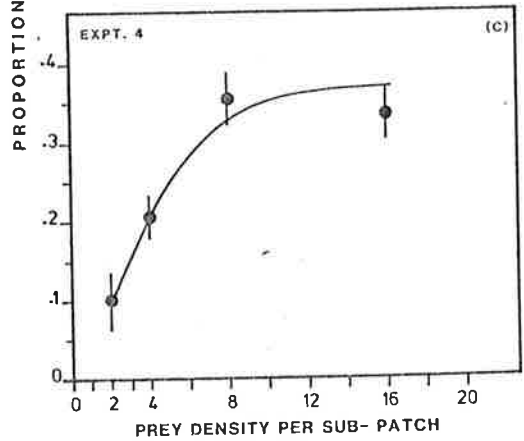
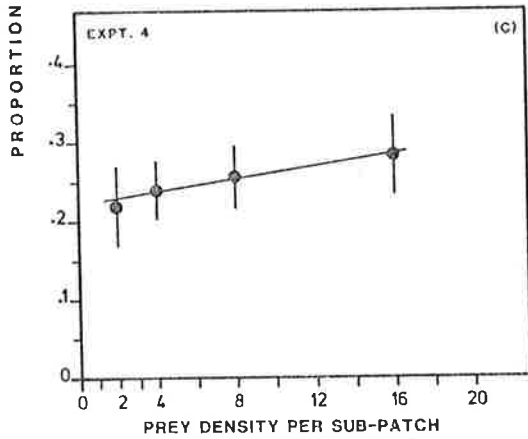
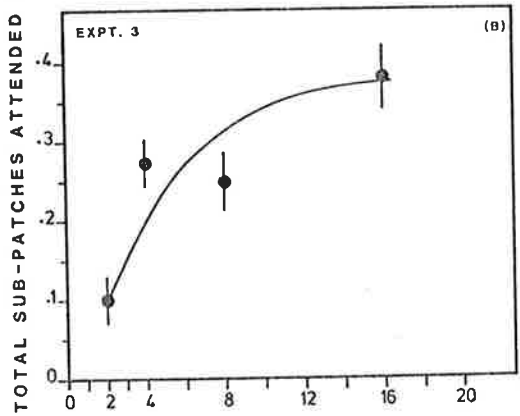
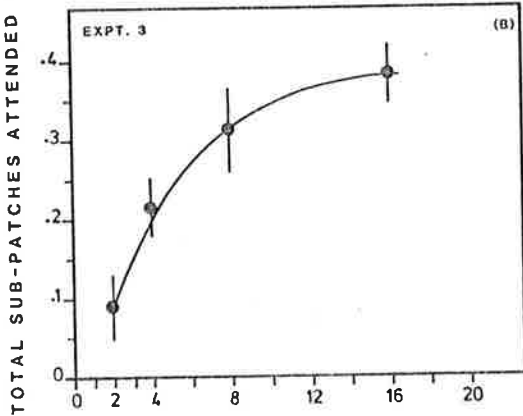
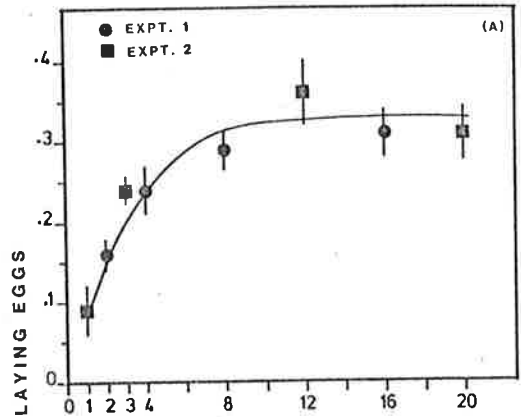
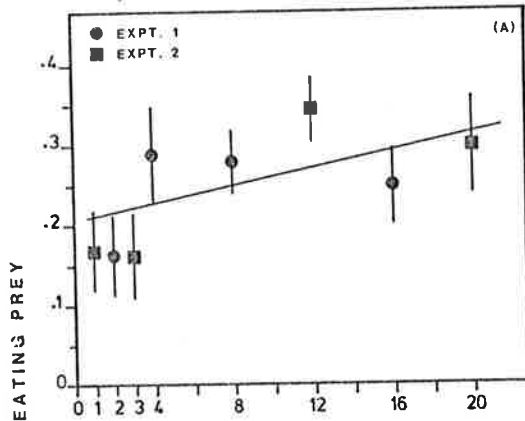
EGGS LAID

Fig. 7.8

Means  $\pm$  S.E. of the proportion of total sub-patches ATTENDED per day for eating prey at patches of different prey densities; in the searching efficiency experiments 1 plus 2 (A), 3 (B), and 4 (C).

Fig. 7.9

Means  $\pm$  S.E. of the proportion of total sub-patches ATTENDED per day for laying eggs at patches of different prey densities; in the searching efficiency experiments 1 plus 2 (A), 3 (B), and 4 (C).



FROM TOTALS OVER FOUR DAYS FOR BEETLE (1) IN EXPT. (1)			
PREY DENS. PER S/PATCH	S/PATCHES ATTENDED FOR EATING PREY	S/PATCHES ATTENDED FOR LAYING EGGS	TOTAL S/PATCHES ATTENDED
2	5	7	10
4	6	7	8
8	6	11	14
16	4	9	10
TOTALS	21	34	42

For the data in Fig. 7.8A the proportions were estimated for beetle (1) Expt. (1) as

$$5/21 (=0.24), \quad 6/21 (=0.29), \quad 6/21 (=0.29), \quad 4/21 (=0.19).$$

For the data in Fig. 7.9A the proportions were estimated for beetle (1) Expt. (1) as

$$7/34 (=0.21), \quad 7/34 (=0.21), \quad 11/34 (0.32), \quad 9/34 (0.27).$$

For the data in Fig. 7.10A the proportions were estimated for beetle (1) Expt. (1) as

$$10/42 (=0.24), \quad 8/42 (=0.19), \quad 14/42 (=0.33), \quad 10/42 (=0.24).$$

The means  $\pm$  S.E. of these proportions, estimated over the three replicates, have been plotted in Figs. 7.8, 7.9, and 7.10. The X-Axis in each figure represents the prey density per sub-patch while the Y-Axis represents the means of the proportions.

(i) PROPORTION OF SUB-PATCHES ATTENDED FOR EATING PREY

As mentioned earlier, the data from Expts. (1) and (2) were combined to obtain more points because the prey densities tested were complementary. The proportions of sub-patches ATTENDED for eating prey (Fig. 7.8A) suggest a linear increase in this proportion with an increase in prey density per sub-patch. A regression line fitted to the data points showed a significant positive slope ( $b=0.0056$  ;  $P<0,05$ ) and a significant positive correlation ( $r=0.63$  ;  $P<0.05$ ). Similar results from Expt. (3) showed a decelerating rise to an upper asymptote (Fig. 7.8B), while the results from Expt. (4) also showed a significant positive slope ( $b=0.004$  ;  $P<0.05$ ) from a linear regression line fitted to the data points (Fig. 7.8C).

(ii) PROPORTION OF SUB-PATCHES ATTENDED FOR LAYING EGGS

The proportion of sub-patches ATTENDED for laying eggs showed a decelerating rise to an upper asymptote for the combined data from Expts. (1) & (2), and also for those from Expts. (3) and (4) (Fig. 7.9).

(iii) PROPORTION OF TOTAL SUB-PATCHES ATTENDED

The proportion of total sub-patches ATTENDED followed trends similar to those of the proportion of sub-patches ATTENDED for laying eggs in all the four experiments (Fig. 7.10).

Thus, the general trend in the relationships between the proportion of sub-patches ATTENDED and the prey density per sub-patch showed an increase with an increase in prey density per patch. In most cases, the graphs showed a decelerating rise to an upper asymptote, and were similar in shape, therefore, to Holling's Type-II Functional Response curve.

(E) THE PATCH FINDING EFFICIENCY

The Patch Finding Efficiency (PFE) of the beetle was estimated from the following expression (discussed in section 7.1.3). In the estimation of the PFE, the values of the parameters were as follows :

$$PFE = (1/PTV).(n/N)$$

P (the No. of searching predators) = 1

T (the duration of search) = 1 day

N (the No. of sub-patches of one prey density present)	= 7
V (volume of the searching arena)	
(i) for Expts. (1), (2), and (3)	= (1.5 x 1.5 x 1.1 = 2.475 cu m)
(ii) for Expt. (4)	= (3 x 3 x 1.1 = 9.9 cu m)

The estimates of PFE for all the four experiments have been tabulated in Appendix Table 19, and are plotted in Fig. 7.11. Generally their trends were similar to those for the total sub-patches ATTENDED (Fig. 7.10), i.e. the PFE values showed a decelerating rise to an upper asymptote. There was a marked difference between the PFE values from Expt. (4) and Expts. (1), (2), and (3). The marked decline in PFE values in Expt. (4) is a result of : (a) a significant decline in the total number of sub-patches ATTENDED per day (Table 7.3), and (b) an increase in the volume of the searching arena from 2.475 cu m, in the first three experiments, to 9.9 cu m in Expt. (4). Generally, one would expect a decline in the number of sub-patches ATTENDED as the searching arena was made more complex (by introducing plants in Expt. (3) or when its size was increased (Expt. 4). Indeed, an analysis of variance of the total numbers of sub-patches ATTENDED per day (Table 7.3) showed that they were significantly higher in Expt. (1) than in either Expts. (3) or (4).

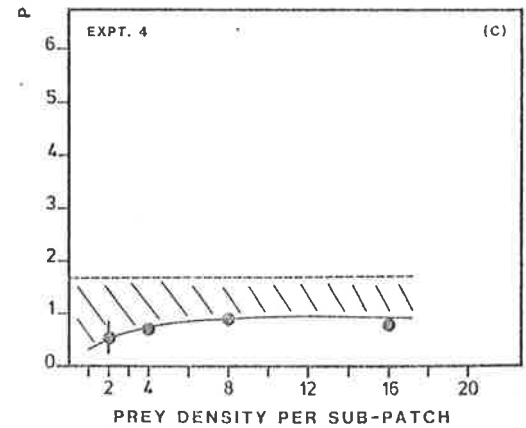
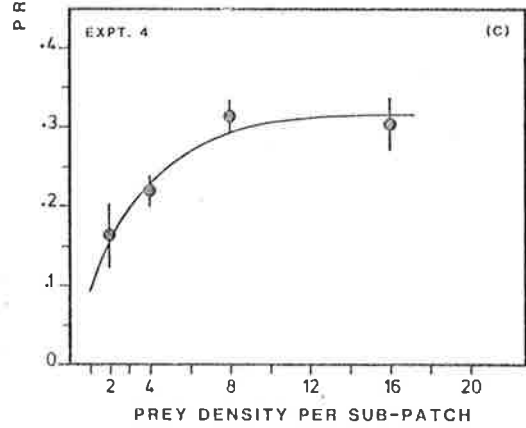
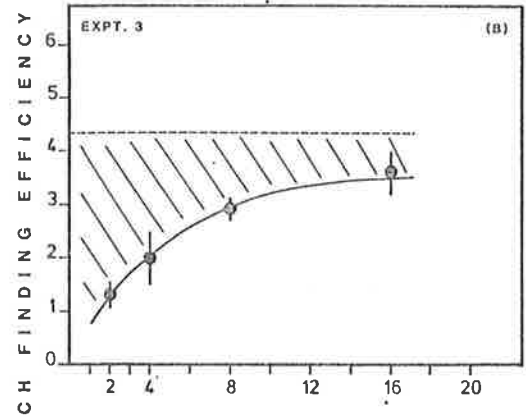
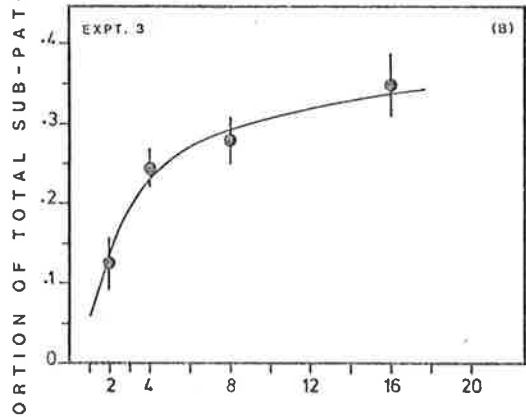
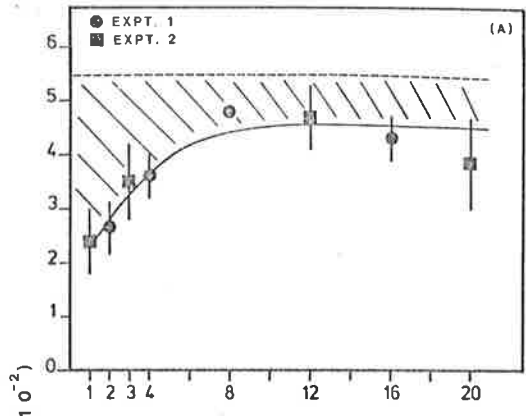
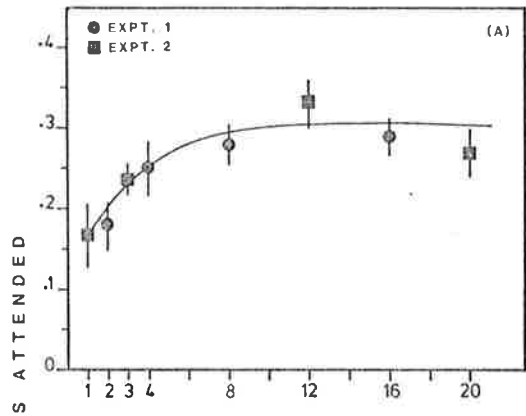
The results for the Patch Finding Process, therefore, indicate that in patch selection, the beetle shows a differential response to sub-patches of different prey densities, which suggests that the beetle is able to distinguish between the sub-patches from a distance, even before it discovers them. One may, therefore, conclude that the searching behaviour of the beetle is not RANDOM but ORIENTED towards sub-patches of higher prey density. Parasites are known to be attracted to patches of higher host density under the influence of the host's sex pheromones or kairomones (see Chapter 1). However, the likelihood of Rodolia responding to any such stimulus appears to be low. Coccinellids, in general, are known to search RANDOMLY for their prey to the extent that they have to bump into their prey to notice them (see Chapter 8.2). A preliminary experiment conducted to test this hypothesis on Rodolia showed that the beetle responded to a prey individual only when it had come to within a few mm of the prey. If the searching by Rodolia is truly random, how does one explain the

Fig. 7.10

Means  $\pm$  S.E. of the total sub-patches of a particular prey density ATTENDED, as a proportion of the TOTAL sub-patches ATTENDED of all prey densities per day; in the searching efficiency experiment 1 plus 2 (A), 3 (B), and 4 (C).

Fig. 7.11

The estimates of Patch Finding Efficiencies (PFE) (Means  $\pm$  S.E.) of the beetle to patches of different prey densities ATTENDED; in searching efficiency experiments 1 and 2 (A), 3 (B), and 4 (C). The straight lines were fitted by eye. The dashed lines are hypothetical lines for PFE for sub-patches VISITED.





relatively higher attendance of sub-patches of higher prey density in the experiments on searching efficiency?

Perhaps the differential response to sub-patches of different prey densities is only apparent because we are only considering the number of sub-patches ATTENDED and not the number of sub-patches VISITED. It might well be that the number of sub-patches of any prey density VISITED is not different and that the discovery of sub-patches is indeed random. Furthermore, once a sub-patch has been discovered, the searching behaviour at the sub-patch may still remain random, i.e. the beetle has to bump into a prey to detect it. Since, at a higher prey density, the chance of the beetle bumping into a prey would be much higher than that at a lower prey density, the beetle's chance of ATTENDING the former would also be greatly enhanced. Moreover, after Rodolia has detected its first prey, its searching behaviour may change as does that of many parasitoids and predators which show an increase in what is called AREA RESTRICTED SEARCH, as a result of Orthokinetic and Klinokinetic responses (see Chapter 8.2). The area restricted search further increases the chance of the predator detecting more prey at sub-patches of higher prey density.

At lower prey densities, the beetle would probably leave the sub-patch after a short unsuccessful search. Thus, if we had data on the number of sub-patches VISITED as well, and the PFE estimates based on them had been plotted in Fig. 7.11, we might expect the PFEs to fall on a horizontal line above the upper asymptote of the curve fitted to the PFEs based on the number of sub-patches ATTENDED. The area between the two lines (see Fig. 7.12) would then represent the difference between the two processes -- sub-patches VISITED and sub-patches ATTENDED.

The importance of distinguishing between sub-patches VISITED and sub-patches ATTENDED is further elaborated in Chapter 8.1, where it was found that sub-patches of lower prey density were, in fact, VISITED more often than those of higher prey density. Such a behavior, it has been argued, represents the beetle's persistence in searching sub-patches of lower prey density.

#### 7.3.1.2.2 THE ATTACK COMPONENT OF SEARCHING EFFICIENCY

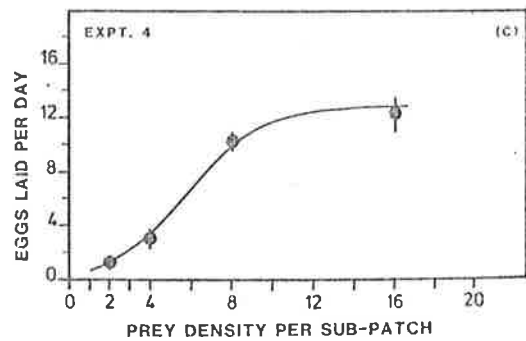
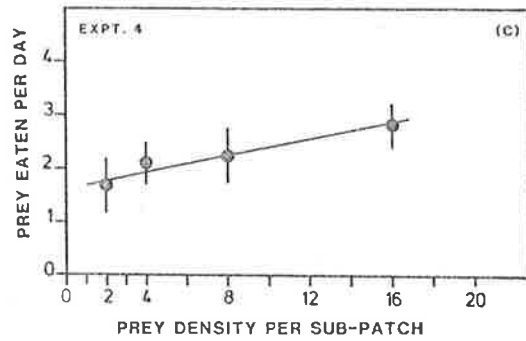
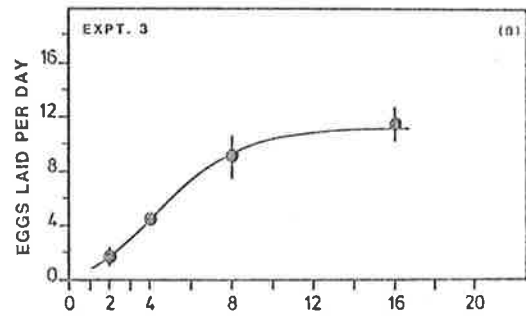
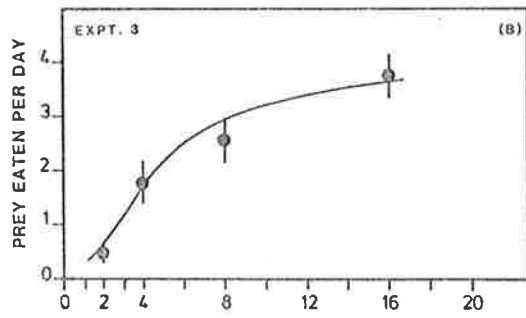
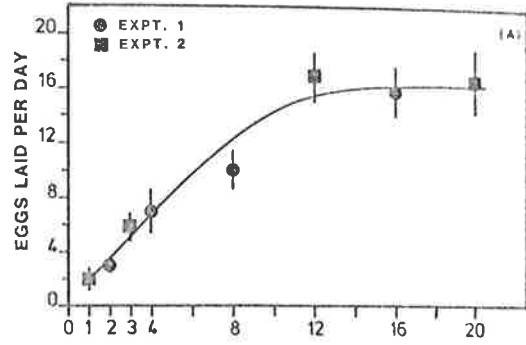
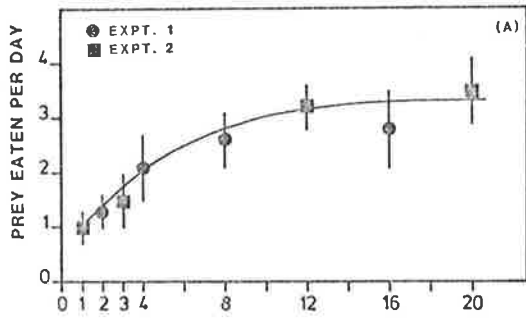
An attack on prey can only take place after a sub-patch containing prey has been discovered, i.e. after the PATCH FINDING PROCESS. Therefore,

Fig. 7.12

The numbers of prey eaten per day (means  $\pm$  S.E.) at patches of different prey densities considering all the sub-patches present; in searching efficiency experiments 1 plus 2 (Fig. A), 3 (Fig. B), and 4 (Fig. C). In Figs. (A) and (B) the lines were fitted by eye, but in Fig. (C) the straight line was fitted by regression ( $Y = 0.076X + 1.64$ ;  $t=6.23$ ,  $P<0.05$ ).

Fig. 7.13

The numbers of eggs laid per day (means  $\pm$  S.E.) at patches of different prey densities considering all the sub-patches present; in searching efficiency experiments 1 plus 2 (Fig. A), 3 (Fig. B), and 4 (Fig. C). The lines were fitted to the data points in each figure by eye.



having discussed the results of the Patch Finding Process, we may now consider a beetle's response at the sub-patches which it discovered.

The numbers of prey eaten and the the numbers of eggs laid by the beetles in each of the four experiments have been presented in Appendix Table (15a to 15D). The mean numbers of prey eaten and eggs laid have been calculated over all the sub-patches of a particular prey density present, and not only those ATTENDED. Thus the means have been estimated over 4 days x 3 replicates (beetles) (see also Table 7.1). In Fig. 7.12 the mean number of prey eaten, and in Fig. 7.13 the mean number of eggs laid in relation to prey density per sub-patch have been plotted. Once again the data for Expts. (1) and (2) have been pooled and plotted in the "A" series figures since the prey densities tested were complementary.

(A) PREY EATEN IN RELATION TO PREY DENSITY (ATTACK RATE)

The mean number of prey eaten was found to increase with an increase in prey density per sub-patch and the curve decelerated to an upper asymptote in Expts. (1), (2), and (3) (Figs. 7.12A and 7.12B), and showed a linear relationship in Expt. (4) (Fig. 7.12C). Thus, except in Expt. (4), the general trend appears analogous to Holling's Type-II functional response.

(B) EGGS LAID IN RELATION TO PREY DENSITY (OVIPOSITIONAL POTENTIAL)

The mean number of eggs laid was also found to increase with an increase in prey density per sub-patch, such that the plotted curve decelerated to an upper asymptote in each of the four experiments (Fig. 7.13). So these curves were also analogous to Holling's Type-II functional response curve.

However, though the shape of the curves appear similar to that of the Type-II functional response, both for the number of prey eaten and the number of eggs laid, the justifications for such a trend in the present case may not necessarily be the same. In the type-II response, the decelerating rise in the numbers of prey killed to an upper asymptote is explained on the grounds that with an increase in prey density, HANDLING TIME starts becoming a limiting factor which is responsible for forcing the curve to an upper asymptote. Such an explanation may not necessarily be true in the present case. This is because, unlike functional response

experiments, the predator here was not provided with only one prey density at a time nor was it confined to that prey density for a fixed period of time. In the present set up, the predator had access to all the prey densities at the same time and it was also free to arrive at or leave a prey density (sub-patch) of its own accord. Therefore, the present system was much more complex than any conventional functional response experiment. In this more complex system, detailed observations on the predator's behaviour at sub-patches of different prey densities are needed to explain the trend. The behavioural results presented in Chapter 8.1 provide an explanation.

#### 7.3.1.2.3 ESTIMATION OF SEARCHING EFFICIENCY (THE OVERALL RESPONSE)

The results on the two separate processes involved in the evaluation of the searching efficiency of a predator, viz. (a) Patch Finding Process, and (b) Attack Rate after a patch has been discovered, were presented in sections 7.3.1.1 and 7.3.1.2 respectively. However, what is really needed is a quantification of the combined influence of both the processes in order to obtain a realistic estimate of the searching efficiency of the beetle. In the following, the results of the two processes have been integrated to obtain a measure of searching efficiency. To achieve this, I considered only the number of prey eaten and the number of eggs laid in those sub-patches that had been ATTENDED by the beetle. This approach was intuitively more realistic, because the number of sub-patches which the beetle did not ATTEND are not relevant in the evaluation of searching efficiency

In Table 7.5 are presented the total number of prey eaten and the corresponding number of sub-patches ATTENDED for eating prey, and also the total number of eggs laid and the corresponding number of sub-patches ATTENDED for laying eggs, summed over the whole experimental period (i.e. 4 days x 3 replicates) at sub-patches of each of the different prey densities, for each of the four experiments (see also Appendix Table 15A to 15D for details). The data in Table 7.5 show that, at any prey density, the number of sub-patches attended for eating prey is not identical to the number of sub-patches attended for laying eggs, because the sub-patch from which prey were eaten was not invariably the sub-patch at which eggs were laid, or vice versa. There were, however, some sub-patches at which both

Table 7.5

THE TOTAL NUMBER OF PREY EATEN (P.E.) WITH CORRESPONDING NUMBERS OF SUB-PATCHES ATTENDED FOR EATING PREY (SPPE) AND THE TOTAL NUMBER OF EGGS LAID (E.L.) WITH CORRESPONDING NUMBERS OF SUB-PATCHES ATTENDED FOR LAYING EGGS (SPEL) BY THREE BEETLES OVER FOUR DAYS IN SEARCHING EFFICIENCY EXPERIMENTS 1, 2, 3, AND 4.

EXPT.	PREY DENS.	P.E.	SPPE	$\frac{P.E.}{SPPE} \pm S.E.*$	E.L.	SPEL	$\frac{E.L.}{SPEL} \pm S.E.*$
	2	16	11	$1.46 \pm 0.16$	37	17	$2.18 \pm 0.27$
EXPT.	4	25	20	$1.25 \pm 0.12$	83	27	$3.07 \pm 0.39$
(1)	8	31	19	$1.63 \pm 0.16$	120	32	$3.75 \pm 0.40$
	16	34	17	$2.00 \pm 0.28$	189	34	$5.56 \pm 0.52$
	1	12	12	$1.00 \pm 0.00$	23	10	$2.30 \pm 0.52$
EXPT.	3	18	15	$1.20 \pm 0.11$	68	25	$2.72 \pm 0.39$
(2)	12	38	23	$1.65 \pm 0.15$	200	37	$5.41 \pm 0.65$
	20	42	20	$2.10 \pm 0.22$	199	30	$6.63 \pm 0.68$
EXPT.	2	6	5	$1.20 \pm 0.20$	20	8	$2.50 \pm 0.60$
(3)	4	22	13	$1.69 \pm 0.21$	54	21	$2.57 \pm 0.36$
	8	31	19	$1.63 \pm 0.19$	109	20	$5.45 \pm 0.69$
	16	45	22	$2.05 \pm 0.21$	129	29	$4.79 \pm 0.52$
	2	20	14	$1.43 \pm 0.14$	15	10	$1.50 \pm 0.17$
EXPT.	4	25	14	$1.79 \pm 0.26$	35	18	$1.94 \pm 0.26$
(4)	8	27	16	$1.69 \pm 0.27$	124	28	$4.43 \pm 0.54$
	16	34	16	$2.13 \pm 0.24$	148	26	$5.69 \pm 0.67$

\* for method of estimation of S.E. see text.

feeding and oviposition had taken place. Since feeding and oviposition are independent activities performed by the beetle and are influenced by different sets of stimuli, they have been considered separately in the evaluation of searching efficiency. Thus, two values of searching efficiency were obtained, one based on the beetle's ATTACKING potential, and the other based on the beetle's OVIPOSITIONAL potential.

By dividing the total number of prey eaten, at sub-patches of a particular prey density, by the number of sub-patches of that prey density ATTENDED for eating prey (and similarly, dividing the total number of eggs laid at sub-patches of a particular prey density ATTENDED for laying eggs), the two processes, viz. (a) the Patch Finding Process and (b) The Attack Rate, are integrated into one process. The resultant values are given in Table 7.5. The standard errors given in Table 7.5 were obtained by the following method (see raw data presented in Appendix Table 15A to 15D) :-

The number of prey eaten at each sub-patch ATTENDED for eating prey was considered as a separate entity. Thus, for each sub-patch ATTENDED for eating prey, the number of prey eaten was divided by one -- the single sub-patch ATTENDED for eating prey (dividing the number by one, therefore, made no difference). The prey eaten at each sub-patch ATTENDED for eating prey was transformed in this manner. The means are, therefore, essentially the same as the values obtained by dividing the total number of prey eaten by the total number of sub-patches ATTENDED for eating prey.

Similar procedures were adopted for data on the number of eggs laid and sub-patches ATTENDED for laying eggs (Table 7.5).

#### (A) SEARCHING EFFICIENCY BASED ON THE ATTACK POTENTIAL

The data on the number of prey eaten per sub-patch ATTENDED for eating prey at different prey densities in each of the four experiments have been plotted against prey density in Fig. 7.14. The trends were obviously linear, so regression lines were fitted to the data points. The slope of each fitted line (Table 7.6B) represents the rate at which the predator finds the sub-patches and ATTACKS prey in relation to prey density while the apparent intercepts provide estimates of the predator's response to patches of lower prey density for ATTACKING PREY. Thus, both the slopes and the intercepts provide information about the SEARCHING EFFICIENCY of the predator on the basis of its ATTACKING potential (see

Fig. 7.14

The numbers of prey eaten per sub-patch ATTENDED (means  $\pm$  S.E.) considering only those sub-patches of different prey densities at which prey were eaten in searching efficiency experiments 1, 2, 3, and 4. The lines were fitted by linear regression :

(A) Expt. 1 :  $Y = 0.047X + 1.23$ ;  $t=3.27$ ,  $P>0.05$ .

(B) Expt. 2 :  $Y = 0.056X + 0.99$ ;  $t=19.1$ ,  $P<0.005$ .

(C) Expt. 3 :  $Y = 0.05X + 1.27$ ;  $t=2.68$ ,  $P>0.05$ .

(D) Expt. 4 :  $Y = 0.042X + 1.45$ ;  $t=2.86$ ,  $P>0.05$ .

Fig. 7.15

The numbers of eggs laid per sub-patch ATTENDED (means  $\pm$  S.E.) considering only those sub-patches of different prey densities at which eggs were laid in searching efficiency experiments 1, 2, 3, and 4. The lines were fitted by linear regression :

(A) Expt. 1 :  $Y = 0.23X + 1.92$ ;  $t=11.32$ ,  $P<0.005$ .

(B) Expt. 2 :  $Y = 0.24X + 2.13$ ;  $t= 9.99$ ,  $P<0.005$ .

(C) Expt. 3 :  $Y = 0.18X + 2.48$ ;  $t= 1.53$ ,  $P>0.05$ .

(C) Expt. 4 :  $Y = 0.31X + 1.07$ ;  $t= 4.55$ ,  $P<0.05$ .



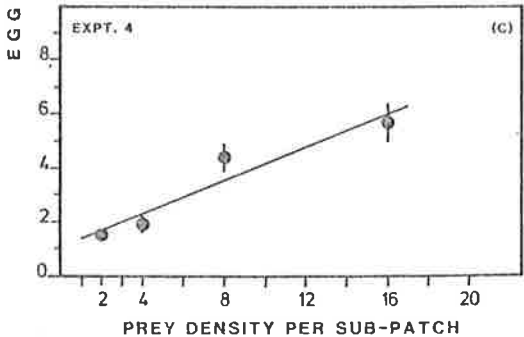
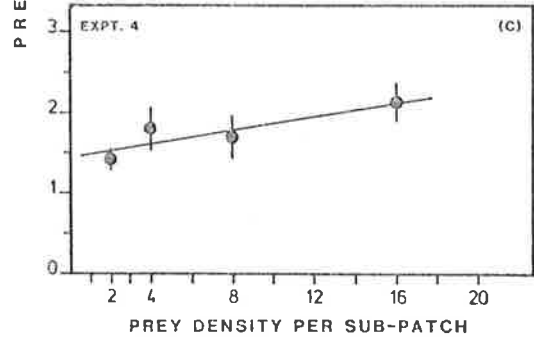
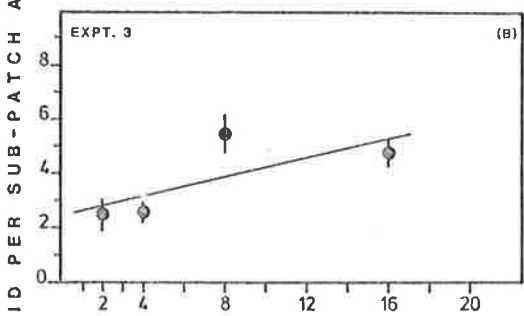
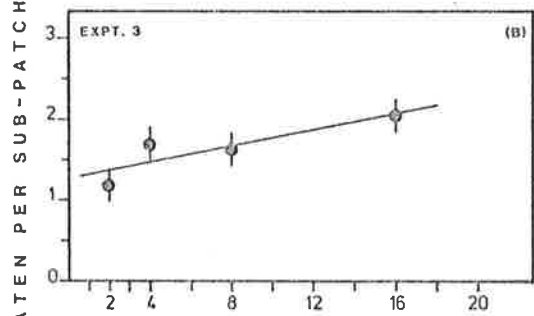
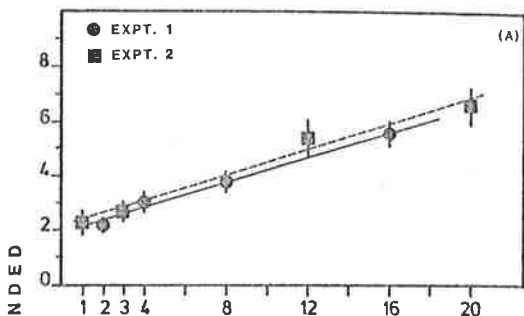
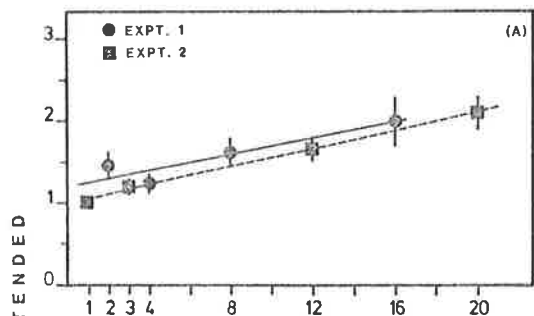


Table (7.6A)

COMPARISON OF SLOPES FROM FIGURES (7.12) AND (7.13) WITH  $b=0$ , AND COMPARISON OF SLOPES AND ELEVATIONS ACROSS SEARCHING EFFICIENCY EXPERIMENTS 1, 2, 3, AND 4.

EXPT.	ATTACK POTENTIAL		OVIPOSITIONAL POTENTIAL	
	t	P	t	P
1	3.27	>0.05	11.32	<0.0005
2	19.06	<0.005	9.99	<0.005
3	2.68	>0.05	1.53	>0.05
4	2.86	>0.05	4.55	<0.05

COMPARISON OF SLOPES ACROSS EXPERIMENTS

F = 0.24 ; P>0.25

F = 0.57 ; P>0.25

COMPARISON OF ELEVATIONS ACROSS EXPERIMENTS

F = 3.91 ; P<0.05

F = 0.41 ; P>0.25

Table (7.6B)

ESTIMATES OF SLOPES AND INTERCEPTS FROM REGRESSION LINES PLOTTED IN FIGURES (7.12) AND (7.13)

EXPT.	ATTACK POTENTIAL		OVIPOS. POTENTIAL	
	SLOPE	ELEVATION	SLOPE	ELEVATION
1	0.047a	1.23b	0.230c	1.92d
2	0.056a	0.99	0.237c	2.13d
3	0.050a	1.27b	0.180c	2.48d
4	0.042a	1.45b	0.310c	1.07d
Common Reg.	0.0501			
Total Reg.			0.241	1.89

Values followed by the same letter are not significantly different at  $P<0.05$ .



sections 7.3.1.2.3C and 7.3.4 below).

The slopes of the fitted lines in Fig. 7.14 were compared with  $b=0$  (Table 7.6A). Only in Expt. (2) was the slope significantly different from zero, indicating that in three out of four experiments the rate at which sub-patches were found and prey attacked did not increase with an increase in prey density per sub-patch.

The slopes and intercepts of the fitted lines were also compared across experiments (Table 7.6A). It was found that the slopes from the four experiments were not significantly different from each other ( $P>0.05$ ), but the intercepts were significantly different ( $P<0.05$ ). The intercept for the fitted line in Expt. (2) was significantly different from that of all the other experiments (Table 7.6B) perhaps because the range of densities in this experiment was different from that in the other three experiments. The lack of significant difference between Expts. (1), (3), and (4) indicates, however, that the searching efficiency of the beetle was not altered by changes in the different arenas in the three experiments. A common value of the slope estimated over all the four experiments was 0.0501 which together with the intercepts from the respective experiments provide information about the searching efficiency of Rodolia on the basis of its ATTACKING POTENTIAL.

#### (B) SEARCHING EFFICIENCY BASED ON OVIPOSITIONAL POTENTIAL

The number of eggs laid per sub-patch attended for laying eggs at different prey densities have been plotted in Fig. 7.15, and regression lines were fitted to the data points. The slopes of these fitted lines represent the rates at which the predator finds sub-patches and LAYS EGGS in relation to prey density while the intercepts provide estimates of the predator's response to patches of lower prey density for LAYING EGGS. These slopes and the intercepts provide information about the SEARCHING EFFICIENCY of the predator, this time on the basis of its OVIPOSITIONAL potential (see sections 7.3.1.2.3C and 7.3.4 below).

The slopes of the fitted lines in Fig. 7.15 were compared with  $b=0$  (Table 7.6A). It was found that all the slopes were significantly different from zero except that in Expt. (3), indicating that, in three out of four experiments, the rate at which sub-patches were found and eggs laid increased with an increase in prey density per sub-patch.

The slopes and intercepts of the fitted lines were also compared across experiments (Table 7.6A). It was found that neither the slopes nor the intercepts from the four experiments were significantly different from each other ( $P > 0.25$ ). These results show that the searching efficiency of the beetle based on its OVIPOSITIONAL potential was not affected by changes in the experimental set up that were tested. Therefore, on the basis of the total regression estimated over all the four experiments the common slope was 0.241 and the common intercept was 1.886. The common slope and the common intercept provide information about the searching efficiency of the Rodolia on the basis of its OVIPOSITIONAL POTENTIAL.

It is of considerable importance to know how the female predator distributes its eggs; for the distribution of eggs would markedly influence the future survival of the predator's progeny. Most larval predators are wingless, so the distance that they can cover to search for their prey is very limited. Therefore, the manner in which the adult predator distributes its eggs is of prime importance to the survival and efficiency of the species as a natural enemy. The results presented here indicate that though Rodolia did not exploit patches of different prey density in a differential manner for KILLING prey (except in Expt. 2), it did show a differential response to patches of different prey density in OVIPOSITION, thereby enhancing the chance of survival of its progeny. Therefore, the searching efficiency of Rodolia in terms of its OVIPOSITIONAL potential is of greater significance for supporting the hypothesis that it is a better and more efficient natural enemy.

(C) BIOLOGICAL SIGNIFICANCE OF INTERCEPTS AND SLOPES  
IN FIGURES 7.14 AND 7.15

The slopes of the regression lines in Fig. 7.14 and 7.15 represent the changes in the RATES at which sub-patches are discovered and prey eaten (Fig. 7.14), and changes in the RATES at which sub-patches are discovered and eggs laid (Fig. 7.15) in relation to patches of different prey densities. The intercepts of the regression lines, on the other hand, provide information about the predator's response to sub-patches of lower prey densities. A predator which would show a better response to sub-patches of lower prey densities (higher values of intercept), would be a more effective predator, since sub-patches of lower prey densities are

more difficult to find and so ATTEND (see Chapter 8.1).

A predator may show a high slope demonstrating a high potential of discrimination among patches of different prey densities and a low intercept demonstrating inefficiency in finding patches of lower prey densities, or vice versa. An ideal predator would be one which would show both, a high slope and a high intercept. But predators with a high slope and a low intercept or with a low slope and a high intercept would still be better than those with a low slope and a low intercept. Thus, the slopes and the intercepts are two important parameters describing the searching behaviour of a predator, and so they provide valuable information about the searching efficiency of the predator.

### 7.3.1.3 APPLICATION OF CHESSON'S MODEL TO THE DATA

Chesson's (1982) model was fitted to the data gathered from the four experiments, and estimates were obtained of  $\beta_n$  (the probability that a sub-patch with  $n$  prey is discovered (VISITED) by the beetle) and  $P_n$  (the probability that a particular prey on an ATTENDED sub-patch is eaten given that there are  $n$  prey on the sub-patch) (Appendix Table 20). The estimates of  $\beta_n$  and  $P_n$  are plotted against prey density per sub-patch in Figs. 7.17 and 7.19 respectively. The proportion of sub-patches ATTENDED from those PRESENT (of a particular prey density) (Appendix Table 19) and the proportion of prey eaten per sub-patch ATTENDED were also plotted alongside plots of  $\beta_n$  and  $P_n$ , in separate Figs. 7.16 and 7.18 respectively.

Chesson's model could not be applied to sub-patches with prey density one, and the model produced erroneous results in conditions when the percentage of sub-patches with only one prey eaten became considerably higher than those with more than one prey eaten. Such limitations of the model were pointed out by Chesson (1982) herself. Therefore, the erroneous estimates of  $\beta_n$  and  $P_n$  were ignored.

The proportion of sub-patches ATTENDED from those PRESENT (of a particular prey density), when plotted against prey density per sub-patch, showed a decelerating rise to an upper asymptote in all the four experiments (Fig. 7.16). A similar plot of  $\beta_n$ , on the other hand, did not follow any trend, except in Expt. (3), where it appeared to show a decelerating rise to an upper asymptote (Fig. 7.17). However, both the proportion of prey eaten per sub-patch ATTENDED (Fig. 7.18) and the

Fig. 7.16

Means  $\pm$  S.E. of the proportion of sub-patches ATTENDED from those of a particular prey density PRESENT (=7) per day; in searching efficiency experiments 1 plus 2 (Fig. A), 3 (Fig. B), 4 (Fig. C). The lines in the figures were fitted to the data points by eye.

Fig. 7.17

The estimates of  $\beta_n$  (means  $\pm$  S.E.) from fitting Chesson's (1982) model to the number of sub-patches of different prey densities that were ATTENDED; from searching efficiency experiments 1, plus 2 (Fig. A), 3 (Fig. B), and 4 (Fig. C).

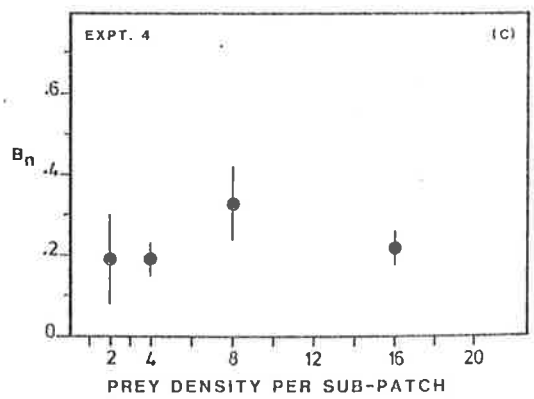
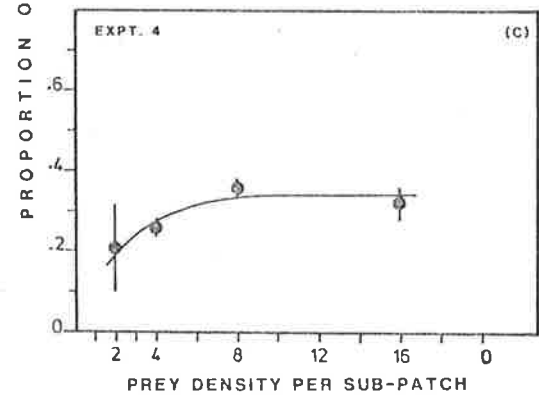
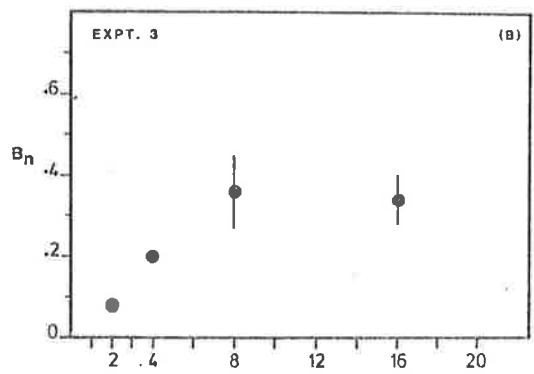
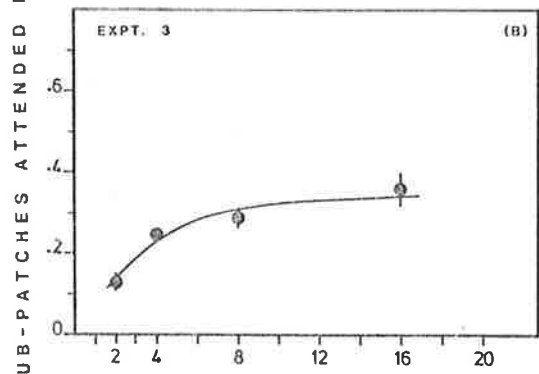
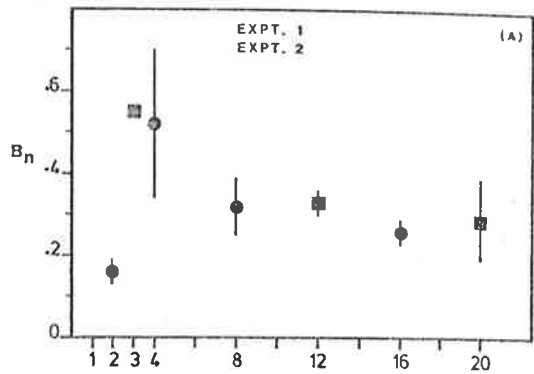
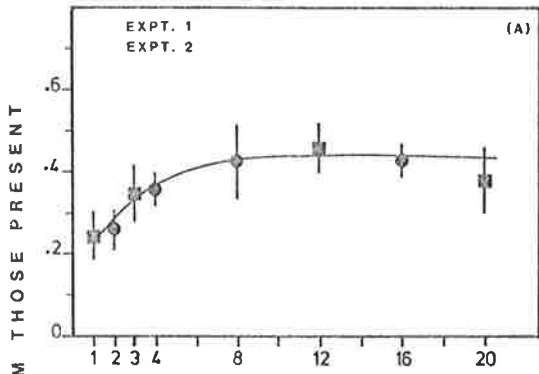


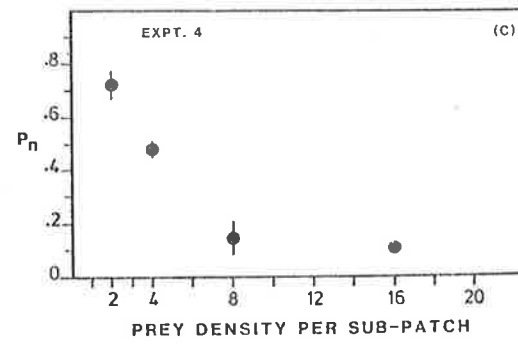
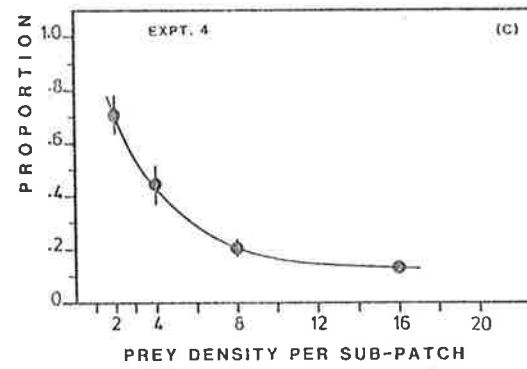
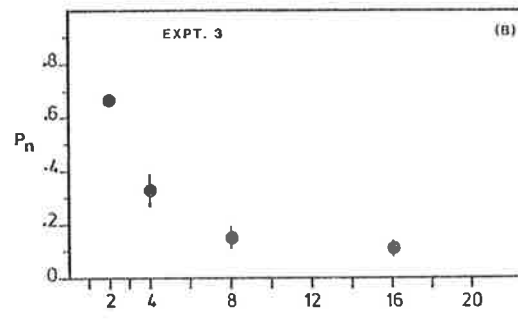
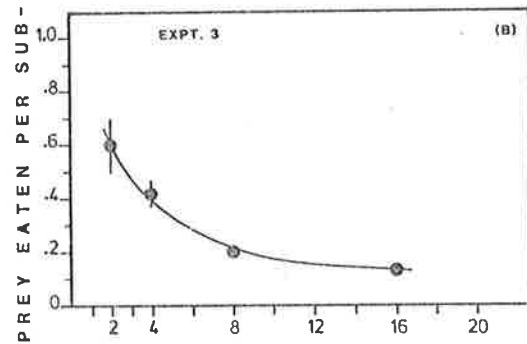
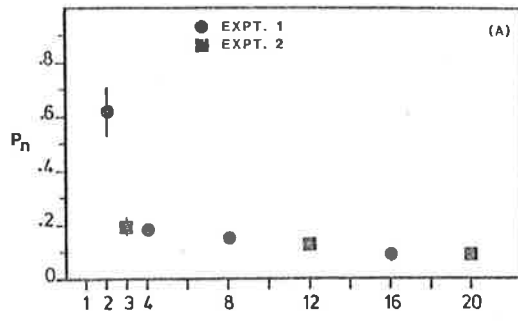
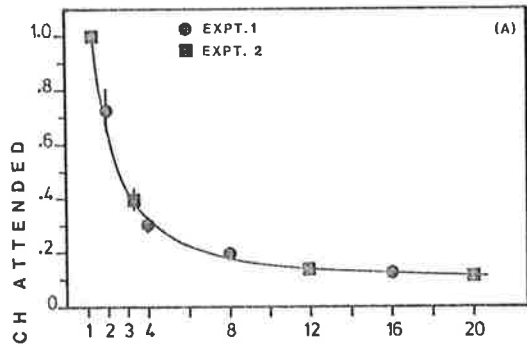
Fig. 7.18

Means  $\pm$  S.E. of the proportion of prey eaten from those prey PRESENT at a sub-patch of a particular prey density that were ATTENDED by beetles; in searching efficiency experiments 1, plus 2 (Fig. A), 3 (Fig. B), and 4 (Fig. C). The lines in the figures were fitted to the data points by eye.

Fig. 7.19

The estimates of  $P_n$  (means  $\pm$  S.E.) from fitting Chesson's (1982) model to the numbers of prey eaten in sub-patches of different prey densities ATTENDED; in searching efficiency experiments 1 and 2 (Fig. A), 3 (Fig. B), and 4 (Fig. C).





estimates of  $P_n$  (Fig. 7.19) showed a decelerating decrease to a lower asymptote when plotted against prey density per sub-patch in all the four experiments.

The estimates of  $\beta_n$  and  $P_n$ , in general, follow the predictions of Chesson (1982) in that the former should increase while the latter should decrease with prey density per sub-patch; and the estimates indicate that sub-patches of higher prey densities had a higher probability of being VISITED and that a typical prey on a sub-patch of a higher prey density had a lower probability of being attacked.

### 7.3.2 SEARCHING EFFICIENCY — EXPERIMENT (5)

#### 7.3.2.1 INTRODUCTION

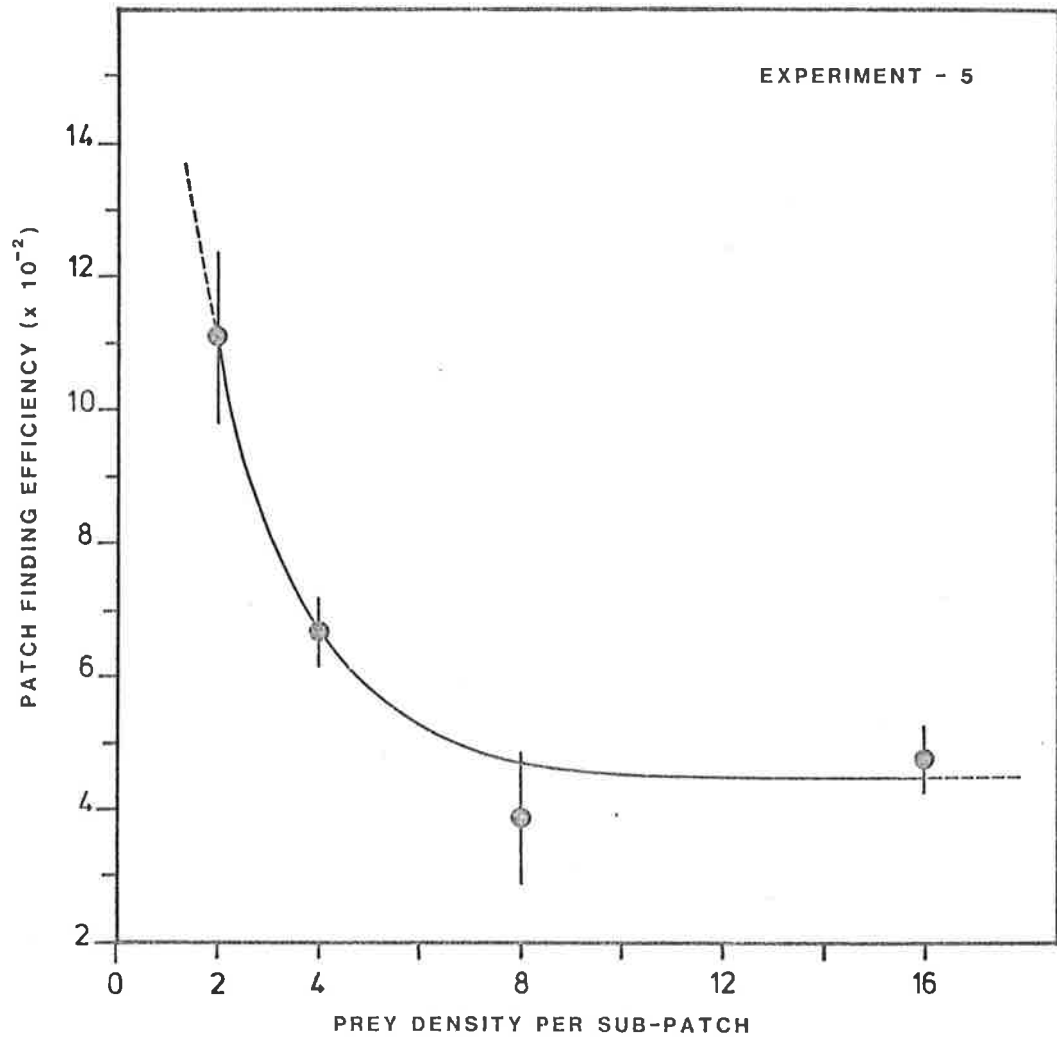
From the first four experiments, there was evidence to show that, when given a choice, the beetle exercised discrimination in attending sub-patches of different prey densities such that it attended a relatively higher proportion of sub-patches of higher prey density (section 7.3.2.1C); and the beetle's Patch Finding Efficiency (PFE) showed a decelerating rise to an upper asymptote in relation to prey density per sub-patch (Fig. 7.20). In an attempt to substantiate these findings further, in the following experiment the beetle was provided with sub-patches of the same prey density at a time, in any single trial. It was expected that the trend in the response to prey density would be reversed, such that a plot of PFE values would decelerate to a lower asymptote with an increase in prey density per sub-patch.

#### 7.3.2.2 RESULTS AND DISCUSSION

The data gathered from this experiment, and the estimated PFE values have been tabulated in Appendix Table 21. The PFE estimates have also been plotted in Fig. 7.20, which shows that the plot of PFE values decelerated to a lower asymptote with an increase in prey density per sub-patch. Such a trend in PFE values would be obtained if the beetle truly possessed an ability to discriminate between sub-patches on the basis of prey density. If all the available sub-patches are of the same prey density, the beetle would not need to attend larger numbers of sub-patches when all the sub-patches are of higher prey density because it would be able to satisfy its needs of feeding on prey and laying its quota of eggs in fewer

Fig. 7.20

The estimates of Patch Finding Efficiency (PFE) (means  $\pm$  S.E.) of the beetles towards sub-patches of different prey densities; in searching efficiency experiment 5.



sub-patches.

Thus, the data gathered from this experiment further support the hypothesis that Rodolia has the potential to differentially exploit prey population in terms of prey density. Not only is it able to exploit a greater proportion of sub-patches of higher prey density when it is given a choice, but it also attacks a larger number of individuals from sub-patches of higher prey density. However, when it is provided with sub-patches of the same prey density, it distributes its energy efficiently, by not attending too many sub-patches when prey density in all sub-patches are higher.

### 7.3.3 MODE OF SEARCHING

An attempt has been made by means of a conceptual model (Fig. 7.21), to understand the whole searching process on the basis of the data gathered from this series of experiments and our existing knowledge on predation from the literature.

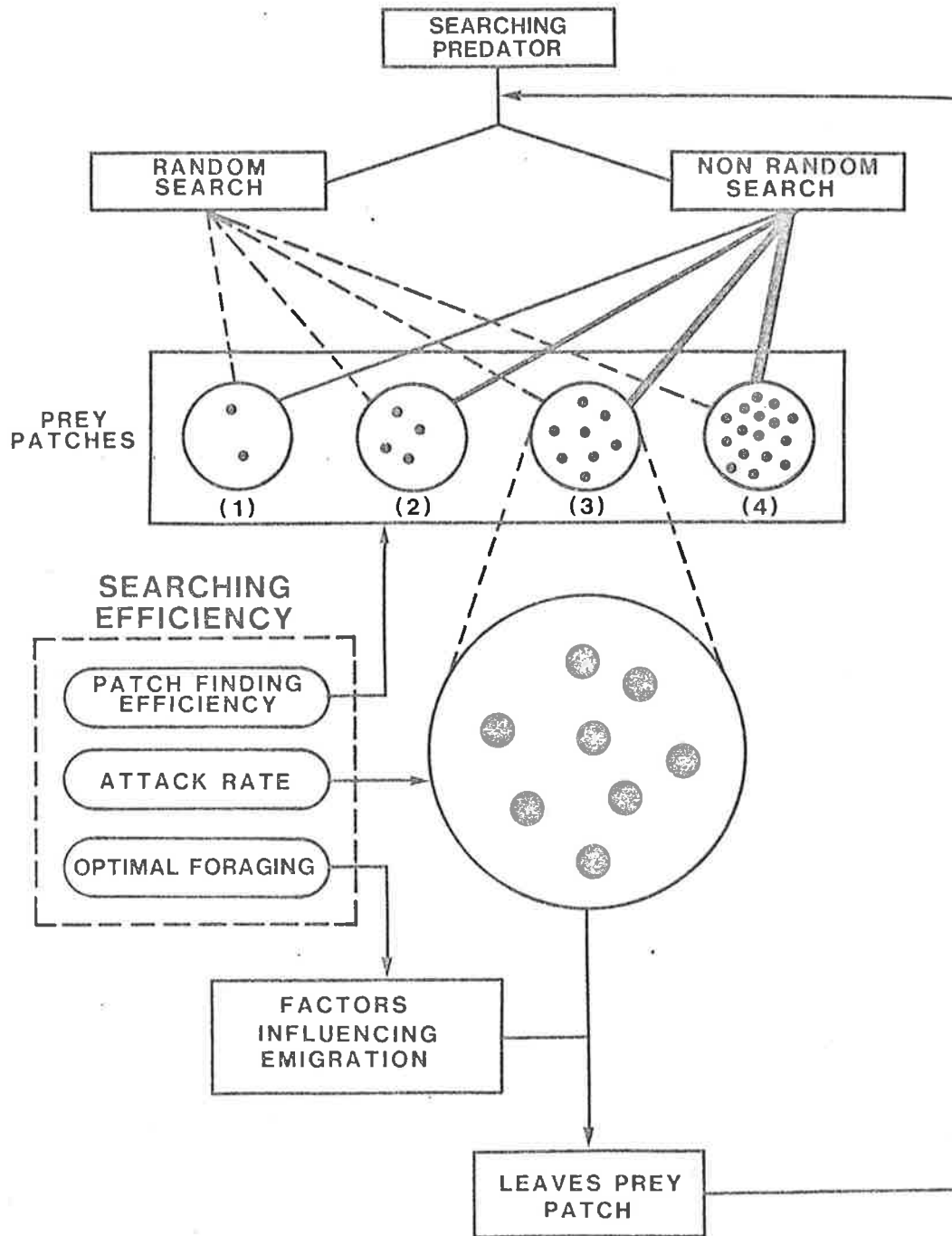
Earlier, it was mentioned that in nature a prey population is generally distributed in patches of varying sizes, that spatial heterogeneity is common and that predators may not necessarily search for their prey at random in relation to prey density. Let us assume that a predator is randomly searching for four patches of prey with prey densities of 2, 4, 8, and 16 prey per patch. Under random search conditions, the probability of the predator finding each of the 4 patches would be the same, and so just by chance, it can land at a patch of any prey density. On the other hand, if we assume a predator which responds to stimuli emitted by the prey from a distance (eg. prey Kairomones etc.), the prey density at the patch would influence the predator's searching process. In the latter case, the probability of discovery of a patch with the highest prey density would be the highest, and that of the lowest prey density the lowest. This has been depicted in the figure by different thicknesses of the arrows.

Let us now assume that prey patch No. 3, with prey density 8 is discovered by a predator searching randomly. The predator lands on the patch and wanders on the patch until it bumps into a prey. Depending on its hunger level and ovipositional urge, it might either feed on the prey or lay eggs (assuming that the searching predator was a female capable of laying eggs). If the hunger level and/or the ovipositional

Fig. 7.21

A conceptual model of the mode of searching describing the new concept of searching efficiency and depicting the series of behavioral steps in the foraging behaviour of the predator that leads to the attack of patchily distributed prey.

# THE MODE OF SEARCHING



urge are not acute, the predator on encountering the first prey may begin a "success motivated" or "area restricted" search of the arena. If the hunger level and/or ovipositional urge is strong, the above searching behaviour may follow the initial feeding and egg laying. The first encounter with a prey and the area restricted search seemingly gives the predator an image of the prey density at the patch. The prey density at the patch greatly influences the behaviour of the predator because at relatively high prey densities the chance of the first encounter with a prey individual is relatively high. Once at the patch, the three factors of hunger level, ovipositional urge and prey density together influence the predator's behaviour in terms of functional and ovipositional responses, the former in the form of the ATTACK potential and the latter in the form of the OVIPOSITIONAL potential.

We further know that, when given a choice any predator does not stay at any place indefinitely, even if the prey individuals are replenished. Predators seem to have an inherent urge to leave any prey patch after some time, despite optimum conditions. The question then arises — what are the factors that govern the predator's decision to emigrate from a prey patch? Students of predation biology have tried to answer this question and have put forward a number of hypotheses, so much so that an altogether new field of study has evolved called Optimal Foraging Theory (see Chapter 8.1). In this vast body of knowledge there are a number of hypotheses which attempt to explain the factors that influence the predator in deciding when to leave a particular patch of prey. However, as is evident from Chapter 8.1, until now no study has examined all of these hypotheses in an integrated manner, and no single hypothesis can explain the behaviour of a general forager. But no matter which of the hypotheses is found applicable to the system under investigation, one thing is certain, namely that the prey density at the patch is directly or indirectly the single most important influence in the predator's decision to remain in or emigrate from a patch of prey.

Once the predator leaves the patch, the whole cycle starts all over again.

It is clear from the above that a comprehensive study of predator searching, and therefore evaluation of searching efficiency, should incorporate all the three processes involved, viz. (a) the Patch Finding Process, (b) the Attack Rate, and (c) the Emigration from the discovered



patch. Any method of evaluation of searching efficiency that does not give due importance to all these three processes would be biologically unrealistic, no matter how sound it is mathematically and statistically.

#### 7.3.4 USES OF THIS METHOD

The concept of searching efficiency has come a long way since the days of Thompson (1924), Lotka (1925), Volterra (1926), and Nicholson and Bailey (1935), but as yet it has remained a theoretical concept with little applied value. On the other hand, the concept of searching efficiency presented here is expected to have wide applicability in the field of applied biological control. Very often applied entomologists are confronted with the problem of making decisions on the importation and release of a worthwhile biological control agent. The vast entomological literature tells us about the possible characteristics to look for -- the foremost being a high searching efficiency. However, it fails to tell us how we go about obtaining realistic values of searching efficiency for different species and comparing them on the basis of such values. Not only that, even if we know from practical experience that one natural enemy is better than the other, we are not able to quantify the greater effectiveness of that species on the basis of any critical characteristic. The present attempt is a step in that direction and the concept it suggests is simple and does not involve complex mathematical and statistical computations. And besides providing a more realistic estimate of the searching efficiency of a predator, the method discussed here also tests the predator's differential response to patches of different prey densities, which is another attribute to be possessed by an efficient natural enemy.

However, the method of gathering data would, perhaps, require modification considering the behaviour of the natural enemy in question.

#### COMPARISON OF MORE THAN ONE PREDATOR

From the data gathered for Rodolia, it appears that a predator can be compared for better effectiveness by means of the slopes and the intercepts of the regression lines in plots similar to those in Figs. 7.13 and 7.14, representing the searching efficiency and the predator's response to patches of lower prey densities, respectively.

Let us assume that we had information on the number of prey eaten and

the number of patches ATTENDED for eating prey from experiments similar to those conducted for Rodolia, for four predators (A), (B), (C), and (D) (Fig. 7.22). Thus, if for these four predators, estimates of the slopes and the apparent intercepts were obtained (Table 7.7A) by fitting regression lines to the data points (Fig. 7.17), in the manner done in Figs. 7.13 and 7.14, we would be able to compare the four predators for better effectiveness in the manner shown in Table 7.7B. The hypothetical results have been considered for extreme sets of conditions. Table 7.7B shows that a predator which shows significantly higher values of both slopes and intercepts would emerge to be the more effective predator, both in terms of its searching efficiency and its response to patches of lower prey densities (comparison numbers 3 & 4). But if a predator shows superiority in terms of only one of the parameters, i.e. the slope or the intercept (comparison numbers 1 & 2 or 5 & 6), then its effectiveness would be superior only in terms of the better parameter. Predators which are found superior in both parameters (slopes -- better differential response in patch selection, and intercepts -- better response to patches of lower prey densities) would show better effectiveness than those showing superiority in terms of a single parameter.

#### 7.4 GENERAL DISCUSSION

From section 7.1.1, it becomes clear that, to date, almost all efforts in the evolution of the concept of searching efficiency of predators have followed along the lines of the Nicholson-Bailey model. Therefore, all previous developmental attempts suffer from some of the same constraints that the Nicholson-Bailey model suffered, viz. assumption of RANDOM search by the predator for randomly distributed prey in a homogeneous environment. In nature, predators do not necessarily search for their prey at random, nor is the prey population distributed in a homogeneous manner; on the contrary, patchy distribution of prey would be the rule rather than the exception. Hassell (1982a) does propose a method of evaluating searching efficiency for a predator searching in a patchily distributed prey population but his method introduces another constraint in the form of information required on the actual searching time for the predator under investigation. All these constraints are serious impediments to the evaluation of the real searching efficiency of predators.

Fig. 7.22

Comparison of predators on the basis of their differential responses to patches of different prey densities (the slopes), and their responses to patches of lower prey densities (the intercepts) by a plot of the numbers of prey killed per patch of a particular prey density ATTENDED estimated; from the new concept of searching efficiency for four hypothetical predators.

(a) Predator (A) :  $Y_1 = a_1 + b_1X$ .

(b) Predator (B) :  $Y_2 = a_2 + b_2X$ .

(c) Predator (C) :  $Y_3 = a_3 + b_3X$ .

(d) Predator (D) :  $Y_4 = a_4 + b_4X$ .

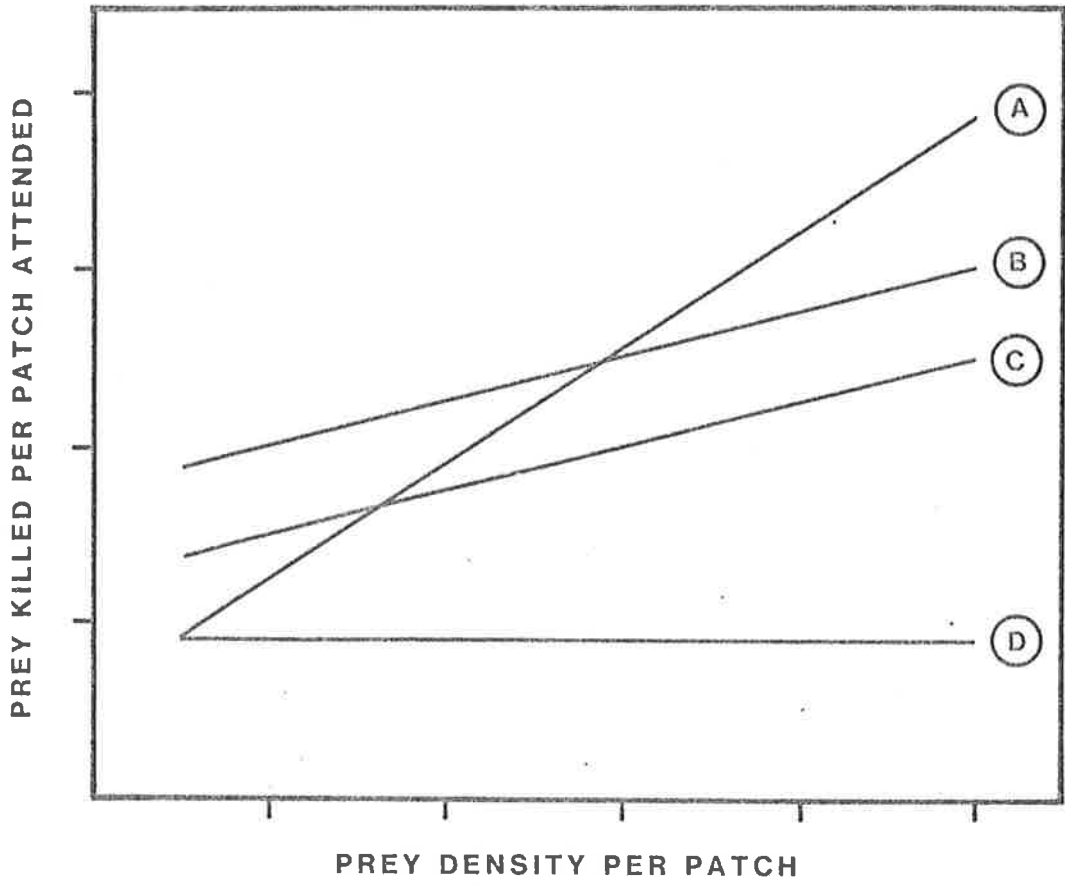


Table 7.7A.

SLOPES AND INTERCEPTS FOR REGRESSIONS IN FIGURE (7.17)

PREDATOR	INTERCEPT	SLOPE
A	a1	b1
B	a2	b2
C	a3	b3
D	a4	b4

Table 7.7B

COMPARISON OF PREDATORS ON THE BASIS OF THEIR SLOPES AND INTERCEPTS  
FROM Table (7.7A)

COMPAR. NUMBER	COMPARE PREDATORS	COMPARE INTERCEPTS	COMPARE SLOPES	INFERENCES DRAWN
1	A & B	$a1 > a2$	$b1 = b2$	A more efficient #
2	C & D	$a3 = a4$	$b3 < b4$	D more efficient *
3	A & C	$a1 > a3$	$b1 > b4$	A more efficient #*
4	B & C	$a2 > a3$	$b2 > b3$	B more efficient #*
5	A & D	$a1 > a4$	$b1 < b4$	A more efficient #
6	B & D	$a2 > a4$	$b2 < b4$	B more efficient #

# effectiveness based on response to patches of lower prey density.

\* effectiveness based on searching efficiency.

Besides, Hassell's (1982a) method is also out of step with the latest developments in predation biology because, though it recognizes the importance of patchiness in the distribution of prey population, it does not evaluate the predator's response to spatial heterogeneity in the distribution of prey, i.e. it fails to evaluate the PATCH FINDING PROCESS (see section 7.1.2). In recent years, students of predation biology (including Hassell (1982b) himself) have come to the conclusion that a predator's response to spatial heterogeneity in the distribution of prey is a vital factor affecting the dynamics of interacting predator-prey populations (Beddington et al., 1978; Waage, 1983; Heads and Lawton, 1983; see also Chapter 6.1). Recognizing the importance of the predator's response to patchiness, Morrison et al. (1980) and Morrison and Strong (1981) stress that in analysing relationships between parasitism and host density per patch, it is necessary to account for both the proportion of patches discovered (i.e. the Patch Finding Process) and, within these, the proportions of host parasitized (i.e. the Attack on hosts in the discovered patch). Theoretical host-parasite models also lead to the conclusion that all those factors which result in a clumped distribution of attacks on a host population tend to contribute to population stability (May, 1978). The unevenness in the distribution of attacks is generally an outcome of behavioural response (an "aggregative response"; see Chapter 6.1) of the predator to patches of different prey densities. The behavioural "aggregative" response leads to an aggregation of predators at patches of higher prey densities, and Hassell (1982b) warns that "The distribution of searching parasitoids itself, however, has no direct impact on population dynamics. It is the resulting pattern of parasitism that is the all-important determinant of a parasitoid's impact upon the host population."

The arguments presented in this chapter lead to the realization of the need for the development of a more realistic concept of searching efficiency of a predator which evaluates its behavioural response both BETWEEN patches and WITHIN patches of prey. Such a concept would not only be closer to biological realism but also permit comparison of more than one predator on the basis of their searching efficiencies. The method of evaluation of searching efficiency should also be relatively easy.

In an attempt to overcome the limitations inherent in the earlier concepts and incorporate the attributes mentioned above, the concept of

searching efficiency that I have proposed was developed by taking into account the series of steps in the searching behaviour of the predator (Fig. 7.21) which results in the attack of prey. As was pointed out in section 7.1.3, Morrison et al. (1980) studied the response of Trichogramma spp. to patchily distributed Heliothis zea eggs and considered the parasitoid's response both between patches and within patches in the manner discussed here but they did not relate it to a concept of searching efficiency.

The estimates of searching efficiency obtained using the new concept provide two-fold information about the searching behaviour of Rodolia in an environment with patchily distributed prey. On the one hand, the method allows the evaluation of the predator's differential response to patches of different prey densities and, on the other, allows the evaluation of the the predator's response to patches of lower prey density. Both these parameters describe the foraging behaviour of Rodolia in a more comprehensive manner.

The series of experiments conducted to evaluate the searching efficiency of Rodolia cardinalis produced two sets of estimates (each set comprising the slope and the intercept; see section 7.3.1.2.3) of searching efficiency, one based on the ATTACK potential of the beetle, and another based on the beetle's OVIPOSITIONAL potential. Both these sets of estimates appeared to remain unaffected by changes in the experimental conditions, which raised the question — is searching efficiency a characteristic attribute of a species and hence a constant, as was assumed by Nicholson (1933)?

Though the results gathered so far appear to indicate that searching efficiency may indeed be a constant, a considerable amount of work needs to be done to substantiate this hypothesis. The indication of searching efficiency being a constant could well be an artifact, because the results obtained here may simply indicate that the alterations in the experimental conditions (that were tested) were not great enough to change the searching efficiency of the beetle. From the literature, there are many reasons to believe that searching efficiency cannot be a constant and characteristic attribute of a species, e.g. it has been shown to be affected by changes in prey density, spatial heterogeneity in the distribution of prey and predators, and also predator density (Hassell, 1978b). Though the effect of prey density and spatial heterogeneity in the distribution of prey had

been taken into account in the design of the experiments that were carried out with Rodolia, the influence of predator density and spatial distribution of predators had not been considered, since the response of an individual predator was only tested.

The influence of predator density usually takes place in the form of MUTUAL INTERFERENCE between searching predators which results in a decline in the number of prey killed per predator and so the searching efficiency (Hassell, 1978b). However, the impact of such mutual interference can only become evident when the predator density rises beyond a certain level, for there must be an optimum number of predators which would maximize the searching efficiency under a given set of conditions. Testing the effects of Mutual Interference on the searching efficiency of predators would produce misleading results without due consideration of the density of parasitoids and the size of the searching arena in relation to the natural habitat of the organisms.

The concept of searching efficiency presented here is still in its infancy and demands further research, both in the consolidation of its theory and the standardization of methodology. However, it is very unlikely that any single procedure would ever be applicable to every predator, for predators not only differ enormously in their foraging behaviour because they have to forage in totally different environments, but also differ vastly in their perception of patches (Heads and Lawton, 1983). Any experimental evaluation procedure which does not take into account such behavioural implications is bound to produce spurious and unrealistic results.

If biological control is to leave the "try-it-and-see" technique that it has been until now and become a scientific enterprise, it would only be as a result of those attempts that give priority to biological realism. Predation biologists who give prime importance to the behaviour of predators are truly the pioneers in attempts to transform biological control from an "art" to "science" (see van Lenteren, 1980).

In the following chapter, the searching behaviour of Rodolia has been studied in detail at the individual patch level in an attempt to understand all those factors that influence the beetle's decision to emigrate from the patch that it once discovers.



**CHAPTER 8**  
**SEARCHING BEHAVIOUR OF RODOLIA WITHIN PATCHES**

## CHAPTER 8

### SEARCHING BEHAVIOUR OF RODOLIA WITHIN PATCHES

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There is something fascinating about science. One gets such a wholesome return of conjecture out of a trifling investment of fact.

-- Mark Twain (1874).

In Science the primary duty of ideas is to be useful and interesting even more than to be "true".

-- Wilfred Trotter.

The great tragedy of Science -- the slaying of a beautiful hypothesis by an ugly fact.

-- T.H. Huxley.

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## 8.1 THE OPTIMAL FORAGING BEHAVIOUR OF THE BEETLE

### 8.1.1 INTRODUCTION

Emlem (1966) and MacArthur and Pianka (1966) first proposed the idea of optimization as an useful approach in the study of foraging behaviour. And since then this bioeconomic approach has been applied to questions such as : allocation of time to play, time a male should invest with a female, space utilization, life-history strategies, levels of aggression, group dynamics, etc. (Howell, 1983). The optimization approach to the study of foraging behaviour has developed into an independent theory referred to as Optimal Foraging Thoery (OFT). A number of reviews on OFT have been published (Schoener, 1971; Pyke et al., 1977; Krebs, 1978; Hassell and Southwood, 1978; Kamil and Sargent, 1981) but Krebs et al.'s (1983) review is the most comprehensive.

At the very heart of the optimization approach to the study of animal behaviour lies the assumption that evolution has occurred by natural selection and that animal behaviour ought to be interpreted in terms of the contributions it makes to the survival and reproduction of its possessors, that is to Darwinian fitness (Smith, 1978). Coupled with this are the assumptions that behaviour is adaptive (Kamil, 1983) and that animals possess the power of learning and memory. And since the theory postulates

that only the most fit individuals can survive, there is also an implicit assumption that natural selection is an optimization process (Krebs, 1979).

The optimization approach to ethology is being elaborated by a lot of theory and consolidated by some experimental evidence from the laboratory (Charnov, 1976b; Cowie, 1977; Cook and Cockerell, 1978; Hubbard and Cook, 1978; Krebs et al., 1978; Bond, 1980, and van Alphen and Galis, 1983) and field studies (Townsend and Hildrew, 1980; Roitberg et al., 1982; Stamp, 1982). However, bitter criticisms have challenged its basic premise. Proponents of the optimization approach have assumed that behaviour is adaptive, but critics assert that the basic hypothesis of adaptation is an untestable hypothesis and therefore unscientific (Popper, 1977; Smith, 1978). Other critics have suggested that the whole program of functional explanation through optimization takes us in circles and that optimization theory based on the theory of natural selection is tautological (Cody, 1974; Popper, 1977). Thus, Cody (1974) argues that natural selection is a "mechanism that maximizes fitness. It leaves only the best adapted or optimal phenotypes for inspection". So having assumed that evolution is an optimizing process, the optimization approach to the study of behaviour attempts to show that foragers indeed behave optimally (Krebs, 1979). Harvey and Mace (1983) similarly argue that the "application of optimization theory to evolutionary biology and ethology do not (and cannot) test the general hypothesis that nature optimizes."

A number of other critics of OFT have suggested that many optimization models are too simple compared to the complex challenges an animal faces in nature (Zach and Smith, 1981). Some of these models are based on assumptions which are not only biologically unrealistic but absurd. For example, Charnov's (1976a) "marginal value theorem" is based on an implicit assumption that foragers are omniscient and rational maximizers of energy intake (Green, 1984); but many biologists would have difficulty accepting that animals are indeed omniscient.

Kamil (1983) has presented a critical review of the criticisms voiced against optimization theory in biology. He dismisses most criticisms as unimportant on the grounds that "concepts such as optimization are theoretical constructs that we use to help us understand and predict behaviour, but are not themselves the objects of study." Krebs (1979) believes that "even though natural selection inevitably pushes towards optimal solution, it can be argued that true optima, even optimal

compromises, are rarely achieved." In the meantime, the literature on optimization studies in biology is becoming voluminous.

Despite the many criticisms of OFT, I think that such an approach to the study of ethology deserves appreciation because it has led to the formulation of many testable hypotheses.

#### 8.1.1.1 THE OPTIMALITY CRITERION

The first step in the optimization test of a behaviour involves the selection of some currency as the optimality criterion. Almost all OFT models assume that the net rate of energy intake is the currency which needs to be maximized when subjected to cost-benefit analysis. Royama (1970, 1971) has argued that searching in "profitable" feeding areas is important for animals, and he defines the profitability of a feeding area as "the amount (biomass) of food the predator can collect for a given amount of hunting effort" (time spent hunting). Other optimal foraging models have used similar assumptions (MacArthur and Pianka, 1966; Schoener, 1971; Charnov, 1976a). In particular, Schoener (1971) suggests that a foraging animal either has a fixed energy requirement and aims to minimize the time spent feeding so as to leave more time for other activities (Time Minimizers), or it has a fixed time in which to feed during which it aims to maximize its energy gain (Energy Maximizers). And Schoener (1971) and Pyke et al. (1977) conclude that, in both these conditions, animals should forage in such a way that their net rate of intake of energy (food) is maximized, assuming that such a foraging strategy would maximize their fitness.

Specific optimal foraging models arrive at their predictions by constructing a model (usually mathematical) of a particular foraging problem and then deriving the optimal solution within the terms of the model. The solution is optimal in the sense that it maximizes energy intake per unit time an animal spends foraging. This is, however, a very simplistic view of the animal. In reality, an animal has to perform a range of activities besides foraging, and the way in which a forager behaves is likely to be a compromise resulting from conflicting selection pressures for different activities (Krebs, 1973). The general problem in finding a good index of fitness is to provide a common currency by means of which the benefits of different aspects of behaviour can be compared. Besides, natural selection may maximize fitness but the measurement of the

exact relation of behaviour and fitness is difficult (Howell, 1983). In fact, biologists are still debating the definition of fitness (Stenseth, 1983, 1984; Owen and Wiegert, 1982; Nur, 1984). A number of methods, however, have been proposed for translating the long-term goal of maximizing fitness into a short-term quantifiable index of fitness that can be subjected to a cost-benefit analysis (Sibly and McFarland, 1976; McFarland, 1977).

#### 8.1.1.2 OPTIMIZATION APPROACH TO FORAGING BEHAVIOUR

Pyke et al. (1977) classified the literature on OFT into four categories, namely (1) Optimal diet choice (2) Optimal patch choice (3) Optimal allocation of time to different patches (4) Optimal patterns and speed of movement. In the following, only two of the above four categories (2 and 3) will be discussed because they bear relevance to my work.

##### 8.1.1.2(A) OPTIMAL PATCH CHOICE

In a classical experiment - the "two-armed-bandit" problem - Krebs et al. (1978) provided great tits (Parus major) with two feeding sites which differed in profitability. They then produced a model which conceptualized the foraging behaviour of the birds as consisting of two discrete stages-- exploration (information gathering), followed by exploitation. The results were qualitatively similar to what the model had predicted, i.e., increasing the difference in payoff rates decreased the length of the exploration phase. Kamil (1983) suggests that such results are commonly found in experimental animal psychology. He also finds strong similarities between the probability learning experiments of animal psychologists and the patch selection experiments of ecologists and points out that Krebs et al.'s findings are a well known result in the animal psychology literature; though in the latter the switching from exploration to exploitation phase is more gradual than abrupt as found by Krebs et al. The well defined results obtained by Krebs et al. probably occurred because they oversimplified the system by providing only two patches for the birds, and in nature a bird is unlikely to have to choose from only two possible feeding sites (McNeil Alexander, 1982). When a number of patches of varying degrees of profitability are provided, the animal does not only feed on the best patch, as Smith and Sweetman (1974) found in their study of titmice. The birds in this latter experiment fed on patches of

different profitability, allocating the greatest amount of time to the area of highest food abundance and progressively less time to progressively worse areas.

Thus, in essence, the theory of optimal patch choice states that an optimal forager should be able to differentially exploit patches in relation to profitability.

#### 8.1.1.2(B) OPTIMAL ALLOCATION OF FORAGING TIME

A number of hypotheses have been proposed to describe the optimal allocation of time in foragers and to predict when foragers should leave the current patch in search of another. Some of the notable hypotheses are as follows:

##### (1) HUNTING BY EXPECTATION

A forager enters a patch with the expectation of capturing prey and leaves the patch when the quota of prey is realized (Gibb, 1962).

##### (2) MARGINAL VALUE THEOREM (MVT)

Charnov (1976a) proposed the "marginal value theorem" (MVT) which states that an animal should leave a patch when its rate of food intake in the patch drops to the average rate for the habitat, and furthermore, that this "marginal" capture rate should be equalized over all patches within a habitat. He showed that - given certain assumptions - an optimal predator would have a fixed giving-up-time rule. McNair (1982) interprets MVT as the strategy of optimal "residence time" (RT).

##### (3) GIVING-UP-TIME (GUT)

The GUT is defined as the time between the last capture and the time at which the predator leaves the patch (Cowie and Krebs, 1979). Though they did not use the term, Tinbergen et al. (1967) measured GUTs for carrion crows, and the term was later coined by Croze (1970). Krebs et al. (1974) produced a model based on the assumptions of the marginal value theorem to predict that an optimal predator would leave a patch, if for some specified time (fixed GUT), it did not find any prey regardless of the quality of the patch. They produced empirical evidence for this conclusion from their study of black-capped chickadees (Parus atricapillus).

McNair (1982) and Green (1984) have criticized Krebs et al.'s method

of identifying GUT with MVT and optimal foraging. Green (1984) argues that the GUT is neither optimal nor equivalent to the MVT and has shown that "the GUT rule will not satisfy the MVT if prey capture is a "random" (i.e., Poisson) event"; and McNair (1982) has shown that for an optimal forager, GUT should be related to the patch quality and not remain constant as inferred by Krebs et al. (1974). So if GUT is viewed as a measure of a forager's persistence in searching for more food in a patch, then in theory, a forager should be more persistent in better quality patches and larger GUTs should be used in such patches.

The GUT concept has drawn much theoretical attention from Hassell and May (1974), Murdoch and Oaten (1975), Breck (1978) (in Green, 1984) and Iwasa et al. (1981). Hassell and May (1974) reviewed the examples of insect predators and birds which distribute their searching effort, measured as a proportion of the total time, according to prey density when offered a simultaneous choice of patches. They concluded that, generally, the allocation of time among patches of different profitability showed a sigmoid relationship which they called the "aggregative" response. Thus predators tend to spend little time in areas of low prey density and do not discriminate strongly between such areas; but they discriminate very strongly at intermediate prey densities, and rather little again at very high prey densities. Hassell and May (1974) suggested that the sigmoid response could result from either :

- (i) area restricted searching - meaning that the predator adjusts its search path immediately after a capture so as to concentrate its search effort near the last prey, or
- (ii) a fixed giving-up-time (GUT) (similar to that of Murdoch and Oaten, 1975) - based on the idea that, after a find, the predator searches in the immediate vicinity for a fixed time and leaves if it does not have another success. If it does find another prey, it simply "resets its clock" and searches again until the waiting time has elapsed with no capture. Such a strategy would allow the predator to concentrate effort in more profitable patches.

Hassell and May (1974) have used the assumption that the actual time between captures is exactly equal to the expected time when calculating the rate of finding prey for an animal that forages at random and uses the GUT

rule. This assumption simplifies the calculation, but it is nonetheless, a mistake (Green, 1984). The more difficult, correct calculations for a Poisson distribution of the number of prey per patch has been described by Murdoch and Oaten (1975) and Iwasa et al. (1981).

#### (4) RANDOM PREDATOR EQUATION

Cook and Hubbard (1977) proposed a model which uses the marginal value conclusions and reanalysed the data of Hassell (1971) describing the parasitism and aggregative response of Nemeritis canescens. They found that the number of prey located in each patch could be described by a modification of the "random predator equation" of Rogers (1972). They also compared their predictions of the optimal allocation of time with the data obtained by watching individual wasps searching for 6 hours in an arena containing five patches of different host density (Hubbard and Cook, 1978). Two of the assumptions of the Cook and Hubbard model are that there is a fixed time and that the animal has some knowledge of the profitability of different areas. Although these results suggest that Nemeritis is capable of approximating the optimal solution, Waage (1979) has suggested that the underlying mechanism is very simple. He showed that the decision made by an individual to leave a patch depends on a mechanism involving habituation to host scent.

(5) van Alphen (1980) lists nine variables that may interact to release emigration behaviour of parasitoids, namely : (a) number of encounters with unparasitized hosts (b) rate of encounter with unparasitized hosts (c) ability of parasite to recognize parasitized hosts (d) presearch ability (e) habituation to host derived arrestment chemicals (f) experience on other patches (g) encounters with non-hosts (h) encounters with unsuitable hosts, and (i) interference from other parasitoids.

#### (6) ASSESSMENT RULE

Most of the above theories are based on the assumption that a forager has some prior information on patch quality even before it enters the patch. Also these theories attempt to predict "when" a forager should leave the current patch in search of another; what they do not say is "how" a forager should make such a decision. The assessment rule of Green (1984) attempts to do that.



In nature a forager has to deal with the problem of unpredictability, because both the quality and location of patches change unpredictably with time. A forager cannot have prior knowledge of these changes as most OF models have assumed but rather it has to gather this information, which leads to the need for a forager to sample various portions of the habitat (Gibb, 1962; Royama, 1970; Krebs et al., 1978). Stochasticity should therefore, be incorporated in foraging models if it can be done conveniently, and Green (1984) proposes a stochastic foraging model which is mathematically tractable and which is based on the idea that animals use their experience in a patch in order to decide when to leave a patch. It tells whether the animal should leave a patch at any particular time according to how many prey have been found up to that time. And since it assumes that search is systematic and prey are distributed at random within each patch, the best stopping rule depends only on the number of prey caught upto a given time, and not on their actual capture times.

Green (1984) compared the assessment rule with the GUT rule and the Fixed Time rule and found it to be the best for assessing patch quality. Smith and Sweetman (1974) found that great tits had the ability to use the factors of prey size and prey density to make an assessment of the average profitability of a feeding area such that they allocated the greatest amount of time to the area of highest food abundance and progressively less time to progressively worse areas.

The two decisions of : which patches to visit (patch selection) and how long to spend in a patch (patch time allocation) are, in fact, inter-related (Waage, 1979, 1983) because patches of higher profitability would be selected against those of lower profitability and the forager would spend a greater proportion of its searching time so as to exploit maximum returns. There are numerous examples in the entomological literature to suggest that predators and parasitoids do, indeed, show a differential response to patches of different prey densities, in that they select and spend more time in higher prey density patches (Hassell, 1978b).

### 8.1.1.3 OBJECTIVES BEHIND MY EXPERIMENT

Having gathered evidence in support of the hypothesis that Rodolia shows a differential response to prey density (Chapters 6 and 7) there was need to understand the mechanism which produced such a response by a

detailed study of the behaviour of the beetle at the single patch level. The following experiment was therefore performed to :

- (i) understand the factors that influence the predator's decision to emigrate from a prey patch,
- (ii) study the foraging behaviour of Rodolia in the light of the optimal foraging theories, and
- (iii) test the hypothesis regarding sub-patches "visited" and sub-patches "attended" proposed in Chapter 7, which stated that a patch "visited" may not necessarily be "attended", and so only a fraction of the patches visited may be attended.

### 8.1.2 MATERIALS AND METHODS

The experiment was conducted in a 24x24x34 cm cage (Fig. 8.1A) which had a metal frame, a wooden base and a clear perspex top. The four sides were covered by polyester voile which was kept free on one side to allow access into the cage. This side was normally kept in position by means of rubber bands. In the centre of the cage was placed a support for a single patch of prey. The support consisted of a 12x12x2 cm block of wood through the centre of which was fixed a vertical 30 cm length of wooden "dowelling" of 1.25 cm dia. To the free end of the dowelling was attached a leaf-disc support for a single prey-patch.

One week old second instar scales and six days old beetles, both reared in the insectary (Chapter 3), were used in the experiment. The beetles were capable of laying eggs and were satiated prior to use in the experiment.

The experiment consisted of four treatments by five replicates. Each treatment consisted of four prey-patches which were provided in different sequences to a single searching predator (Table 8.1.1; following page).

The experiment was started at around 1000 h. A single predator, released on the floor of the cage, was allowed to find the prey-patch, attack the prey and/or lay eggs. If the predator left the prey-patch, it was allowed to return to the prey-patch within 4 min, after which the patch was changed to the patch with the next prey density in the sequence. Before the patch was changed, the number of prey eaten and the number of eggs laid were recorded. This method was repeated for all four prey-patches in the sequence of a treatment.

Fig. 8.1.1A

Photograph of the polyester voile cage with a single patch  
of prey on a citrus leaf-disc.



Table 8.1.1

DESIGN OF EXPERIMENT -- ALLOCATION OF PATCHES OF  
FOUR PREY DENSITIES TO FOUR TREATMENTS COMPRISING  
FOUR DIFFERENT SEQUENCES

TREATMENT	PREY-PATCH SEQUENCE			
	(1)	(2)	(3)	(4)
	PREY DENSITY PER PATCH			
I	2	4	8	16
II	16	8	4	2
III	2	2	2	2
IV	16	16	16	16

The experiment was conducted at a constant temperature of  $28 \pm 2^{\circ}$  C in the insectary. Light was provided by a pair of 60 cm long, 20W fluorescent tubes hung 30 cm above the cage.

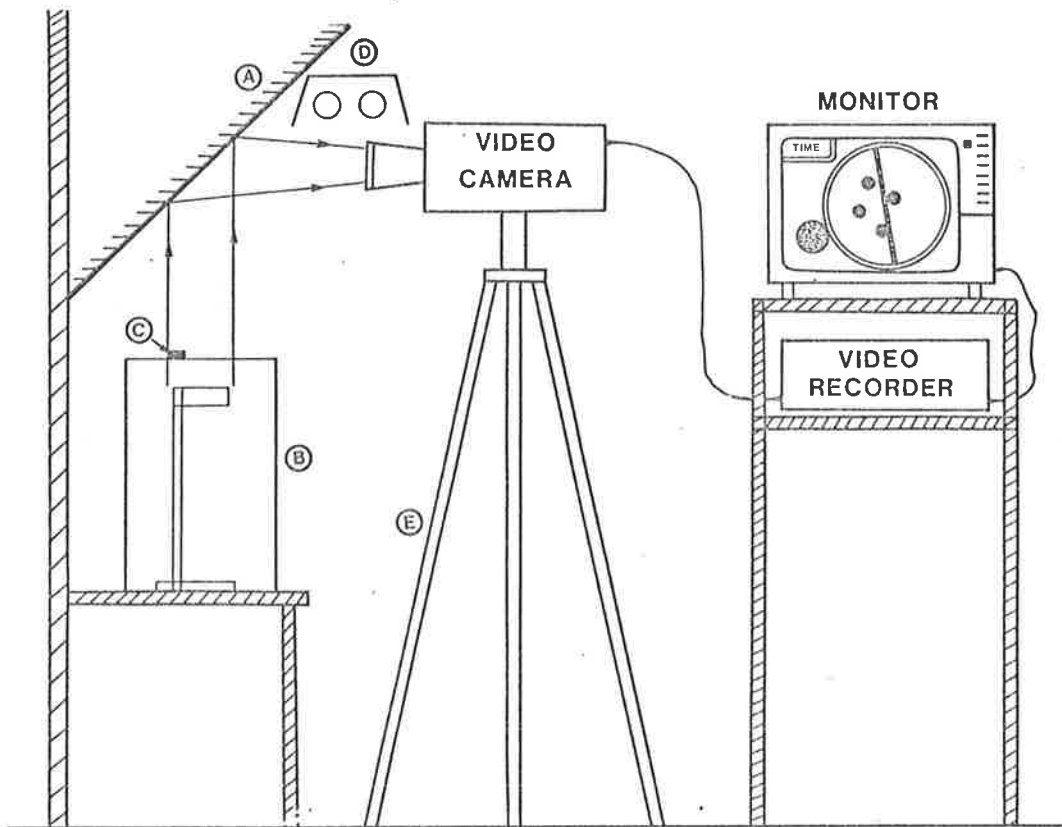
Video recording equipment was employed to record the behaviour of the beetle on and around the prey-patch. The video camera was positioned horizontally so that it received a reflected image of the prey-patch in the cage from the top, through a mirror fixed at an angle of 45 (Fig. 8.1B). A digital clock was also placed within the field of the camera to keep track of time.

#### USE OF COMPUTER AS AN EVENT RECORDER :

An Apple IIE computer was used as an event recorder. In a special programme written for the purpose, twenty buttons of the computer's keyboard were coded for twenty different events. To use the programme, the prerecorded video tapes of the experiment were played. While observing the activities of the predator on the monitor, the computer was simultaneously used as an event recorder. After having entered an initial time as the start of the experiment, one of the coded buttons of the keyboard was pressed to allow the computer program to record the coded event together with the time at that instant drawn from the clock. In this manner, the activities of the beetle were categorized as events which were translated directly into data on the computer for later analysis.

Fig. 8.1.1B

Diagrammatic representation of the experimental set-up for studying the foraging behavior of Rodolia using video recording equipment.



### 8.1.3 RESULTS AND DISCUSSION

#### 8.1.3.1 SUMMARY OF BEHAVIOURAL OBSERVATIONS

A summary of the detailed behavioural observations collected in this experiment is presented in a diagrammatic form in Fig. 8.2, by the help of a main figure (Fig. 8.2A) and an overlay (Fig. 8.2B). This figure was constructed by the computer with the aid of another special programme written for the purpose. Each line in the figure represents, on an hourly scale, the duration and sequence of various activities performed by the beetle in a particular treatment/replicate combination (TR-I, # 1 to 5; TR-II, # 6 to 10; TR-III, # 11 to 15; TR-IV, # 16 to 20). The main figure represents the events : (a) experiment started or patch changed, (b) entering patch and leaving patch, (c) encounters with prey, and (d) feeding. The overlay, on the otherhand, represents the events : (a) entering patch vicinity and leaving patch vicinity, (b) resting on disc and starting from rest, and (c) encounters leading to ovipositions, or other stoppages on the prey. By careful observation of the details of the figures, one can notice the sequence of events that took place. The format used in the figure thereby allows a summary of the entire observations to be represented in a coherent manner.

Certain main conclusions may initially be drawn from the data, namely :

- (a) there was no obvious trend in the time interval between experiment started or patch changed AND entering into patch vicinity or entering onto the patch itself,
- (b) not all entries into the patch vicinity resulted in an entry onto the patch,
- (c) not all entries onto the patch resulted in an encounter with prey,
- (d) in most instances, resting on the disc bore some relationship with feeding and the former generally followed the latter.

#### 8.1.3.2 FORM OF DATA PRESENTATION

The data gathered for different events followed a set pattern, and samples of the pattern for three events have been presented in Fig. 8.1.3 as mean eggs laid, total encounters and percentage of total encounters resulting in feeding, oviposition or other stoppages at the prey, plotted against patch type sequence. The trend lines for TR-I, with patch type sequence of 2, 4, 8, and 16 prey per patch appeared to approximate a mirror



Fig. 8.1.2

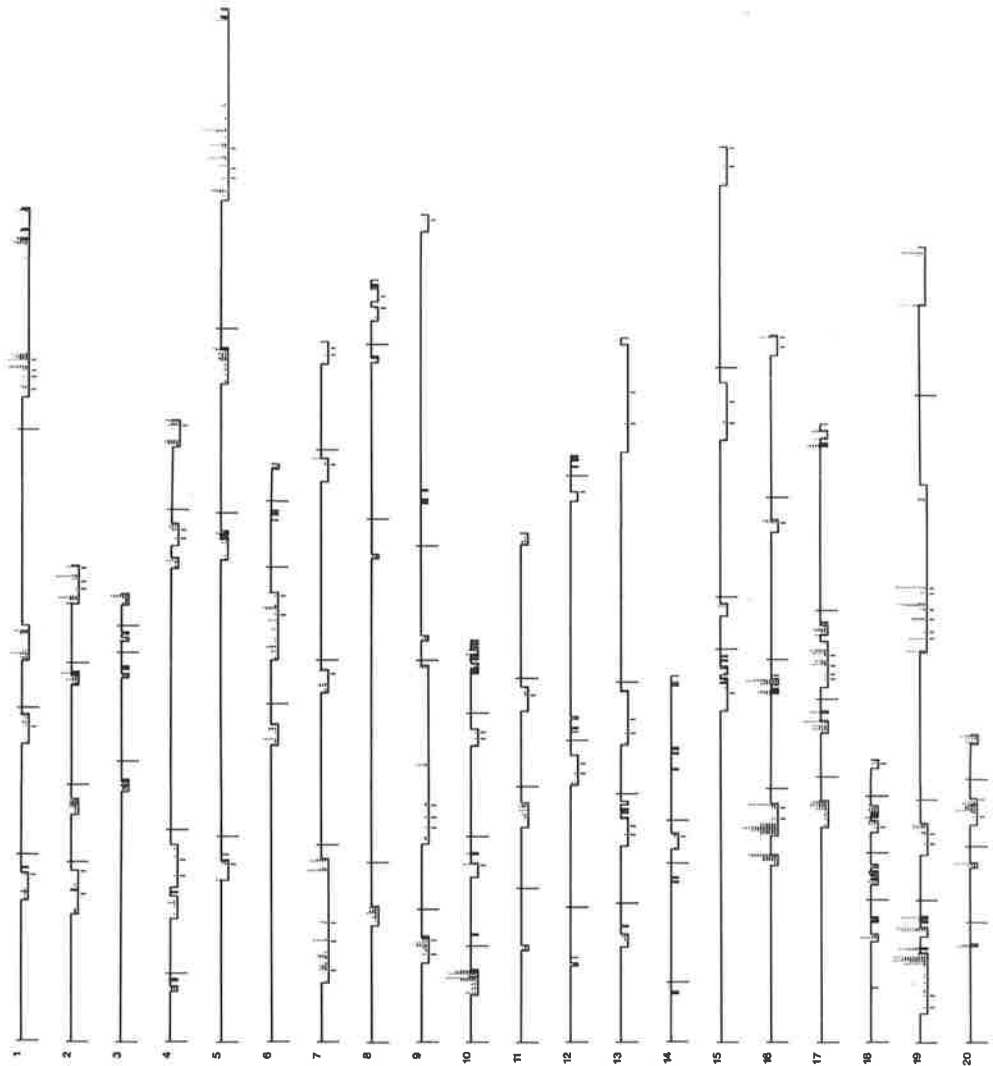
Diagrammatic representation of the data gathered from a study of the behavioural response of each of five Rodolia beetles to patches of different prey densities in each of four treatments. The data for the following events and numbers have been presented on an hourly scale by means of a main figure and an overlay.

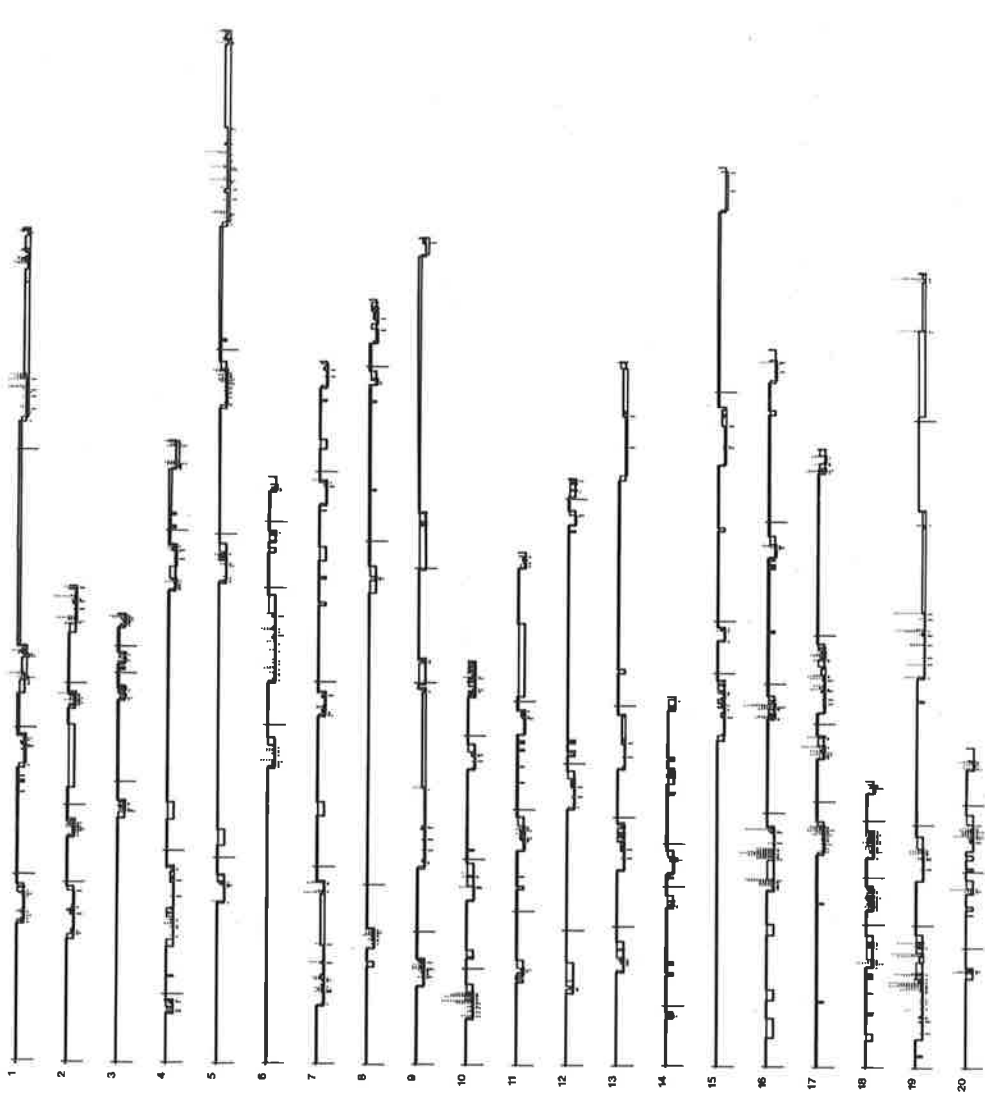
(A) MAIN FIGURE

(a) Experiment started	:	┐
(b) Patch changed	:	┐+
(c) Enter disc	:	┐┐
(d) Leave disc	:	┐┐
(e) Total encounters with prey	:	┐┐┐
(f) Encounters resulting in Feeding on Prey	:	┐┐

(B) OVERLAY

(a) Enter patch vicinity	:	┐┐
(b) Leave patch vicinity	:	┐┐
(c) Rests on disc	:	┐┐┐
(d) Starts from rest	:	┐┐┐
(e) Encounters resulting in oviposition or other stoppages on prey.	:	┐┐┐





HOURS

Fig. 8.1.3

Sample of the data showing the general trends in the results obtained from the behavioural response of Rodolia to patches of different prey densities (patch types) presented in different sequences.

- (A) The mean numbers of eggs laid by the beetles plotted against patch type sequence .
- (B) The mean of the TOTAL encounters with prey plotted against patch type sequence.
- (C) The means of the percentages of the TOTAL encounters with prey, that resulted in feeding, oviposition, or other stoppages on prey.

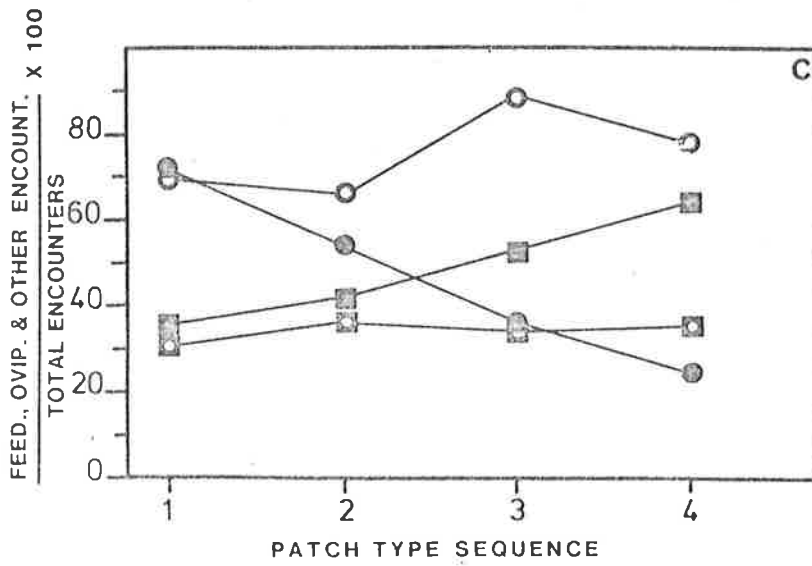
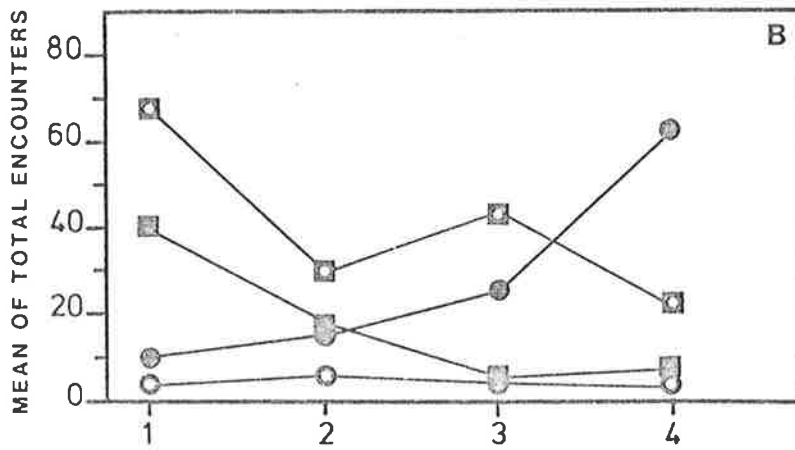
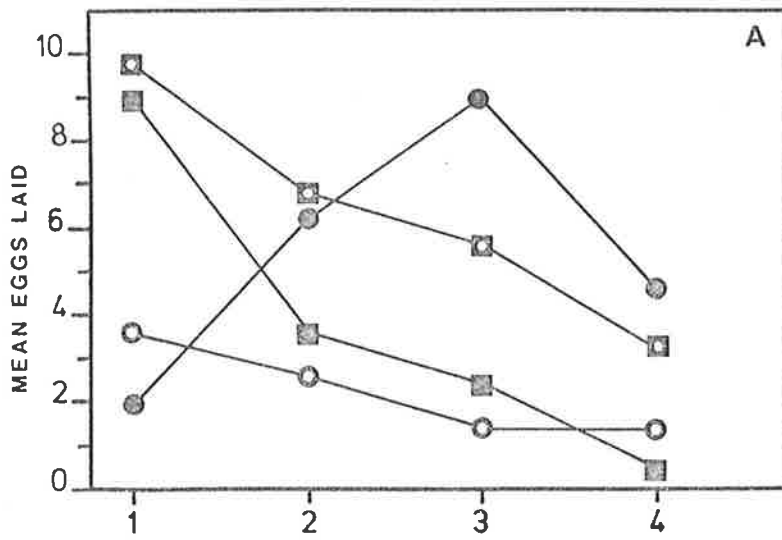


image of those of TR-II, which had a patch type sequence of 16, 8, 4, and 2 prey per patch. However, the trend lines for TR-III (which had all patches of prey density 2), remained above that of TR-IV (which had all patches of prey density 16) for some events (Fig. 8.1.3C) or below it for others (Figs. 8.1.3A and 8.1.3B).

Therefore, in an attempt to show a better representation of the beetle's general response to patches of different prey densities, the data are presented in the following manner. Two sets of graphs are plotted for data collected for each event. The data for patches of the same prey density from both TR-I and TR-II were pooled and are plotted against patch type as (A)-series figures to illustrate the influence of four different densities, namely 2, 4, 8, and 16 prey per patch. The pooled response assumes, therefore, that the sequence of the patch types in TR-I and TR-II had no effect on the results. Such an assumption was generally true, as has been shown by the mirror image trends in Fig. 8.1.3. The data from TR-III and TR-IV, on the other hand, were plotted in a manner similar to that in Fig. 8.1.3, and are referred to as (B)-series figures. In these figures, the prey density does not vary with patch type sequence, and the only comparison is between a prey density of 2 (in each patch type) and another one of 16.

Most of the plots in the (A)-series figures show a trend which is similar to that of Holling's Type-II functional response curve in the sense that the graphs decelerate to an upper asymptote. I have borrowed the phrase "Type-II curve" from the functional response concept to refer to such curves, though no relationship between the two is implied.

### 8.1.3.3 OPTIMAL PATCH CHOICE

In essence the theory of Optimal Patch Choice states that the foraging behaviour of an animal would be optimal if it demonstrated differential exploitation of patches of different profitability when given a choice. Thus, "better" quality patches (patches with higher prey density) ought to be exploited relatively more than "worse" ones. In this experiment the predator was provided with only one patch type at a time and so its response to patches of different prey density can only be inferred from its activities within the patch and the outcome of its activities, i.e. the degree of exploitation of patches.

(A) THE OUTCOME OF PREDATOR SEARCH (DIFFERENTIAL RESPONSE)

(i) Prey Eaten : The pooled response of TR-I and TR-II suggested that the number of prey eaten increased with an increase in prey density per patch (Fig. 8.1.4A). But a regression line fitted to the data points gave a slope ( $b = 0.061$ ), which was not significantly different from zero at  $P=0.05$ . On the other hand, an increase in the number of prey eaten (Fig. 8.1.4B) upto the third patch in the sequence was found in both TR-III and TR-IV, after which there was a decline. The ascending phase of the latter graph could be a result of an increase in the hunger level, while the descending phase of the graph was, perhaps, due to satiation. A more detailed analysis of the feeding behaviour of the beetle is presented in Sec.(8.1.3.7) below.

(ii) Eggs Laid : The number of eggs laid at a patch also showed a positive relationship with patch type and the pooled response of TR-I and TR-II gave a Type-II curve (Fig. 8.1.5A). By contrast, the curves for both TR-III and TR-IV (Fig. 8.1.5B) showed a declining trend with patch type sequence; but they remained separate from one another, with the line for TR-III lying much below that of TR-IV, which shows that consistently more eggs were laid in TR-IV with 16 prey per patch than in TR-III with only 2 prey per patch.

(iii) Total Time Spent : The pooled data from TR-I and TR-II for the total time spent on the patches gave a sigmoid curve when plotted against patch type (Fig. 8.1.6A), which signifies that the beetle demonstrates differential allocation of foraging time in relation to prey density per patch. In TR-III (Fig. 8.1.6B), there was a general increase in the amount of time spent on the patch in relation to patch type sequence, which shows that when consecutive patches of lower prey density are provided, the later patches are searched more intensely. The graph for TR-IV, however, shows an oscillation between higher and lower values for time spent in relation to patch type sequence (Fig. 8.1.6B), which suggests that the time spent at a patch does not depend only on the prey density at the patch but perhaps it is also influenced by other factors such as hunger level and ovipositional urge. The influence of the latter becomes apparent only when patches of higher prey density are consistently provided to the predator.

Similar trends in the numbers of prey eaten, eggs laid, and the time

Fig. 8.1.4

The numbers of prey eaten (means  $\pm$  S.E.) from patches of different prey densities (patch types).

- (A) Pooled data from TR-I and TR-II. The linear regression ( $Y = 0.061X + 0.54$ ) fitted to the data points was not significant ( $t=1.84$ ;  $P<0.1$ ).
- (B) Data from TR-III (●) and TR-IV (■) plotted against patch type sequence.

Fig. 8.1.5

The numbers of eggs laid (means  $\pm$  S.E.) at patches of different prey densities (patch types).

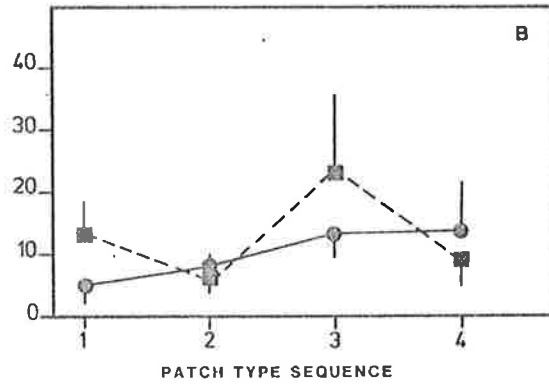
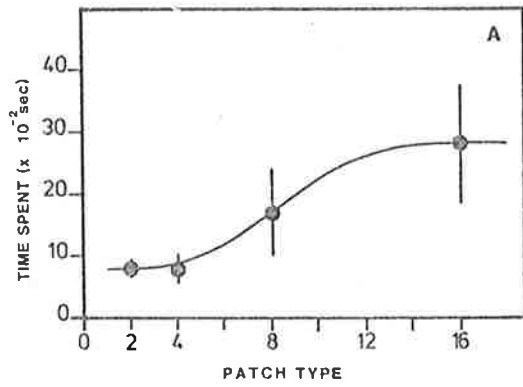
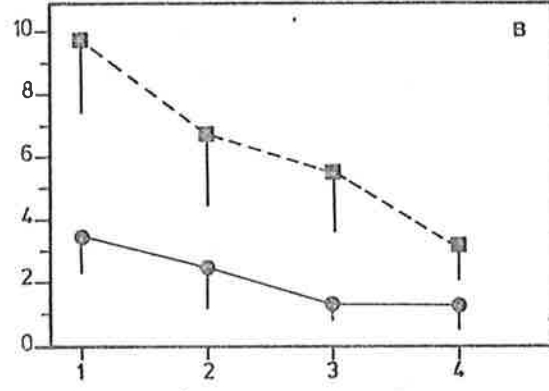
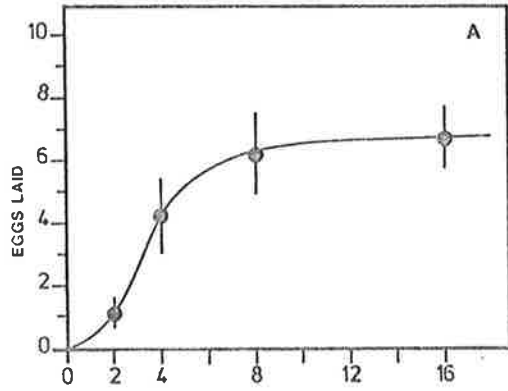
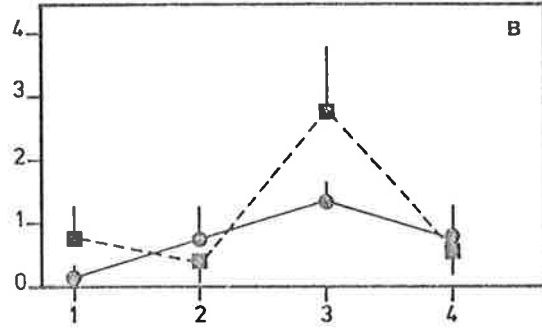
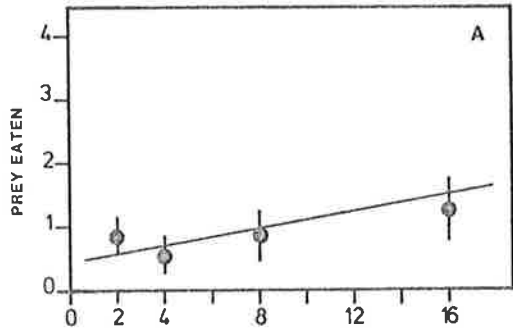
- (A) Pooled data from TR-I and TR-II. The line was fitted to the data points by eye.
- (B) Data from TR-III (●) and TR-IV (■) plotted against patch type sequence.

Fig. 8.1.6

Time spent ( $\times 10^{-2}$  sec) (mean  $\pm$  S.E.) at patches of different prey densities (patch types).

- (A) Pooled data from TR-I and TR-II. The line was fitted to the data points by eye.
- (B) Data from TR-III (●) and TR-IV (■) plotted against patch type sequence.





spent in relation to patch type were found in the experiments described in Chapters 6 and 7. Thus the trends have remained consistent in all the three experiments conducted under three different sets of conditions.

(B) ANALYSIS OF SEARCH BEHAVIOUR PRODUCING DIFFERENTIAL RESPONSE

(a) Number of visits to patches : The number of times the beetle visited a particular patch type was found to decrease with an increase in prey density per patch (Fig. 8.1.7). The graph in the pooled response decelerates to a lower asymptote with increase in prey density per patch (Fig. 8.1.7A). A general decline in the number of visits to a patch was also noticed in TR-III and TR-IV (Fig. 8.1.7B). However, the decline in TR-III was followed by a steep increase after the 3rd patch in the sequence. This trend is an index of a beetle's "persistence" to patches of different prey density and suggests that it searches patches with lower prey density more thoroughly.

(b) Visits resulting in encounter with prey : The data from TR-I and TR-II on the relationship between patch type and the percentage of visits to a patch that lead to an encounter with prey also follows a Type-II curve (Fig. 8.1.8A), and the trends for TR-III and TR-IV are spread apart, with the former lying below the latter (Fig. 8.1.8B). These trends therefore suggest, as may be expected, that an increase in prey density at a patch increases the predator's chance of encountering prey.

(c) Visits leading to patch ATTENDED : The percentage of visits to any patch type that lead to it being ATTENDED (visits resulting in prey eaten and/or eggs laid) was also found to increase with patch type (Fig. 8.1.9). The pooled response of TR-I and TR-II once again follows the Type-II curve (Fig. 8.1.9A), and the line for TR-III lies below that of TR-IV (Fig. 8.1.9B). The trends in the "A" and "B" figures indicate that at patches of lower prey density the proportion of visits that lead to patch ATTENDED is lower than that at patches of higher prey density. The higher prey density, therefore, seems to stimulate the predator to eat prey and/or lay eggs.

(d) Prey Finding Time (PFT) : The Prey Finding Time (PFT) will be defined as the time interval between entry into patch and the first encounter with

Fig. 8.1.7

The numbers of VISITS (mean  $\pm$  S.E.) to patches of different prey densities (Patch types).

(A) Pooled data from TR-I and TR-II. The line was fitted to the data points by eye.

(B) Data from TR-III (●) and TR-IV (■) plotted against patch type sequence.

Fig. 8.1.8

The percentage of VISITS (means  $\pm$  S.E.) to patches of different prey densities (patch types) resulting in encounter with prey.

(A) Pooled data from TR-I and TR-II. The line was fitted to the data points by eye.

(B) Data from TR-III (●) and TR-IV (■) plotted against patch type sequence.

Fig. 8.1.9

The percentage of VISITS (means  $\pm$  S.E.) to patches of different prey densities (patch types) resulting in the ATTENDING of the patch.

(A) Pooled data from TR-I and TR-II. The line was fitted to the data points by eye.

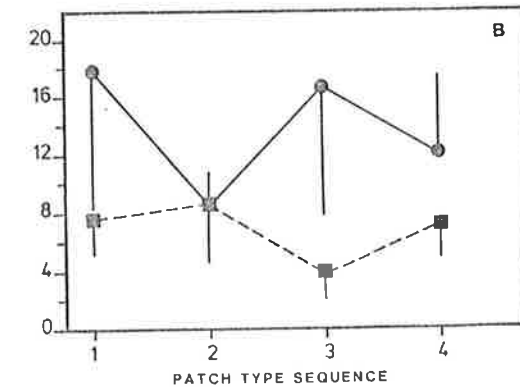
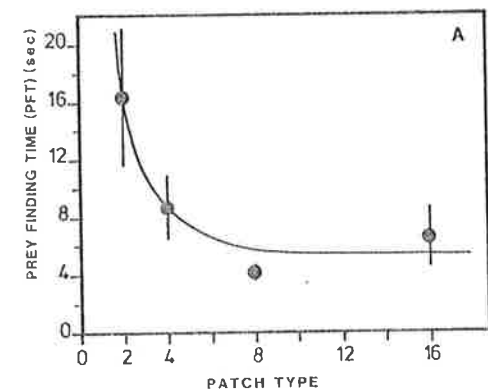
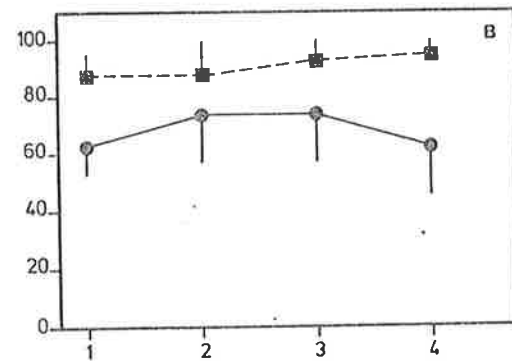
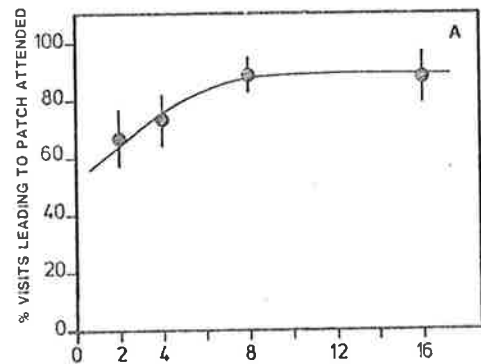
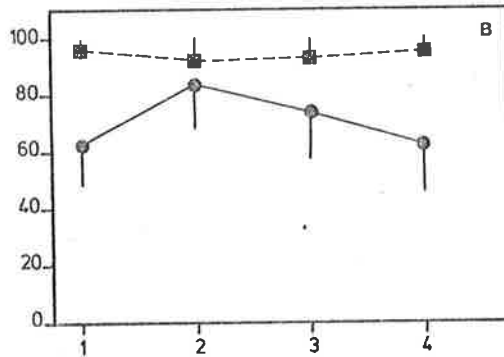
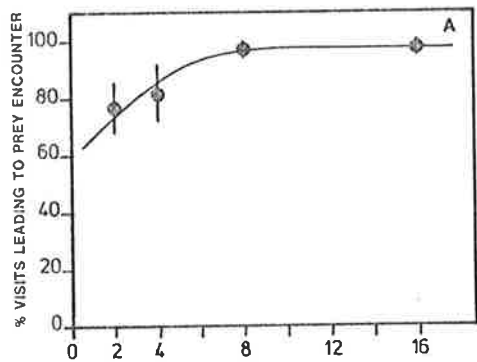
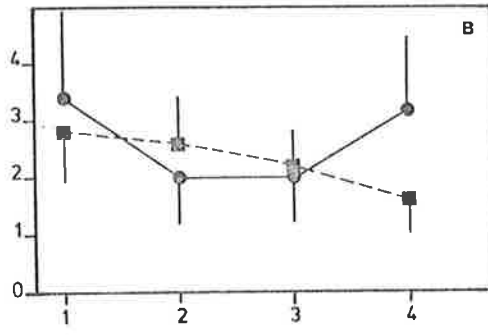
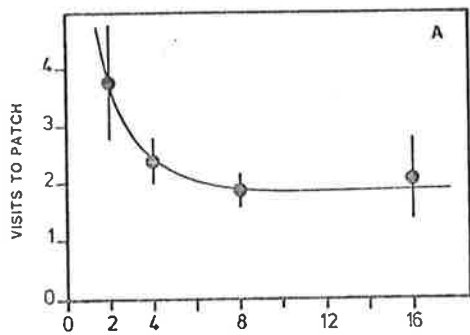
(B) Data from TR-III (●) and TR-IV (■) plotted against patch type sequence.

Fig. 8.1.10

The prey finding time (PFT) (means  $\pm$  S.E.) at patches of different prey densities (patch types).

(A) Pooled data from TR-I and TR-II. The line fitted to the data points by eye.

(B) Data from TR-III (●) and TR-IV (■) plotted against patch type sequence.



prey. The pooled response of TR-I and TR-II decreased with an increase in prey density per patch and then decelerates to a lower asymptote (Fig. 8.1.10A); and the curve for TR-III (the lower density) lies above that of TR-IV (the higher density) (Fig. 8.1.10B), showing that the prey density at the patch influences the chance of the predator's encounter with the first prey. A higher PFT at patches of lower prey density indicates that the beetle is not attracted to the prey from a distance and so the results provide an indication that the searching behaviour of the beetle could be random.

(e) Encounters with prey : Assuming a fixed mean distance between prey, an increase in the number of prey in a patch of a given size would lead to an increase in the area covered by the prey's distribution. The probability of a predator encountering a prey ought then to increase with an increase in prey density, and one would expect the total number of encounters with prey to increase with an increase in prey density per patch.

The pooled response of TR-I and TR-II is given in Fig. 8.1.11A. As expected, the total number of encounters with prey followed a linear relationship and it increased with an increase in prey density per patch (Fig. 8.1.11A). The fitted regression line had a positive slope which was significantly different from zero ( $t=6.26$ ;  $P<0.001$ ). The trend for TR-III was a line parallel to the horizontal which lay well below that of TR-IV (Fig. 8.1.11B), indicating a consistently large difference in the results of the two treatments. The general decline in the total number of encounters in TR-IV was, perhaps, due to the beetle's acclimatization to patches of higher prey density, satiation and/or temporary exhaustion of egg supply.

(f) Interval between encounters : From a follow-up of the above, we may expect that the number of encounters per unit time would also increase with an increase in prey density per patch. And as a corollary, the time interval between encounters should decrease with an increase in patch quality.

The pooled response of TR-I and TR-II is given in Fig. 8.1.12A. As expected, there was a decline in the time interval between successive encounters when the pooled response of TR-I and TR-II was plotted against

Fig. 8.1.11

Total numbers of encounters with prey (means  $\pm$  S.E.) at patches of different prey densities (patch types).

- (A) Pooled data from TR-I and TR-II. The linear regression ( $Y = 3.18X + 1.14$ ) fitted to the data points was significant ( $t=6.26$ ;  $P<0.001$ ).
- (B) Data from TR-III (●) and TR-IV (■) plotted against patch type sequence.

Fig. 8.1.12

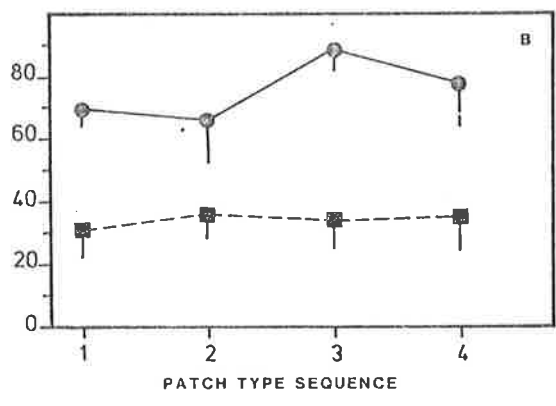
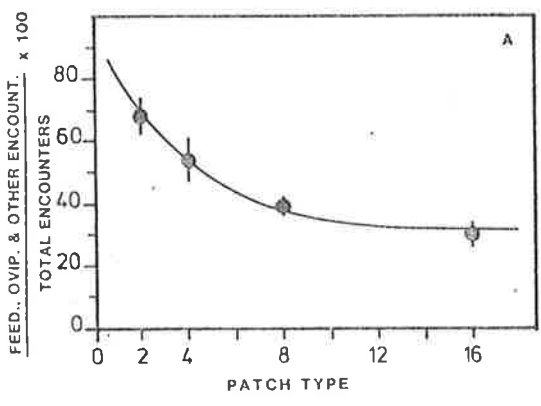
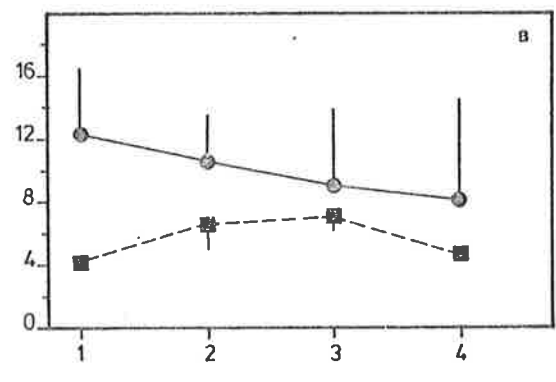
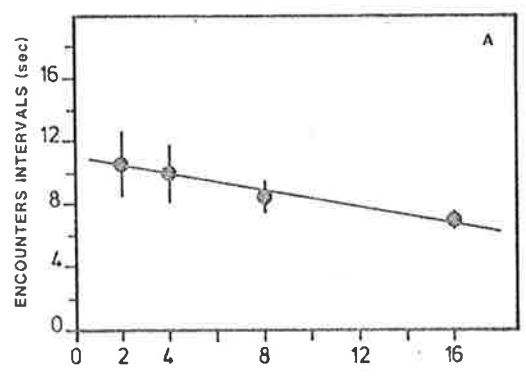
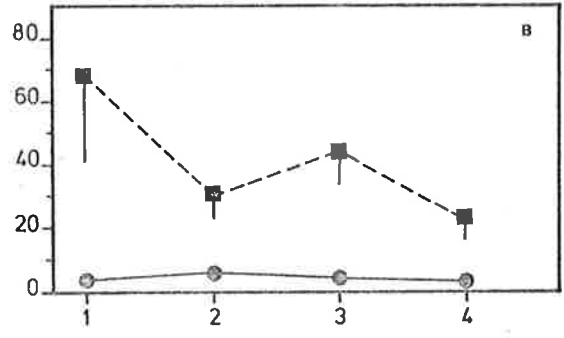
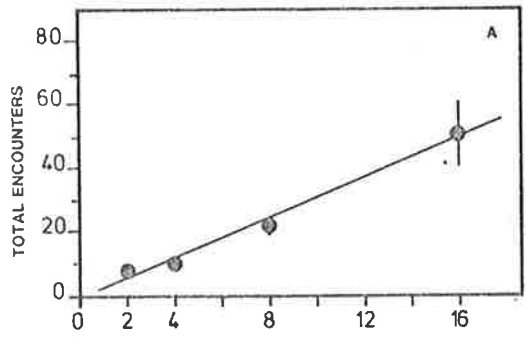
The intervals between successive encounters with prey (means  $\pm$  S.E.) at patches of different prey densities (patch types).

- (A) Pooled data from TR-I and TR-II. The linear regression ( $Y = -0.27X + 11.05$ ) fitted to the data points was significant ( $t=8.12$ ;  $P<0.05$ ).
- (B) Data from TR-III (●) and TR-IV (■) plotted against patch type sequence.

Fig. 8.1.13

Means  $\pm$  S.E. of the percentages of the TOTAL encounters with prey, that resulted in feeding, oviposition, or other stoppages on prey.

- (A) Pooled data from TR-I and TR-II. The line was fitted to the data points by eye.
- (B) Data from TR-III (●) and TR-IV (■) plotted against patch type sequence.



patch type, and the fitted regression showed a negative slope ( $Y = -0.267X + 11.05$ ) which was significantly different from zero ( $t=8.1231$ ;  $P<0.05$ ) (Fig. 8.1.12A). The responses for TR-III and TR-IV were again widely separated lines (Fig. 8.1.12B) with the line for the former lying much above that of the latter.

Since an increase in prey density per patch decreases the time interval between encounters (Fig. 8.1.12A), there would be an increase in the frequency of encounters with prey at patches of higher prey densities. If every encounter with prey results in the recording of an event in the predator's memory; then the frequency of these recorded events would help the predator assess the profitability of the patch; an increase in frequency of encounters would "show" a higher prey density, and a more profitable patch.

(g) Encounters leading to an outcome (prey eaten and/or eggs laid) : The next question that arises is the relation between the number of encounters with prey and the number of feeds or ovipositions.

The percentage of encounters that result in an outcome (i.e., feeding, oviposition or other stoppages on the prey) is shown in Fig. 8.1.13A for the pooled response of TR-I and TR-II. The percentage of encounters resulting in an outcome, decelerated to a lower asymptote with an increase in prey density per patch (Fig. 8.1.13A). In Fig. 8.1.13B, the line for TR-III was situated above that of TR-IV. The results from Fig. 8.1.13A suggest that an increase in the number of encounters with prey does not result in a corresponding increase in the number of prey eaten and/or eggs laid as the prey density per patch increases. Or, in other words, the rate at which the number of encounters increase is not the same as the rate at which the number of prey eaten and/or eggs laid increase.

### (C) OPTIMAL PATCH CHOICE — MAIN CONCLUSIONS

The main inferences drawn from the analysis of the searching behaviour of the beetle are as follows :

- (1) the number of VISITS to a patch decreases with an increase in prey density per patch (Fig. 8.1.7A),
- (2) the number of VISITS resulting in an encounter with prey increases with an increase in prey density per patch (Fig. 8.1.8A),



- (3) the number of VISITS resulting in the patch ATTENDED (prey eaten and/or eggs laid) increases with an increase in prey density per patch (Fig. 8.1.9A),
- (4) the prey finding time (PFT) decreases with an increase in prey density per patch (Fig. 8.1.10A),
- (5) there is a positive linear relationship between the number of encounters with prey and prey density per patch (Fig. 8.1.11A),
- (6) the interval between encounters decreases with an increase in prey density per patch (Fig. 8.1.12A), and
- (7) the percentage of encounters that result in an outcome (prey eaten and/or eggs laid) decreases with an increase in prey density per patch (Fig. 8.1.13A).

The results presented above provide evidence that the predator exercises discrimination among patch types on the basis of the prey density per patch, and that the latter directly influences the number and frequency of encounters with prey by which the predator is able to "assess" the profitability of the patch and then respond differentially by eating relatively more prey, laying more eggs, and spending more time at patches of higher prey density. Smith and Sweetman (1974) also found that great tits, (Parus major), had the ability to use prey size and prey density to make an assessment of the average profitability of a feeding area and differentially allocate their foraging time on the basis of such an assessment.

An assessment of the profitability of a patch through the frequency of encounters with prey implies the presence of some sort of "memory" in the forager. If this is so, the question is -- what is the life of such a memory? Does this memory last through the period between leaving one patch and finding another and so influence the outcome of search in the subsequent patch? If the memory does last through the duration of search between patches, the outcome of search within a patch would not only be influenced by the hunger level, the ovipositional urge and the prey density at the patch but also by the predator's "experience" at the last patch. The prey density at the last patch attended would then also influence the outcome of search in the subsequent patch. Therefore, the sequence in which prey patches of different prey densities are found should be of vital significance in influencing the outcome of search within a patch.

However, the results presented above show that if patches of different prey densities are provided to a searching predator in an opposite sequence (TR-I and TR-II), the trend in the results are reversed (Fig. 8.1.3), which demonstrates that the prey density at the patch plays a more important role than the sequence in which patches of prey density are provided. Also, even when patches of the same prey density are provided in a sequence (TR-III and TR-IV), the influence of prey density at the patch appears to be more pronounced. The plot of the data for different parameters from TR-III lies either above or below that of TR-IV depending on the nature of the event (B-series figures). There were few instances in which some trend in the B-series figures were discernible, viz. prey eaten (Fig. 8.1.4) and eggs laid (Fig. 8.1.5), but these can be explained on the basis of changes in hunger level and ovipositional urge, which in turn influence the motivation to search for prey (note the effect of hunger level on the index of activity; Chapter 6.2). Thus, though there is an indication of the presence of short term "memory", which the predator uses to assess the profitability of the patch, there was no evidence to indicate that such a memory lasts over the period of search between leaving one patch and finding another.

The "assessment rule" of Green (1984) also gives credence to the idea that animals use their experience in a patch in order to decide when to leave a patch. It tells whether the animal should leave a patch at any time according to how many prey have been found up to that time. Therefore, it is implied in the "assessment rule" that some sort of "memory" is involved in the assessment of the profitability of the patch. Thus, the explanations provided in support of the trends observed in the results discussed above are in tune with the basic concept of the assessment rule. However, by ignoring the motivational and physical state of the forager, the assessment rule adopts a very simplistic view of the whole foraging process, i.e. the assessment rule overlooks the the influence of past history of the forager on the outcome of search in the current patch. The data obtained from TR-III and TR-IV, and presented in the (B)-series figures, stress the need to recognize the past history of the forager in drawing conclusions on its searching behaviour in the current patch.

#### 8.1.3.4 DIFFERENTIAL ALLOCATION OF FORAGING TIME

##### (A) THE TOTAL TIME

The total time spent at a patch, presented in Fig. 8.1.6 and discussed in section 8.1.3.1(iii), indicated that the beetle demonstrated differential allocation of searching time in relation to patches of different prey densities. The results of the pooled response of TR-I and TR-II have been replotted in Fig. 8.1.14, for the sake of convenience in the following discussion. As pointed out earlier, the relationship was of a sigmoid form, and a similar trend in the relation between time spent at a patch and prey density per patch was also found in the experiment described in Chapter 6, in spite of the design of the two experiments being very different. The results expressed by the sigmoid curve follow the theoretical predictions of Hassell and May (1974) who referred to such differential allocation of searching time as the "aggregative" response in predators. Using a behavioural model, based on the searching behaviour of the predator before and after an encounter with prey (Fig. 8.1.15), Hassell and May (1974) explained that the graph took a sigmoid form because the predators were unable to discriminate strongly in areas of lower prey densities and again in areas of higher prey densities; but they discriminate very strongly at intermediate prey densities. Considering a hypothetical ideal situation, they divided the searching behaviour of a predator into two phases : (a) Phase-I : corresponding to a period of high turning rate and low speed of movement following an encounter, and (b) Phase-II : corresponding to a "normal" pattern of movement with lower turning rate and greater speed prior to encounter and following Phase-I behaviour. After an encounter with a prey, the movement of the predator remains in phase-I for a short period. If no prey are encountered during the phase-I, it is followed by phase-II until another prey is encountered or the "edge" of the area reached; then the predator leaves.

Their behavioural model produced two plateaux, one lower and another higher for low and high prey densities respectively. These were joined by a line with a steep slope for intermediate prey densities (Fig. 8.1.15). In the region of the lower plateau, either the predator has to leave the patch without finding any prey or if one is found, without encountering a further one. In the region of the higher plateau, the prey density is so high that successive prey are encountered while the predator's searching behaviour remains in phase-I; and the predator remains in this phase until

Fig. 8.1.14

Time spent ( $\times 10^{-2}$  sec) (mean  $\pm$  S.E.) at patches of different prey densities (patch types). Pooled data from TR-I and TR-II. The line was fitted to the data points by eye.

Fig. 8.1.15

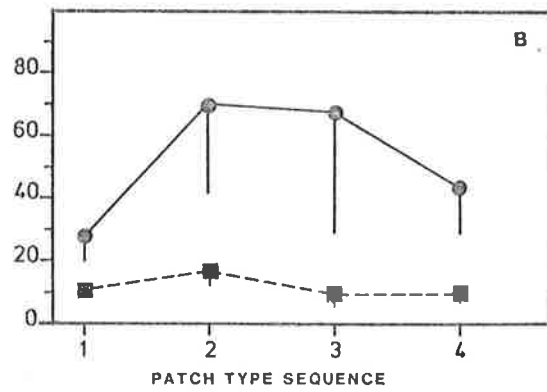
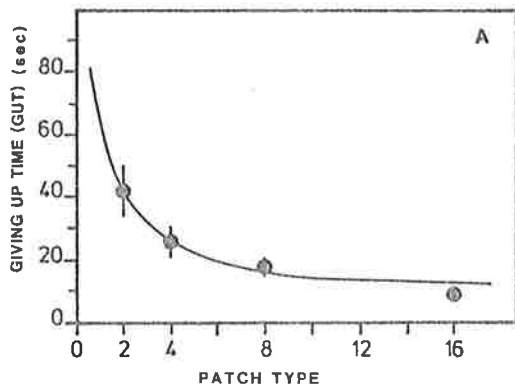
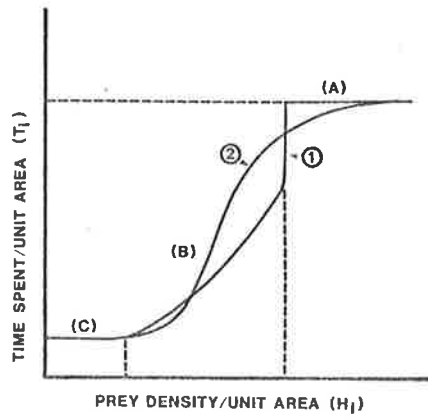
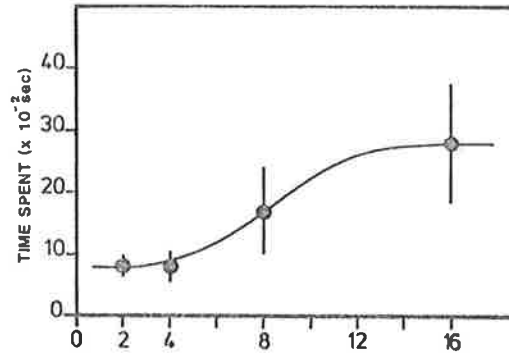
Behavioural model of Hassell and May (1974) for the optimal allocation of foraging time by a predator searching for prey in areas of different prey densities, (1) assuming a FIXED distance between prey, and (2) assuming a VARIABLE distance between prey.

- (A) areas of high prey densities
- (B) areas of intermediate prey densities
- (C) area of low prey densities

Fig. 8.1.16

The giving-up-time (GUT) (means  $\pm$  S.E.) of beetles searching for patches of different prey densities (patch types).

- (A) Pooled data from TR-I and TR-II. The line fitted to the data points by eye.
- (B) Data from TR-III (  $\oplus$  ) and TR-IV (  $\blacksquare$  ) plotted against patch type sequence.



leaving the patch. At intermediate prey densities, the predator encounters a further prey only after reverting to phase-II behaviour. Therefore, there is a continuous oscillation between phase-I and phase-II behaviours, and this results in more time spent in areas of higher rather than lower prey densities.

The above predictions were based on the idealized assumption that the prey individuals were placed exactly unit distances apart. However, when variable distances between prey were included in the model, the sharp edges were smoothed out and the graph adopted a true sigmoid form. Hassell and May pointed out that "the response to prey density per unit area can, over any particular range, vary from markedly sigmoid to apparently convex, depending on where the transition regions in the basic model occur". Hassell (1978b) provides numerous examples from the literature of the "aggregative responses" of parasites and predators adopting various forms, ranging from convex to sigmoid. Bond (1980) found an alternation of phase-I and phase-II in the searching behaviour of the green lacewing, Chrysopa carnea.

No attempt was made to fit Hassell and May's model to the present data because information on a number of parameters required by the model was lacking. So the explanation of the results on the basis of the predictions of the model is only qualitative. An analysis of the searching behaviour of the beetle in terms of turning rates and speed of movement in relation to encounters with prey (Chapter 8.2) also appears to support the above explanation based on the predictions of the behavioural model of Hassell and May (1974).

#### (B) THE GIVING-UP-TIME (GUT)

The GUT defined as the time interval between the last encounter with a prey and the time of leaving a patch, has been plotted against patch type in Fig. 8.1.16. The results show an interesting exception to what has been reported in the literature. In Fig. 8.1.16A, the graph for the pooled response of TR-I and TR-II decelerates to a lower asymptote with an increase in prey density per patch. In Fig. 8.1.16B, the plot of GUT for TR-III lies above that of TR-IV showing that the GUT is consistently higher at prey density 2 than at prey density 16.

A number of models have predicted what form the GUT should take, but it is still a debatable issue. One hypothesis predicts a fixed GUT

regardless of the patch quality (Krebs et al., 1974; Hassell and May, 1974; Murdoch and Oaten, 1975; and Cook and Hubbard, 1977). A second hypothesis predicts that GUT should increase with an increase in patch quality (McNair, 1982; van Alphen and Galis, 1983; Green, 1984). Proponents of the second hypothesis consider GUT as an index of the persistence of a predator and argue that a predator ought to be more persistent in patches of higher profitability.

My results show that neither of these hypotheses is true for Rodolia, but rather that the GUT decreases with an increase in patch quality, as was true for a frugivorous parasite, Rhagoletis pomonella (Roitberg et al., 1982). In fact, one can argue that a higher GUT at patches of lower quality is also indicative of the persistence of a predator, and that such persistence shows that even patches of lower quality are thoroughly searched once the first prey has been encountered. In addition, patches of lower quality are more frequently visited than those of higher quality (section 8.1.3.3.2 above). Thus higher frequency of visits plus a higher GUT at patches of lower quality may be expected to increase the overall efficiency of the predator.

Another reason for the different trend of my results could be as follows. The first hypothesis (fixed GUT) may be false because it wrongly draws conclusions about GUT from the marginal value theorem (McNair, 1982; Green, 1984). And the second hypothesis (increase in GUT with an increase in patch quality) assumes that the profitability of the patches are not good enough to satiate the predator within the period of investigation i.e., no importance is given to the hunger level of the predator (or to the limitation of egg supply with ovipositing predators). However, in my experiments, the patches of higher prey density (with prey density 8 & 16) were more than enough to satiate the predator. Rodolia eats an average of 8 II-instar scales per day, and at each feeding bout up to a maximum of 3 prey are eaten (see section 8.1.3.7 below). Therefore patches with prey densities of 4 and above would always be more than enough to temporarily satiate the beetle. Thus what is observed as GUT at patches of prey density 4 and above are only estimates of the PHASIC BEHAVIOUR of the predator which suggests that an animal does not necessarily stay at a patch even if optimum conditions are provided (Amos and Waterhouse, 1967).

My results, therefore, indicate that most of the models concerning time spent on a patch have to be rejected for Rodolia : the fixed time

hypothesis (Krebs, 1973), the fixed number hypothesis (Gibb, 1962), the fixed GUT hypothesis (Krebs et al., 1974; Murdoch and Oaten, 1975; Cook and Hubbard, 1977); increasing GUT hypothesis (McNair, 1982) and also Waage's (1979) behavioural model based on the waning of the response to the patch edge. My results are, however, in agreement with the behavioural model of the "aggregative response" proposed by Hassell and May (1974).

#### 8.1.3.5 PATCH SELECTION AND PATCH TIME ALLOCATION AS ASPECTS OF THE SAME PHENOMENON

From the foregoing results, it is therefore clear that patches of higher profitability are given preference to those of lower profitability both in terms of exploitation and the duration for which the predator stays at those patches. Thus, the phenomenon of patch selection and patch time allocation are indeed inter-related, as pointed out by Waage (1979, 1983). Both feeding and oviposition are time consuming activities; therefore, if relatively more prey are eaten and more eggs are laid at patches of higher prey densities, then the searching predator must spend relatively more time at such patches. Thus, to consider the phenomenon of patch selection (Optimal Patch Choice) as divorced from that of patch time allocation (Optimal Allocation of Foraging Time) is to ignore biological realism.

#### 8.1.3.6 A CONCEPTUAL MODEL OF OPTIMAL FORAGING

By the help of a flow diagram (Fig. 8.1.17), an attempt has been made to summarize the sequence of events that might be operating to influence the predator's decision to emigrate from a prey patch.

Normally the hunger level and the prey density at a patch should influence any predator's decision to emigrate from a patch, but since we are dealing with a female predator which is also capable of laying eggs, a third factor, its ovipositional urge, would also be of immense importance.

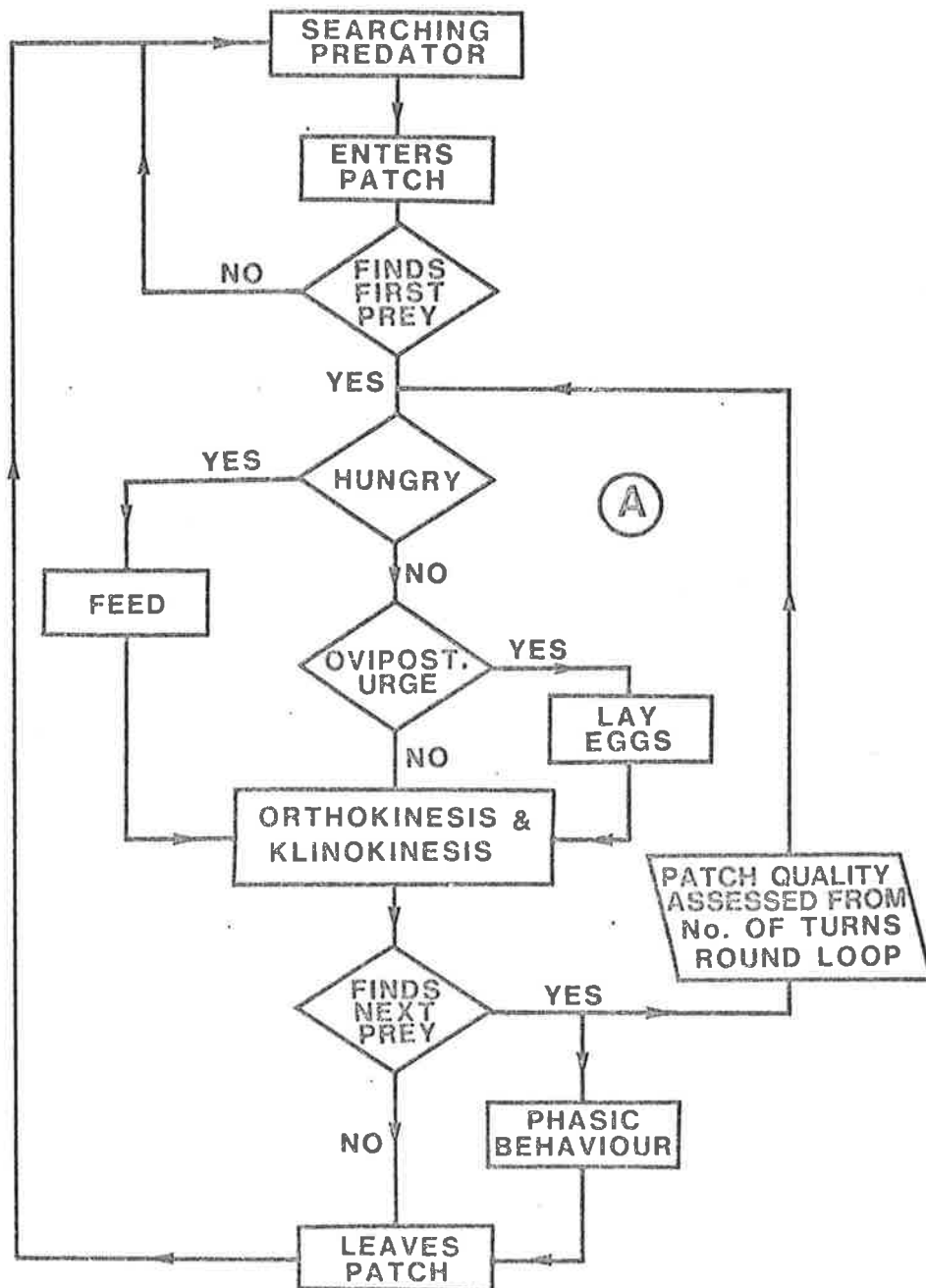
Let us assume that a female predator is searching "randomly" in an arena which has a number of patches with varying prey densities. If this predator enters a patch and wanders in search of prey, it might spend some time in exploration; if it does not find any prey, it will leave the patch in search of another. This duration of unsuccessful exploration would depend on its hunger level and its ovipositional urge, increasing as these increase. In other words, the predator would be more "persistent" in its search as its hunger level and ovipositional urge increased. In another



Fig. 8.1.17

- Conceptual model of searching by a predator for patchily distributed prey, describing the factors affecting the predator's decision to emigrate from a prey patch.

# CONCEPTUAL MODEL OF SEARCHING



laboratory experiment, the index of activity was found to increase with an increase in hunger level, later declining till death. Such a trend in the index of activity can be interpreted as an increase in "persistence" in searching activity with an increase in hunger (see Chapter 6.2).

On the other hand, if the predator finds a prey, the interval between entry into the patch and the first encounter with prey would depend on the prey density at the patch, simply because every extra prey present would increase the probability of the predator's encounter with a prey (PFT; Fig. 8.1.10). Having found the first prey, the predator could either feed on it, lay eggs or just walk away in search of more prey. The decision whether to feed or oviposit would depend on the hunger level and ovipositional urge respectively. (When the prey is very large in size (e.g. adult scales) the feeding and egg laying may take place on the same prey). The feeding decision would have priority over the decision to oviposit, because the motivation for self survival would always have priority over the survival of its progeny. There are numerous examples of insects, including Coccinellids, which reabsorb their eggs or feed on those already laid when food is scarce.

After an encounter with the first prey, the searching behaviour of the predator is altered. The predator shows ORTHOKINETIC (reduction in walking speed) and KLINOKINETIC (increase in turning rates) responses (Hassell and May's (1974) Phase-I searching behaviour). Such a behaviour increases the predator's chances of finding more prey, especially when prey distribution is contagious. If there are no more prey present, the predator would leave the patch in search of another. However, if there are more prey, with each subsequent encounter with another prey, the predator would go through the same decision making processes over and over again till it has eaten up all the prey present or until it is satiated and has temporarily exhausted its egg supply. So if the prey density is higher than the predator's immediate needs, the predator may still leave the patch because no predator stays in a patch indefinitely even if optimum conditions are provided in accordance to what has been termed PHASIC BEHAVIOUR in animals (Amos and Waterhouse, 1967).

Each time the predator encounters another prey and goes through the decision loop "A", it registers an event in its "memory". As a result of the frequency with which these events are registered (the rate of finding prey), the predator acquires an estimate of the prey density at the patch,

Table 8.1.2

DURATIONS (IN SECONDS) OF FEEDS AND RESTS AND OF THE INTERVALS BETWEEN THEM FOR EACH FEED FOR EACH OF THE FIVE BEETLES IN EACH OF THE FOUR TREATMENTS.

TREAT	BEETLE	FEED No.	FEEDING DURATION	INTERVAL BET. FEEDS	INTO	RESTS AND INTERVALS BETWEEN THEM						
						RS1	INT1	RS2	INT2	RS3	INT3	RS4
I	1	1	641	6358*	-	-	-	-	-	-	-	-
		2	645	5536	5	13	214	122	-	-	-	-
		3	284	13868	-	-	-	-	-	-	-	-
		4	398	148	-	-	-	-	-	-	-	-
		5	254	18	-	-	-	-	-	-	-	-
		6	235	190	272	4041	5	520	-	-	-	-
I	2	1	604	5614*	96	42	-	-	-	-	-	-
		2	566	401	-	-	-	-	-	-	-	-
		3	333	11497	-	-	-	-	-	-	-	-
		4	303	2	50	28	43	63	-	-	-	-
		5	322	265	-	-	-	-	-	-	-	-
I	3	0	-	-	-	-	-	-	-	-	-	
I	4	1	447	6557*	-	-	-	-	-	-	-	-
		2	664	0	7	110	62	10	20	244	-	-
		3	311	13195	-	-	-	-	-	-	-	-
		4	346	1	102	48	-	-	-	-	-	-
		5	632	3741	-	-	-	-	-	-	-	-
I	5	1	671	6833*	-	-	-	-	-	-	-	-
		2	477	28309	-	-	-	-	-	-	-	-
		3	422	6	1	91	-	-	-	-	-	-
		4	381	466	1154	62	640	3514	-	-	-	-
II	1	1	232	17721*	1	24	327	32	-	-	-	-
		2	395	387	108	17	-	-	-	-	-	-
II	2	1	456	2601*	627	123	-	-	-	-	-	-
		2	424	760	35	10	-	-	-	-	-	-
		3	686	87	54	2134	-	-	-	-	-	-
		4	426	10016	9	93	-	-	-	-	-	-
		5	712	8070	-	-	-	-	-	-	-	-
		6	347	4285	-	-	-	-	-	-	-	-
		7	272	2	85	155	-	-	-	-	-	-
II	3	1	419	30484*	-	-	-	-	-	-	-	-
		2	229	270	4	70	20	47	26	67	-	-

(continued)

TREAT = TREATMENTS (for details refer Table 8.1.1).

INTO = interval between FEED and first REST

INT1 to INT3 represent intervals between subsequent RESTS after the first REST

RS1 to RS4 represent successive RESTS after a FEED

\* Time interval from the start of experiment to first FEED

| | Represents one FEEDING BOUT (including consecutive FEEDS within 30 sec)

Table 8.1.2 (continued)

TREAT	BEETLE	FEED No.	FEEDING DURATION	INTERVAL BET. FEEDS	INTO	RESTS AND INTERVALS BETWEEN THEM						
						RS1	INT1	RS2	INT2	RS3	INT3	RS4
II	4	1	361	3356*	411	70	-	-	-	-	-	-
		2	80	499	36	66	-	-	-	-	-	-
		3	433	4303	-	-	-	-	-	-	-	-
		4	418	1	-	-	-	-	-	-	-	-
		5	499	1	34	39	1654	4043	-	-	-	-
		6	491	24114	39	6	37	79	6	27	-	-
II	5	1	491	6963*	-	-	-	-	-	-	-	-
		2	275	5037	-	-	-	-	-	-	-	-
		3	236	0	35	103	-	-	-	-	-	-
III	1	1	686	13911*	111	28	13	30	31	100	-	-
III	2	1	374	10880*	-	-	-	-	-	-	-	-
		2	437	1	13	21	33	9	54	88	49	57
		3	374	11022	-	-	-	-	-	-	-	-
III	3	1	521	8246*	-	-	-	-	-	-	-	-
		2	331	6	15	75	44	91	7	4	30	30
		3	399	3457	-	-	-	-	-	-	-	-
		4	584	2	6	164	16	14	39	935	-	-
		5	1189	11293	-	-	-	-	-	-	-	-
		6	1289	1	5	142	42	33	19	21	4	1764
III	4	1	511	8147*	11	30	48	14	-	-	-	-
III	5	1	687	14023*	6	59	18	115	-	-	-	-
		2	704	10630	-	-	-	-	-	-	-	-
		3	831	66	19	415	34	21	60	155	-	-
		4	723	9167	-	-	-	-	-	-	-	-
		5	744	5	-	-	-	-	-	-	-	-
IV	1	1	232	9207*	-	-	-	-	-	-	-	-
		2	452	4	11	26	-	-	-	-	-	-
		3	359	11536	-	-	-	-	-	-	-	-
		4	342	7092	-	-	-	-	-	-	-	-
		5	377	10	-	-	-	-	-	-	-	-
IV	2	1	341	14931*	-	-	-	-	-	-	-	-
		2	165	3	-	-	-	-	-	-	-	-
		3	366	3	-	-	-	-	-	-	-	-
		4	213	232	266	290	-	-	-	-	-	-

(continued)

TREAT = TREATMENTS (for details refer Table 8.1.1).

INTO = interval between FEED and first REST

INT1 to INT3 represent intervals between subsequent RESTS after the first REST

RS1 to RS4 represent successive RESTS after a FEED

\* Time interval from the start of experiment to first FEED

| Represents one FEEDING BOUT (including consecutive FEEDS within 30 sec)

Table 8.1.2 (continued)

TREAT	BEETLE	FEED No.	FEEDING DURATION	INTERVAL BET. FEEDS	INTO	RESTS AND INTERVALS BETWEEN THEM						
						RS1	INT1	RS2	INT2	RS3	INT3	RS4
IV	3	1	222	8850*	37	42	-	-	-	-	-	-
		2	223	2436	17	83	-	-	-	-	-	-
IV	4	1	259	1254*	-	-	-	-	-	-	-	-
		2	464	4	7	7	193	22	-	-	-	-
		3	500	5922	-	-	-	-	-	-	-	-
		4	387	2	-	-	-	-	-	-	-	-
		5	491	7689	-	-	-	-	-	-	-	-
		6	278	24	-	-	-	-	-	-	-	-
		7	512	1	-	-	-	-	-	-	-	-
		8	370	45	50	7	3	89	-	-	-	-
		9	427	267	-	-	-	-	-	-	-	-
		10	201	16	66	3572	82	584	-	-	-	-
IV	5	1	352	112*	41	106	-	-	-	-	-	
		2	112	623	-	-	-	-	-	-	-	

TREAT = TREATMENTS (for details refer Table 8.1.1).

INTO = interval between FEED and first REST

INT1 to INT3 represent intervals between subsequent RESTS after the first REST

RS1 to RS4 represent successive RESTS after a FEED

\* Time interval from the start of experiment to first FEED

| | Represents one FEEDING BOUT (including consecutive FEEDS within 30 sec)

thus assessing its profitability. The decision when to leave the patch is based on this assessment of patch quality i.e., how many prey have been found upto that time (Green, 1984). However, the mechanism by which this works would follow the behavioural model of "AGGREGATIVE RESPONSE" produced by Hassell and May (1974), discussed earlier.

Once the predator leaves the current patch and enters another patch, the whole process begins all over again.

#### 8.1.3.7 FEEDING BEHAVIOUR

In section 8.1.3.3.1(i), it was pointed out that the number of prey eaten per patch was not only influenced by the prey density at the patch but also by the changes in the hunger level of the predator. A detailed analysis of the feeding behaviour revealed that the distribution of FEEDS (FEED -- the act of eating ONE prey) followed a cyclic pattern, which was also influenced by the prey density of the patch.

The frequency distribution of FEEDS through the duration of the experiment has been presented in Fig. 8.1.18, and Table 8.1.2 provides data on the duration of feeding, time interval between FEEDS and the rests that follow FEEDS with intervals in between. On average, the predator takes  $441.1 \pm 23.2$  sec (Mean  $\pm$  S.E.; n=79) to consume a single II-instar prey.

The time intervals between FEEDS that are given in Table 8.1.2 are not, however, representative of the true feeding intervals because the predator did not have access to prey at all times during the course of the experiment. Still, the data show a cyclic trend in that a larger interval between FEEDS is generally followed by a few smaller intervals, thereby signifying an increase in the motivation to eat more prey with an increase in hunger level. If FEEDS separated by no more than 30 sec are considered as a single FEEDING BOUT, a maximum of three 2nd instar prey are eaten in any single FEEDING BOUT (Table 8.1.2). Thus, three 2nd instar prey can be taken as the filling capacity of the gut.

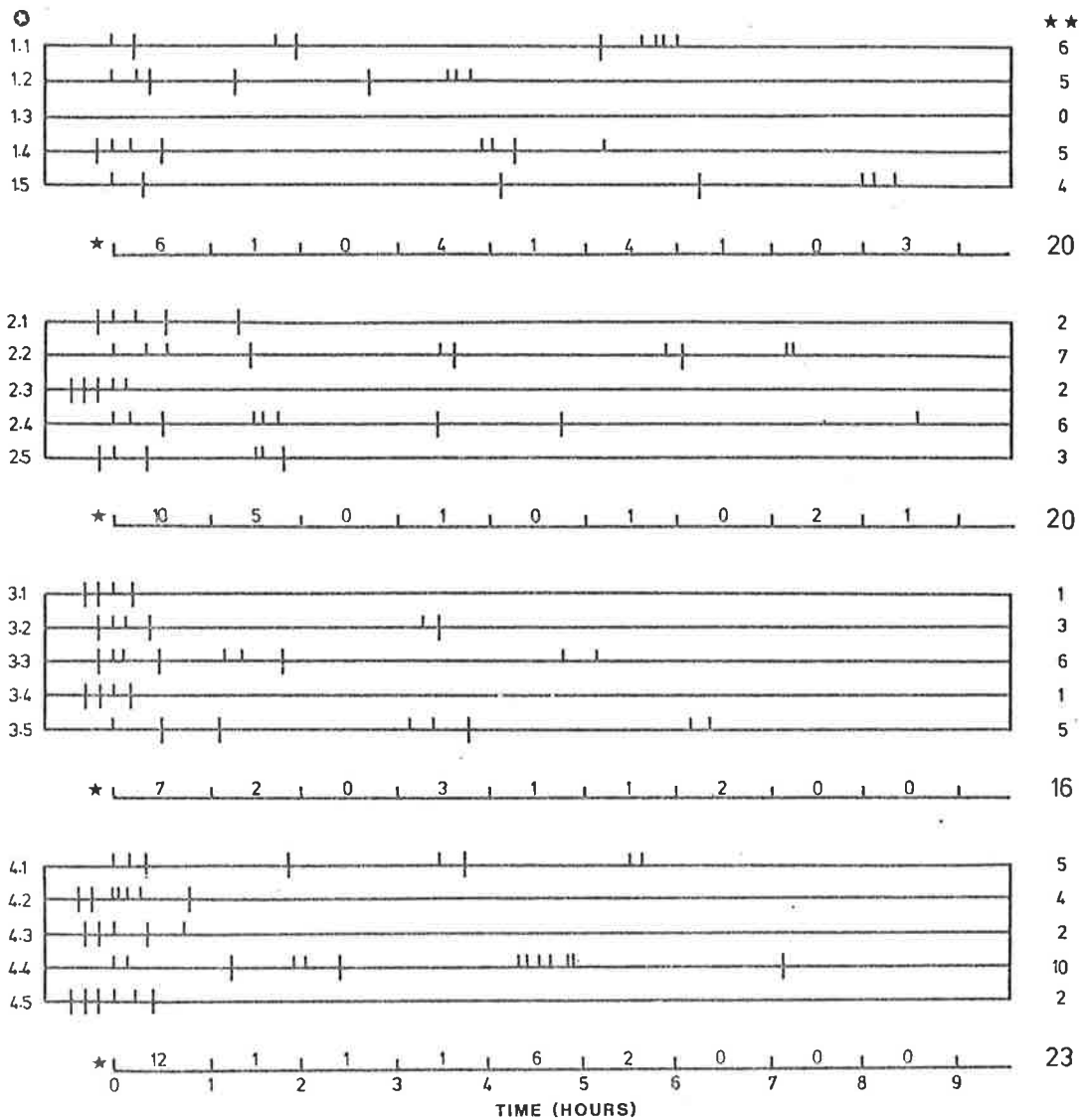
The temporal occurrences of the FEEDS with reference to the first FEED are represented as a plot on a time scale in Fig. 8.1.18. Six and seven prey were eaten within an hour of the first FEED in TR-I and TR-III respectively, where the first patch type in the sequence had a prey density of 2, while 10 and 12 prey were eaten within an hour of the first FEED in TR-II and TR-IV respectively, where the first patch type in the sequence

Fig. 8.1.18

. Diagrammatic representation of the temporal distribution of FEEDS in relation to the first FEED by each of the five beetles searching for patches of prey of different prey densities (patch types) provided in different sequences in each of the four treatments (see Table 8.1.1).

(a) Feed :  $\perp$   
(b) Patch changed :  $\oplus$





★ PREY EATEN (HOURLY TOTALS)  
 ★ ★ PREY EATEN (TOTALS PER REPLICATE)  
 ⊙ TREATMENT.REPLICATE

Table 8.1.3

PERCENTAGE OF THE TOTAL FEEDING BOUTS THAT WERE FOLLOWED BY NO-RESTS AND RESTS AND THE FREQUENCY DISTRIBUTION OF THE RESTS IN RELATION TO THE TIME INTERVALS BETWEEN THE END OF A FEEDING BOUT AND THE START OF THE RESTS

	NO RESTS	RESTS				
% OF TOTAL FEEDING BOUT	33.93	66.07				
		RESTS WITHIN INTERVALS AFTER THE END OF A FEEDING BOUT (SEC)				
		30	60	90	120	>120
% OF TOTAL FEEDING BOUT		28.57	17.86	3.57	7.14	8.93
		(SUM UP TO 66.07)				

had a prey density of 16. However, the large numbers of prey eaten within the first hour of the first FEED in TR-II and TR-IV were not all eaten from the first patch in the sequence. The numbers of prey eaten within an hour of the first FEED, therefore, indicate that prey density has an influence on the predator's motivation to feed.

A total of 20 prey were eaten in TR-I and TR-II, in which the total number of prey provided during a single run of the experiment ( $2+4+8+16 = 30$ ) was the same. Only 16 prey were eaten in TR-III, in which the total prey provided during a single run of the experiment was  $(2+2+2+2) = 8$  as compared to 23 in TR-IV, in which the total prey provided in a single run of the experiment was  $(16+16+16+16) = 64$ . The history of the feeding sequence, therefore, suggests that the beetle's feeding response is stimulated by its experience of higher prey density patches.

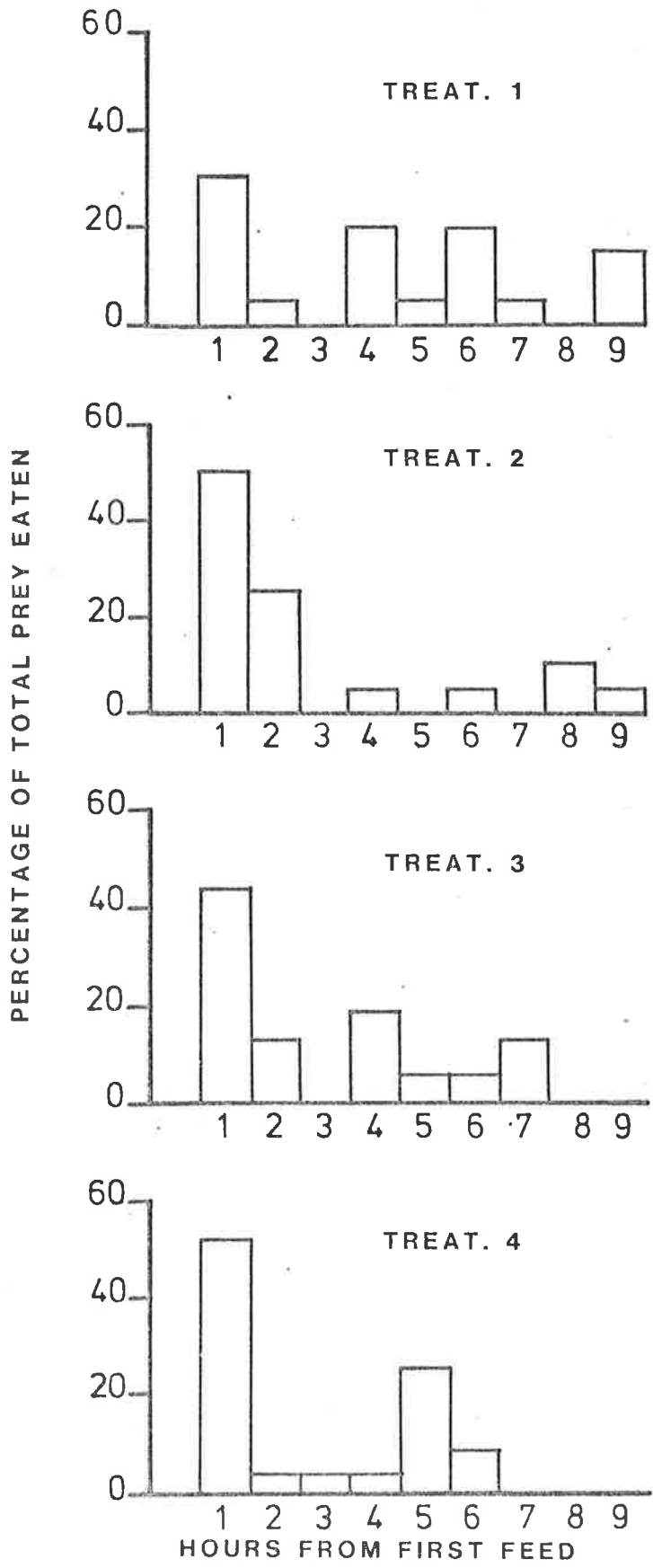
The histograms in Fig. 8.1.19 show the frequency distribution, for each treatment, of the percentage of the total prey eaten in hourly intervals from the first FEED. In estimating the percentages, first, the hourly FEEDS and the total FEEDS were summed up for the three beetles in any treatment, and then the hourly FEEDS were estimated as a percent of the total FEEDS per day (see prey eaten (hourly totals) in Fig. 8.1.18; e.g. in TR-I,  $6/20 = 0.30$ ). Between 30 and 50% of the total prey eaten were consumed within the first hour of the first FEED in any treatment.

The number and duration of rests which follow FEEDS (Table 8.1.2) show that both the time interval between a FEED and the first rest, and the duration of the rests themselves, vary widely. Many of the first rests which followed the FEEDS were subsequently followed by more rests (Table 8.1.2). These rests do not represent the digestive pause of Holling (1966), since they are not followed by more FEEDS when prey are present.

Table 8.1.3 shows that sixty six percent of the FEEDING BOUTS (comprising of FEEDS separated by no more than 30 sec) were followed by rests before the predator left the leaf-disc, and 34 % of the FEEDING BOUTS were not followed by rests (Table 8.1.3A). Of these 66 % of the FEEDING BOUTS that were followed by rests 29 % of them began within 30 sec and 17 % within 60 sec of the end of the FEEDING BOUT.

Fig. 8.1.19

Frequency distribution of the percentage of total prey eaten in different hours from the FIRST FEED; estimated from the totals for all the five beetles tested in each of the four treatments.



### A CONCEPTUAL MODEL OF THE FEEDING CYCLE

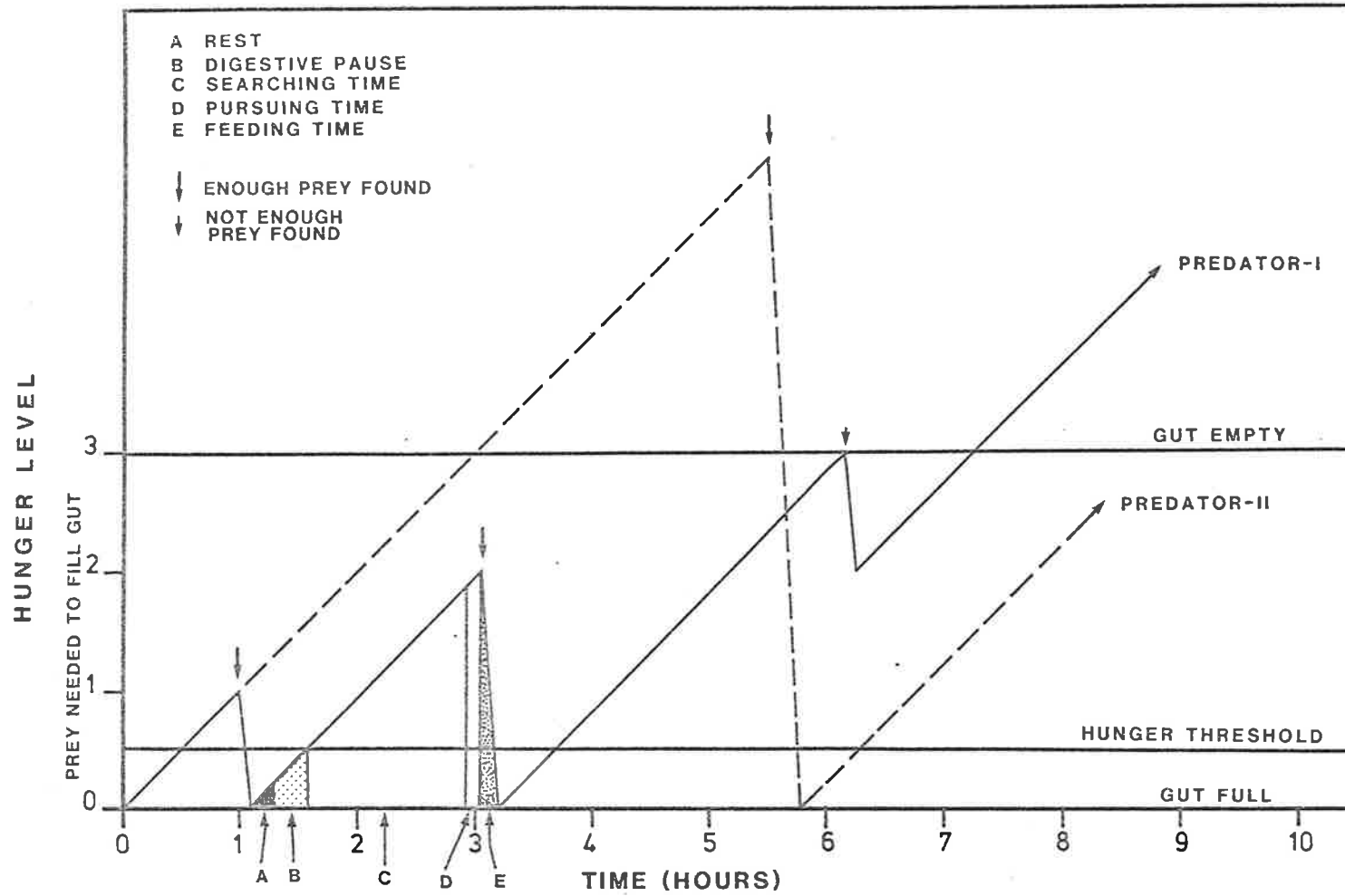
A conceptual model of the feeding cycle is presented in Fig. 8.1.20. On the basis of data presented in Table 8.1.2 the number of prey needed to fill the gut of the predator (satiated) was assumed to be three II-instar scales, i.e. equivalent to a single FEEDING BOUT. It was also assumed that the hunger level was linearly related to time, and that there was a hunger threshold below which the predator would not feed even if prey was provided.

Let us consider a predator (I), whose hunger level gradually increases after satiation with the passage of time. After an hour, when its hunger level has crossed the hunger threshold, and it is provided with prey, it would eat only one prey because that would be enough to drop its hunger level below the threshold and make the gut full (satiated). This FEED would be followed by a period of rest (A) after which the predator would resume activity (e.g. oviposition, etc.) but would not feed. Activities other than feeding would go on until the hunger level reached the hunger threshold, and (A+B) would be the duration of the digestive pause. After the digestive pause, the predator would begin searching for prey for feeding (C). In the meantime, the predator's hunger level would keep rising and the search would be intensified with rising hunger. If prey was encountered, the predator would probe it for a short period (D) and then begin feeding. The act of feeding would last for the duration (E), and then the whole cycle would be repeated. In another scenario, if the predator's hunger level had risen until the gut was empty, and it found less prey than can lower its hunger below the hunger threshold, it would be left hungry even after feeding. In still another scenario, in which the predator (II) was starved for a very long time, far beyond the gut-empty stage, it would begin to use its stored energy reserves. If the latter type of predator was then provided with many prey, it can still feed on only the number of prey that the gut can hold and not more. This number would, thus, be the maximum number of prey that can be eaten by the predator in a single FEEDING BOUT. This maximum number of prey would lower the hunger level of the predator below the threshold to satiation, and another feeding cycle would then be repeated. The data on the temporal distribution of FEEDS presented in Fig. 8.1.18 and Table 8.1.2 followed the above pattern in a very general way.

Fig. 8.1.20

Conceptual model of the feeding cycle of Rodolia searching for prey in three different conditions.

## CONCEPTUAL MODEL OF FEEDING CYCLE





In a detailed theoretical study of the feeding behaviour of predators, Holling (1966) also came to the conclusion that the frequency of feeding followed a cyclic pattern which was driven by the hunger level of the predator. He considered hunger as "an internal motivational state" and defined it as a "measure of the weight of food necessary to return the animal to a condition of complete satiation, since this weight is a measure of the emptiness of the digestive tract". Holling's attack cycle is very similar to the feeding cycle presented in the conceptual model discussed above, except that here each FEED is characterized by the attack of a number of prey within a FEEDING BOUT.

As mentioned above, the number of prey eaten in each FEEDING BOUT was found to be related to the hunger level of the predator within the constraints of the capacity of the gut. Holling's analysis of feeding behaviour also resulted in similar findings. He also lists three features as characteristic of his system :

- (1) it is basically discontinuous, for there are relatively few contacts between predator and prey, and every prey consumed abruptly changes the condition of the predator,
- (2) there is a strong historical element, for what happens at any moment depends not only on the conditions at that moment, but in the past as well,
- (3) thresholds and limits are extremely important features of attack.

The features two and three are directly applicable to the present system, while the first is only partly true. In the present system, the contacts between predator and prey remain more or less continuous so long as the predator remains on the patch. Beyond that, the contact breaks down until a patch with prey is rediscovered. The latter, perhaps, is the reason for the wide variability in the results on the interfeeding intervals. Though the present experiment was not designed to study the detailed feeding behaviour of the beetle, the general pattern of the results obtained are similar to Holling's findings.

#### 8.1.4 GENERAL DISCUSSIONS AND CONCLUSIONS

The findings on the foraging behaviour of Rodolia are indeed in agreement with the general conclusions of the optimal foraging theory i.e., an optimal forager ought to forage and spend a greater part of its foraging

time in relatively more profitable patches. That many foragers are sensitive to changes in patch quality and adjust their search effort accordingly to maximize returns per unit effort has been substantiated by much experimental evidence (see Hassell, 1978b; Krebs et al., 1983). However, in their review of the published literature on OFT, Krebs et al. (1983) reject many such studies as mere "observations that are more or less consistent with some of the assumptions of patch and prey models; for example ..... predators spend more time in more profitable patches" and not a "test of the predictions of optimal foraging models". Perhaps, the results presented here also fall in such a category. But, in an attempt to defend OFT from the bitter criticisms of its critics, Krebs et al. (1983) concede that OFT "cannot be used to test the proposition that animals are (or are not) optimal but only the proposition that one particular hypothesis, for example, maximizing net rate of intake subject to constraints a, b, and c describes the animal's foraging behaviour". If the aim of such studies is simply to identify the constraints which describe the foraging behaviour of an animal, it is hard to believe that any single OFT model would be able to predict the foraging behaviour of more than one type of animal in more than one environment.

In recent developments of OFT, attempts are being made to incorporate specific details of the biology of the system under study, in order to achieve greater predictive accuracy (Krebs et al., 1983). Such models would obviously gain predictive accuracy at the cost of generality because identical systems can only be produced in controlled conditions. This then justifies the criticism that "optimal foraging models are all right in simple laboratory environments but they cannot handle the complexities of nature, where predation risks etc. impinge on foraging behaviour" (Zach and Smith, 1981). Thus Krebs et al.'s (1983) discontent that "Too many papers use the catch phrase "optimal foraging" to dress up a study of feeding ecology that has little, or nothing, to do with testing OFT...." may be true but such studies do produce experimental evidence to show that animals possess the power of learning, memory and discrimination, which they use to their advantage in adopting an efficient foraging strategy. Testing OFT in such systems, in the manner Krebs et al. point out, can be the next step, but for the present the usefulness of such data deserves appreciation. And though the theorists are trying to bring OFT to firmer grounds, much of it

is still a topic of debate. In the meantime, data which merely provide a support of the general conclusions of OFT would help untangle some of the confusion and also provide a sense of direction to later OFT models.

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N.B.

When this chapter was with the typist, attention was drawn to the latest review on 'Optimal Foraging Theory' by Pyke (1984).

## 8.2 ANALYSIS OF THE SEARCHING BEHAVIOUR OF THE BEETLE

### 8.2.1 INTRODUCTION

The development of mathematical models, which attempt to describe the outcome of parasitoid or predator search, has necessitated a detailed study of the foraging behaviour of parasitoids and predators. One of the basic assumptions of foraging models is that animals search for their prey at random. This assumption is mathematically convenient but observations of the searching behaviour have shown that it may not necessarily be true.

Some foragers are attracted over long distances under the influence of some stimulus, usually olfactory, emitted by the host or the host's immediate environment (see Chapter 5). Others appear to search at random but whose behaviour is markedly altered after the first successful attack on a prey. In many foragers, including a housefly (a pseudopredator) searching for sugar droplets distributed in clumps on the floor of the searching arena (Murdie and Hassell, 1973), a pronounced increase in turning rate (klinokinesis) and a reduction in speed of movement (orthokinesis) after the first successful attack on a prey has been noticed. Similar responses have been found in parasitoids such as Trichogramma evanescens Westwood (Laing, 1937), Diaeretiella rapae Curt (Hafez, 1961), and Amitus hesperidum Silvestri and Encarsia opulenta (Silvestri) (Dowell et al., 1981). Predators like Anthocoris confusus (Reuter) (Evans, 1976), Orius tristicolor (White) (Shields and Watson, 1980) and many coccinellids also behave in a similar manner. Predatory coccinellids evidently do not perceive their prey until physical contact occurs and that this contact seems to play a role in eliciting attack (Fleshner, 1950; Robinson, 1952; Putman, 1955; Banks, 1954, 1957; Dixon, 1959; Kehat, 1968; Storch, 1976; Stubbs, 1980; Nakamuta, 1982). Thus, Coccinella septempunctata, foraging for aphids (Nakamuta, 1983) and Pharoscymnus numidicus foraging for coccids (Kehat, 1968) were unable to orientate themselves towards their prey from a distance, though Stethorus punctum was capable of detecting its mite prey by the latter's scent (Colburn and Asquith, 1970). C. septempunctata, however, responded to visual stimuli from its prey and had a perceptive distance of 7 mm (2-7 mm) (Nakamuta, 1984) which was less than the 1.04 cm reported by Stubbs (1980). C. septempunctata also orientated towards a dummy prey at less than 8 mm, but on average it orientated towards an aphid prey from a greater distance than it did towards the dummy prey. Nakamuta (1984) concluded that C. septempunctata only used vision for short range ( $\leq 7$  mm) detection of

the first prey item and that physical contact was an aspect of short range orientation.

Anastis ocellata which feeds on the larvae of the Jack-pine budworm, Choristoneura pinus, also responds to visual stimuli from the prey and has a perceptive distance of 1.27 to 1.91 cm (Allen et al., 1970).

Many foragers tend to spend more of their searching time in areas of high prey density. Such a behaviour leads to "aggregation" of foragers in areas of higher prey density resulting in a differential exploitation of prey patches. It has been argued that, besides the olfactory response to prey density the klinokinetic and orthokinetic behaviour of foragers, discussed above, also assist in such an outcome (Hassell and May, 1974; also see Chapter 8.1).

So having gathered evidence to support the hypothesis that Rodolia cardinalis has the potential to differentially exploit patches of prey in relation to prey density, the next obvious question was, what was the mechanism by which it achieved this discriminatory ability? Was it attracted to prey from a distance in response to olfactory stimuli from the prey or that it searched randomly? In an attempt to answer these questions the observations gathered on the video tapes in the optimal foraging experiment discussed in Chapter 8.1 were further analyzed.

### 8.2.2 MATERIALS AND METHODS

The design of the experiment (Table 8.2.1; following page) and the method in which it was conducted has been described in Chapter 8.1 (section 8.1.2). From the different patches tested a few were selected for the analysis of the searching behaviour of the beetle. The patches selected were done in the manner described below.

#### (A) THE PATCHES SELECTED FOR ANALYSIS

From the four prey densities tested in four treatments each with five replicates (beetles) (Table 8.2.1), only patches with prey density 2 were considered for analysis of the searching behaviour of the beetle because at higher prey densities it was very difficult to find track lengths of 5 sec of walking time (henceforth referred to ONE UNIT; selected for the estimation and comparison of parameters; see below) before and after encounter with prey. At patches of higher prey densities, there were very few instances in which there was an UNIT walking time between entry into

Table 8.2.1

DESIGN OF EXPERIMENT -- ALLOCATION OF PATCHES OF  
FOUR PREY DENSITIES TO FOUR TREATMENTS COMPRISING  
FOUR DIFFERENT SEQUENCES

TREATMENT	PREY-PATCH SEQUENCE			
	(1)	(2)	(3)	(4)
	PREY DENSITY PER PATCH			
I	2	4	8	16
II	16	8	4	2
III	2	2	2	2
IV	16	16	16	16

patch and the first encounter with prey. Also at patches of prey densities greater than 2, consecutive encounters with prey within an UNIT time of leaving the first prey were common, because there were more prey spread in a small area. Such limitations were also present in a few patches of prey density 2, and they were also omitted from the analysis.

#### (B) DECIPHERING OF INFORMATION FROM RECORDED VIDEO TAPES

As the video tape was played, the path traversed by a beetle was traced on a transparent acetate sheet fixed on the screen of the monitor. The path followed by a beetle over a period of 60 to 75 sec of the actual walking time from the time the beetle entered the patch (unless the beetle left the patch earlier) was traced. The beetle's position at every 5 sec was marked on the traced path. The positions of the prey were also marked on the sheet.

An acetate sheet with the traced path of a beetle was then placed on an Apple Graphics Tablet which, in conjunction with an Apple IIe minicomputer and a special programme developed for the purpose, allowed points on the track to be converted into coordinates. The conversion of points on the track into coordinates was achieved in the following manner.

Keys of the computer keyboard were coded to mark (a) start -- S, (b) turning points -- T, (c) encounter with prey -- P, and (d) a 5 sec point on the path -- X. The pressing of one of the coded keyboard buttons for a point marked on the Graphics Tablet, using a special electronic pen, resulted in the recording of X and Y coordinates of that point together

with the coded letter for the event. The coordinates for the points on the track were then stored as data files on floppy discs. The computer analysed the data files for the coordinates and printed out estimates for four parameters : (a) turning rates per sec, (b) turning rates per mm, (c) speed of travel (mm per sec), and (d) ratio of the beeline (straight) distance (DB) and the actual distance (DT) travelled between successive 5 sec points. The programme was also equipped with data for the conversion of the size of the patch on the monitor screen into the actual size of the patch (508 mm dia). The estimates of the parameters were then corrected for the actual size of the patch prior to printing.

### 8.2.3 RESULTS AND DISCUSSION

#### 8.2.3.1 QUALITATIVE DESCRIPTION OF SEARCHING BEHAVIOUR

Samples of the path traversed by the beetle at patches of different prey densities have been presented in Fig. 8.2.1. The figure shows that the beetles covered major parts of the area of the patches and showed tendencies to walk around the edges of the patch more often, which suggests that the shape of the patch influenced the path adopted by the beetle. The paths do not follow obviously different patterns in patches of different prey densities. However, in general, the beetle's activities appeared to be concentrated in the region of aggregation of prey.

#### 8.2.3.2 QUANTITATIVE ANALYSIS OF SEARCHING BEHAVIOUR

The estimates of turning rates per sec, turning rates per mm, speed of travel, and ratio of DB/DT have been presented in Tables 8.2.2, 8.2.3, 8.2.4, and 8.2.5 respectively. The estimates of the parameters were classified into two GROUPS :

- (i) GROUP A : those estimates which came from patches in which the first encounter with prey after entry into patch was NOT followed by another encounter with prey within an UNIT walking time.
- (ii) GROUP B : those estimates which came from patches in which the first encounter with prey after entry into patch was followed by a second encounter within an UNIT walking time.

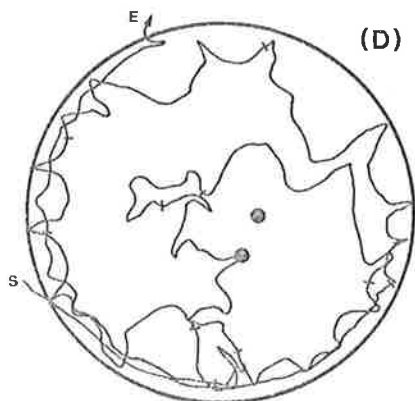
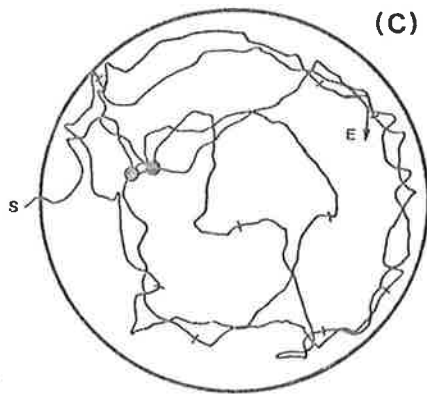
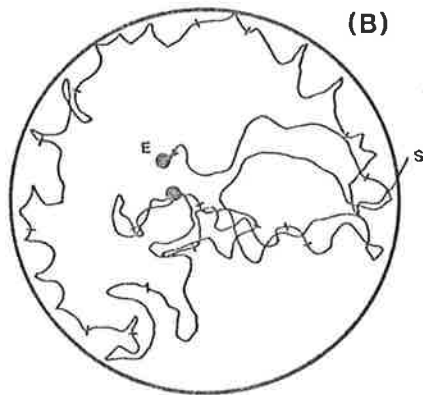
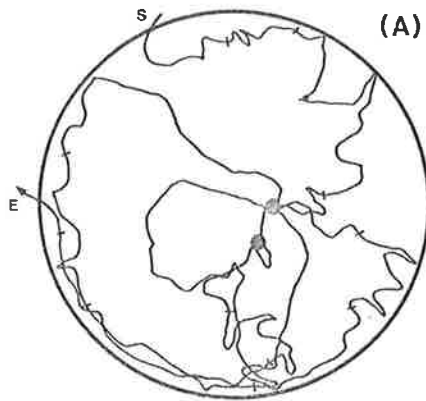
The two groups of estimates were separately analysed to test the null hypothesis of no change in the searching behaviour of the beetle in response to an encounter with prey.

Fig. 8.2.1

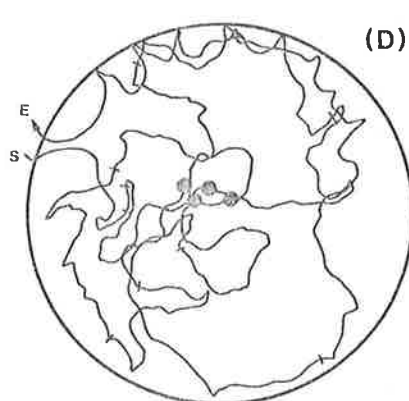
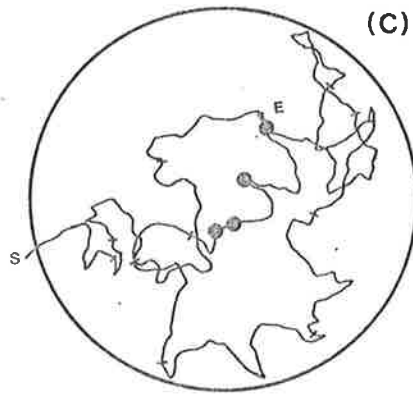
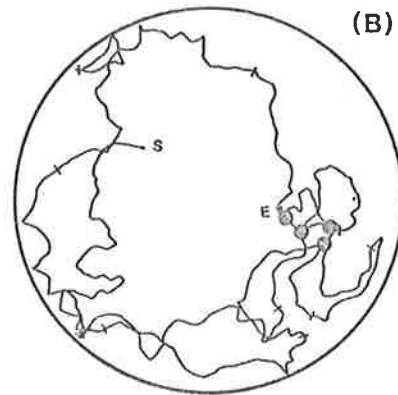
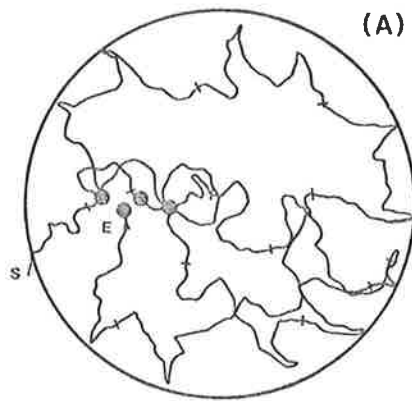
The paths traversed by each of the four beetles (A, B, C, and D) searching for prey at patches of four different prey densities over ca. one minute of walking time. S : start; E : end; and the crosses on the paths represent 5 sec intervals.



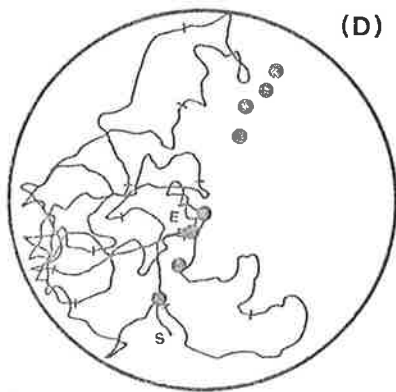
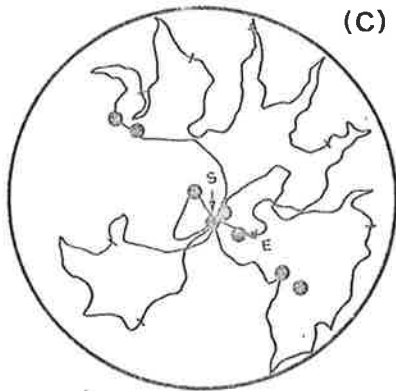
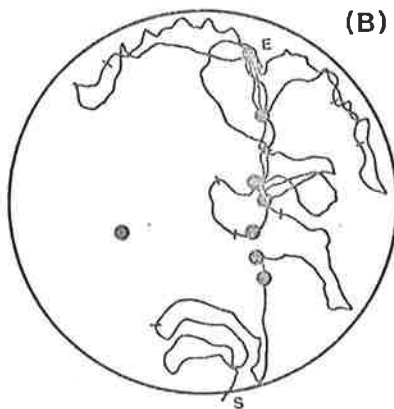
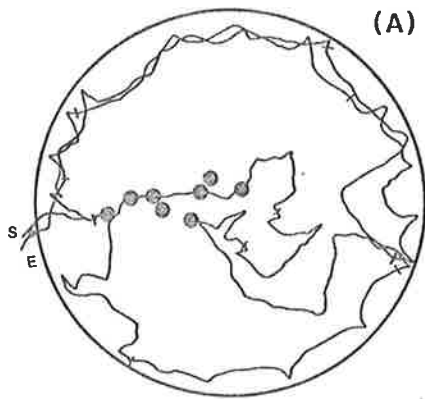
PREY DENSITY (2)



PREY DENSITY (4)



PREY DENSITY (8)



PREY DENSITY (16)

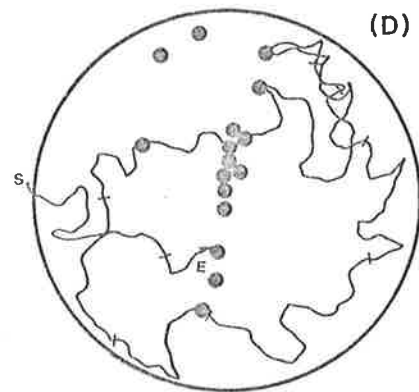
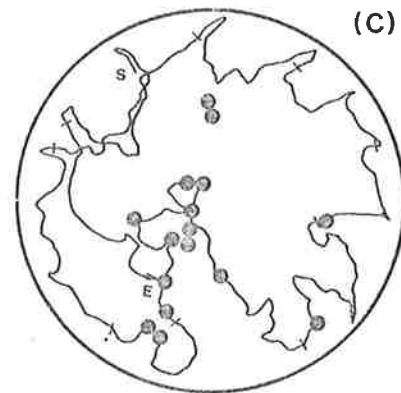
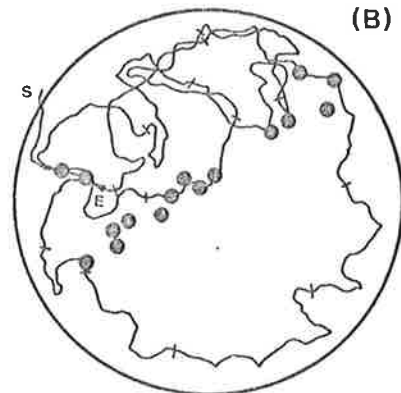
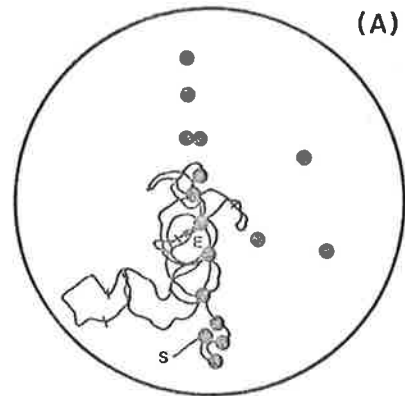


Table 8.2.2

ESTIMATES OF TURNING RATES (PER SEC) BEFORE AND AFTER FIRST ENCOUNTER WITH PREY AFTER ENTRY INTO PATCHES OF PREY DENSITY 2; FOR SELECTED BEETLES FROM OPTIMAL FORAGING EXPERIMENT

(# represents serial number, BEETLE the replicate and SEQUENCE the patch-type sequence (see Table 8.2.1)); TEST STATISTIC = the product of Student's "t" value for (n-1) d.f. and the standard error (S.E.) of the mean)

GROUP (A) : BEETLES WHICH FIRST MADE A SINGLE ENCOUNTER WITH PREY

#	TREAT	BEETLE	SEQUENCE	BEFORE	AFTER	BEFORE - AFTER
1	I	1	1	1.79	1.20	0.59
2	I	2	1	1.79	2.00	-0.21
3	I	3	1	1.20	1.20	0
4	II	5	4	3.40	2.00	1.40
5	III	5	1	1.20	1.20	0
6	III	4	2	3.40	2.59	0.81
7	III	5	4	2.59	2.59	0

MEAN = 0.37  
 S.E. = 0.22  
 TEST STATISTIC = 0.54 (P>0.05)

GROUP (B) : BEETLES WHICH FIRST MADE TWO CONSECUTIVE ENCOUNTERS WITH PREY WITH AN INTERVAL BETWEEN ENCOUNTERS OF <5 sec

#	TREAT	BEETLE	SEQUENCE	BEFORE	AFTER	BEFORE - AFTER
1	II	1	4	0.80	2.20	-1.40
2	III	4	1	3.79	2.59	1.20
3	III	2	3	2.79	3.00	-0.21
4	III	3	3	4.19	1.00	3.19
5	III	4	3	3.00	2.00	1.00
6	III	1	4	3.00	1.20	1.80
7	III	2	4	1.60	2.79	-1.19
8	III	3	4	3.20	1.60	1.60

MEAN = 0.75  
 S.E. = 0.56  
 TEST STATISTIC = 1.32 (P>0.05)

Table 8.2.3

ESTIMATES OF TURNING RATES (PER MM) BEFORE AND AFTER FIRST ENCOUNTER WITH PREY AFTER ENTRY INTO PATCHES OF PREY DENSITY 2; FOR SELECTED BEETLES FROM OPTIMAL FORAGING EXPERIMENT

(# represents serial number, BEETLE the replicate and SEQUENCE the patch-type sequence (see Table 8.2.1)); TEST STATISTIC = the product of Student's "t" value for (n-1) d.f. and the standard error (S.E.) of the mean)

GROUP (A) : BEETLES WHICH FIRST MADE A SINGLE ENCOUNTER WITH PREY

#	TREAT	BEETLE	SEQUENCE	BEFORE	AFTER	BEFORE - AFTER
1	I	1	1	0.45	0.47	-0.02
2	I	2	1	0.34	0.56	-0.22
3	I	3	1	0.59	0.35	0.24
4	II	5	4	0.48	0.22	0.26
5	III	5	1	0.42	0.44	-0.02
6	III	4	2	0.33	0.27	0.06
7	III	5	4	0.54	0.30	0.24

MEAN = 0.08  
 S.E. = 0.07  
 TEST STATISTIC = 0.17 (P>0.05)

GROUP (B) : BEETLES WHICH MADE FIRST TWO CONSECUTIVE ENCOUNTERS WITH PREY WITH AN INTERVAL BETWEEN ENCOUNTERS OF <5 sec.

#	TREAT	BEETLE	SEQUENCE	BEFORE	AFTER	BEFORE - AFTER
1	II	1	4	0.39	0.36	0.03
2	III	4	1	0.35	0.28	0.07
3	III	2	3	0.27	0.28	-0.01
4	III	3	3	0.33	0.27	0.06
5	III	4	3	0.31	0.45	-0.14
6	III	1	4	0.41	0.26	0.15
7	III	2	4	0.35	0.25	0.10
8	III	3	4	0.43	0.43	0

MEAN = 0.033  
 S.E. = 0.031  
 TEST STATISTIC = 0.07 (P>0.05)

Table 8.2.4

ESTIMATES OF SPEED OF TRAVEL (MM PER SEC) BEFORE AND AFTER FIRST ENCOUNTER WITH PREY AFTER ENTRY INTO PATCHES OF PREY DENSITY 2; FOR SELECTED BEETLES FROM OPTIMAL FORAGING EXPERIMENT

(# represents serial number, BEETLE the replicate and SEQUENCE the patch-type sequence (see Table 8.2.1); TEST STATISTIC = the product of Student's "t" value for (n-1) d.f. and the standard error (S.E.) of the mean)

GROUP (A) : BEETLES WHICH FIRST MADE A SINGLE ENCOUNTER WITH PREY

#	TREAT	BEETLE	SEQUENCE	BEFORE	AFTER	BEFORE - AFTER
1	I	1	1	3.91	2.54	1.37
2	I	2	1	5.25	3.56	1.69
3	I	3	1	2.02	3.34	-1.32
4	II	5	4	7.06	8.94	-1.88
5	III	5	1	2.80	2.71	0.09
6	III	4	2	10.27	9.54	0.73
7	III	5	4	4.73	8.40	-3.67
				MEAN = -0.43		
				S.E. = 0.74		
				TEST STATISTIC = 1.80 (P>0.05)		

GROUP (B) : BEETLES WHICH MADE FIRST TWO CONSECUTIVE ENCOUNTERS WITH PREY WITH AN INTERVAL BETWEEN ENCOUNTERS OF <5 sec.

#	TREAT	BEETLE	SEQUENCE	BEFORE	AFTER	BEFORE - AFTER
1	II	1	4	2.00	6.09	-4.09
2	III	4	1	10.72	9.03	1.69
3	III	2	3	10.32	10.65	-0.33
4	III	3	3	12.59	3.62	8.97
5	III	4	3	9.55	4.36	5.19
6	III	1	4	7.18	4.53	2.65
7	III	2	4	4.56	10.83	-6.27
8	III	3	4	7.36	3.64	3.72
				MEAN = 1.44		
				S.E. = 1.75		
				TEST STATISTIC = 4.13 (P>0.05)		

Table 8.2.5

ESTIMATES OF THE RATIO OF DB (the BEELINE (straight) distance between consecutive 5 sec points on track) AND DT (the TRACK distance between consecutive 5 sec points on track) BEFORE AND AFTER FIRST ENCOUNTER WITH PREY AFTER ENTRY INTO PATCHES OF PREY DENSITY 2; FOR SELECTED BEETLES FROM OPTIMAL FORAGING EXPERIMENT

(# represents serial number, BEETLE the replicate and SEQUENCE the patch-type sequence (see Table 8.2.1); TEST STATISTIC = the product of Student's "t" value for (n-1) d.f. and the standard error (S.E.) of the mean)

GROUP (A) : BEETLES WHICH FIRST MADE A SINGLE ENCOUNTER WITH PREY

#	TREAT	BEETLE	SEQUENCE	BEFORE	AFTER	BEFORE - AFTER
1	I	1	1	0.43	0.64	-0.21
2	I	2	1	0.55	0.25	0.30
3	I	3	1	0.70	0.52	0.20
4	II	5	4	0.47	0.51	-0.04
5	III	5	1	0.90	0.56	0.34
6	III	4	2	0.29	0.61	-0.32
7	III	5	4	0.44	0.56	-0.12
				MEAN = 0.02		
				S.E. = 0.10		
				TEST STATISTIC = 0.24 (P>0.05)		

GROUP (B) : BEETLES WHICH MADE FIRST TWO CONSECUTIVE ENCOUNTERS WITH PREY WITH AN INTERVAL BETWEEN ENCOUNTERS OF <5 sec.

#	TREAT	BEETLE	SEQUENCE	BEFORE	AFTER	BEFORE - AFTER
1	II	1	4	0.64	0.59	0.05
2	III	4	1	0.44	0.52	-0.08
3	III	2	3	0.47	0.30	0.17
4	III	3	3	0.31	0.19	0.12
5	III	4	3	0.50	0.45	0.05
6	III	1	4	0.63	0.86	-0.23
7	III	2	4	0.59	0.61	-0.02
8	III	3	4	0.21	0.53	-0.32
				MEAN = -0.03		
				S.E. = 0.06		
				TEST STATISTIC = 0.14 (P>0.05)		

The test involved the estimation of the means and standard errors (S.E.) of the differences between pairs of estimates BEFORE and AFTER an encounter (or two encounters). The means were tested against a product of Student's "t" value for (n-1) d.f. at  $P=0.05$  and the S.E. of the mean (Snedecor and Cochran, 1968). If the absolute value of the mean was LESS than  $t \times S.E.$  ( $P=0.05$ ), then the decrease or increase in parameter estimates following encounter(s) was NOT SIGNIFICANT at  $P<0.05$ .

Contrary to expectation, both the turning rates per sec (Table 8.2.2) and the turning rates per mm (Table 8.2.3) showed a tendency to decrease following encounter(s) in both Group A and Group B. The speed of travel showed a tendency to increase in Group A, but a tendency to decrease in Group B (Table 8.2.4) when a decrease in speed of travel following encounter was expected. The ratio of  $DB/DT$ , which was expected to decrease (a more convoluted path) following encounter with prey, showed a tendency to decrease in Group A but a tendency to increase in Group B (Table 8.2.5). However, as would be evident from the tables, none of these trends were significant.

The results obtained from the analysis of the searching behaviour of Rodolia contradict the findings of previous workers for other predators. Both theory and some experimental evidence (see section 8.2.1) suggested that both orthokinetic (reduction in speed of movement) and klinokinetic (increase in turning rates) responses might follow an encounter with prey, and hence a decrease in the ratio,  $DB/DT$ .

A possible reason for the contradiction in the findings could be due to differences in the methods of experiments. Most experiments designed to test the influence of encounters with prey on the searching behaviour of predators are performed in a more controlled manner (as discussed below) than my experiment.

In most experiments designed to test the influence of an encounter with prey on the searching behaviour, the predator is starved for a fixed period of time (usually 24 h) prior to its use in the experiment (Evans, 1976; Carter and Dixon, 1982; Nakamuta, 1982). The starvation of the predator can usually make it "excited" and more active as shown in the data presented in Chapter 6.2 on the Index of Activity. Thus, if a starved, hyper-active predator is provided with prey, it would be expected to become

sluggish following a feed. The degree of sluggishness would depend on the remaining level of hunger and the temperature (see Chapter 6.2). The sluggishness of the predator would result in a reduction in speed of movement and wandering around, which is perhaps what has been found by other workers in the past and is not a real change in behaviour.

When predators are starved prior to use in an experiment, the first encounter with prey usually results in FEEDING (or oviposition in parasitoids), therefore the changes in the searching behaviour that are observed are also strictly of "encounters which result in FEEDING". Thus, findings reported in the literature can be considered only as a special case of those encounters that result in feeding.

Many experimenters use brushes to transfer predators from vials or culture systems to the test (searching) arena. But handling of insects with brushes etc. alters their behaviour. In particular, it renders unusual alarm in animals which generally respond either by swift movement away or by feigning death (as Rodolia) prior to swift movement away. Both of these behaviours would provide indications of changes in behaviour (especially orthokinetic responses) following an encounter with prey, and so result in spurious findings about the true searching behaviour of predators if they are not provided with enough time to "acclimatize" with the searching arena before observations are taken.

My experiment was designed to avoid the above problems and to study the behaviour of Rodolia in a more realistic manner. The beetles tested were fully fed prior to release at the base of a searching arena which had a single patch of prey (see section 8.1.2). On average the beetle spent over 2 h wandering or resting before it discovered the patch and the prey therein (Table 8.1.2 in section 8.1.3.7). Also, the results on the searching behaviour were based on only those encounters which did not result in feeding. After spending various amounts of time on the patch, the beetle left the patch in search of another, again undisturbed. All these provisions allowed the beetles to behave as naturally as possible.

My method of studying the searching behaviour of the beetle was, however, fraught with other problems. The results obtained, though more realistic, were more variable and difficult to analyse, and consistent conclusions were difficult to find.



In summary , the results on the searching behaviour of Rodolia indicate that it is not influenced by encounters with prey and so the path traversed also appears to remain independent of the numbers of prey present on the patch. Thus, the results provide no evidence against RANDOM search for prey in Rodolia. The evidence supporting the beetle's differential response to prey density, presented in the previous chapters, must therefore be a result of larger numbers of encounters with larger numbers of prey at patches of higher prey densities which results from closer proximity of prey.

**CHAPTER 9**  
**GENERAL DISCUSSION**

GENERAL DISCUSSION

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I think that there is only one way to science -- or to philosophy, for that matter : to meet a problem, to see its beauty and fall in love with it; to get married to it; and to live with it happily, till death do ye part -- unless you should meet another and even more fascinating problem, or unless, indeed, you should obtain a solution. But even if you do obtain a solution, you may then discover, to your delight, the existence of a whole family of enchanting though perhaps difficult problem children for whose welfare you may work, with a purpose, to the end of your days.

-- Karl Popper.

What we call the beginning is often the end and to make an end is to make a beginning. The end is where we start from.

-- T. S. Eliot.

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Every naturalist from Darwin onwards has pondered over the question of population fluctuations. "Fluctuations occur in every group of animals and in every habitat that has been investigated. Although the amplitude of fluctuations is often very great, scarcity alternating with high abundance every so many years, two things that we might expect often do not happen, the first, complete destruction of vegetation by herbivorous animals, and the second, complete destruction over wide area of either predators or prey. The factors controlling the limitations of these fluctuations are therefore of great interest, since they are the factors that critically affect the survival or extinction of species,....." (Elton, 1938, pp. 130-131).

The natural populations of prey and predators are often characterized by cyclic oscillations most often with the predator population lagging behind that of the prey. Despite these oscillations, the natural predator-prey populations are in some sense "stable", in contrast to those of pest species which are characterized by violent fluctuations, and thus appear to be relatively less "stable". Any attempt to identify the causes of this stability or otherwise, is a formidable task, and the analysis of such stability would include "the effect of refuges, spatial heterogeneity,

population movements, seasonal events, relative growth rates of prey and predator, their reproductive and death rates, the influence of prey and predator densities and age distribution upon attack rates and so on." (Murdoch and Oaten, 1975).

Stability, a term borrowed from physics, is used by both field ecologists and mathematical ecologists in explaining fluctuations in animal numbers. However, ecologists tend to avoid a rigorous definition of what they mean by stability. Murdoch and Oaten (1975) in their review of "Predation and Population Stability" leave it to "the reader's own experience and intuition", though they point out that "Roughly speaking, stability in general models is 'return to equilibrium after perturbation', and in experiments and models dealing with functional response, stability is equivalent to requiring that the attack rate of the predator increases faster than proportionately as prey density increases. We assume, as do most ecologists, that these two concepts of stability -- a rough and ready description of the field situation and the rigorous mathematical definition -- are related, and that features that lend stability to models will also tend to add stability to field populations.". However, Usher and Williamson (1974) in their book on "Ecological Stability" do attempt to define the term in the following manner : "Roughly speaking, ecological stability is the strength of the tendency for the population or a set of populations to come to an equilibrium point or to a limit cycle, and also, related to that, the ability of a population system to counteract perturbations.". Thus, in definitions of ecological stability, the stress appears to be on the "return to equilibrium after perturbation".

#### ROLE OF PREDATION ON THE STABILITY OF PREDATOR-PREY SYSTEMS

Depending on the nature of the system, predation can have both destabilizing or stabilizing influences on predator-prey systems.

That predation can have destabilizing influences on a predator-prey system has been well documented by examples from the aquatic environment (see Murdoch and Oaten, 1975). Instability in predator-prey systems can also result if the prey population escapes from the control of the predator. The spruce budworm may have become a pest in Canada at regular intervals, even though it is a native species, because combinations of suitable conditions sometimes allow it to increase so rapidly that the predators cannot keep up (Morris, 1963). In Australia, the whitefly,

Trialeurodes vaporariorum has assumed the status of a pest since the mid 1970's, after being uncommon since the mid 1930's following the introduction of its Chalcid parasite, Encarsia formosa; the reasons for the apparent breakdown of biological control are, however, not known.

That predation can have a stabilizing influence on the dynamics of a predator-prey system can be substantiated by examples from the biological control literature. Many species of animals and plants which have been accidentally introduced into a new environment and have assumed the status of pests have been brought under control after the introduction of their natural enemies from their native habitats. Such examples of successes in biological control are reviewed in several texts on biological control (Huffaker, 1971; van den Bosch, and Messenger, 1973; DeBach, 1974; Huffaker and Messenger, 1976). Unfortunately the successful examples are generally not studied, their success being reward enough. The control of Icerya purchasi by its natural enemies in California and some other 50 countries is one such example.

#### THE ICERYA-RODOLIA SYSTEM

Icerya purchasi persists in California orchards and has done so together with its predator Rodolia cardinalis and parasite Cryptochaetum iceryae for 90 years or so, after the natural enemies were introduced in the late 1880's. Icerya persists at very low densities, and almost all of its mortality is caused by these enemies (Quezada and DeBach, 1973). It is not known whether local populations of Icerya are stable or exist intermittently, but the system as a whole appears to be more stable than was the prey alone, and more stable than when the predator is accidentally reduced by insecticides (Murdoch and Oaten, 1975). In its native land, Australia, the numbers of both Icerya and its natural enemies have always been very low (see Chapter 4.1), and so the system appears to remain "stable".

The aim of the present investigation has been to attempt to understand the factors responsible for this apparent stability. Of the few possible factors that are likely to influence ecological stability and which are listed by Murdoch and Oaten (1975), the response of the predator to spatial heterogeneity in the distribution of prey was investigated at different levels of prey organization.

As pointed out in Chapter 6.1, the predator's response to spatial heterogeneity is expressed in the form of an "aggregative response" which results in the aggregation of more predators at patches of higher prey densities and leads to an increase in the numbers of prey killed and also in the amount of time predators spend at these patches. Such an aggregative response has been referred to as "numerical aggregative response" (Bryan and Wratten, 1984). Alternatively, a predator can respond to spatial heterogeneity in the distribution of prey at the individual level by showing behavioural changes to patches of different prey densities. The outcome of such "behavioural aggregative response" is also similar, i.e. greater exploitation of patches of higher prey densities due to the predator spending more time at such patches. Intuitively, predators possessing the latter type of ability should be more efficient.

Theoretical studies of predator-prey interaction have suggested that such aggregative responses of predators to a patchily distributed prey population imparts stabilizing influences on predator-prey interactions, and they are believed to be one of the important reasons for the success of some biological control programmes (Hassell, 1978b; Beddington et al., 1978; Putman and Wratten, 1984). As a result, during the last few years, spatial heterogeneity has emerged unequivocally as the crucially important factor affecting a population's dynamics (Hassell, 1982b). This realization has made ecologists focus their attention on the foraging behaviour of predators which is recognized as the "major determinant of their effectiveness" (Waage, 1983).

Discussions of a predator's response to spatial heterogeneity in the distribution of prey obviously lead to the question -- what constitutes a patch? This is because in nature one is confronted with the problem of "patches within patches" (Waage, 1979). The aggregative responses to spatial heterogeneity, which are behavioural in origin, would obviously depend on what the FORAGER considers a "patch". Therefore, studies of a predator's response to spatial heterogeneity in the distribution of prey must take into account the structure of prey organization in nature to permit extrapolation of inferences to the real world.

If the essence of predation biology is a study of the "predator's response to prey density" (Chapter 6.1), and the various forms in which this response gets expressed is the major determinant of the dynamics of interacting predator-prey populations (Waage, 1983), then as Heads and

Lawton (1983) suggest "... if we wish to examine patterns of mortality imposed by potential biological control agents in the field, it may be necessary to study victim mortality or enemy behaviour over a series of spatial scales before pronouncing on the presence, or absence of aggregative responses.". A detailed study of the behaviour of predators at the individual patch level must also be conducted before any conclusion relating to its density-dependent response is made (Morrison and Lewis, 1984).

Bearing such ideas as the above in mind, in the present project attempts were made to study the reponse of Rodolia at different levels of prey organization (spatial scales) : in the field (Chapter 5), its response BETWEEN and WITHIN patches in different types of searching arenas (Chapters 6 and 7), and a detailed study of its response in an individual patch (Chapter 8).

It is interesting to note that the response of the beetle to patches of different prey densities, even as an individual (in most experiments the response of a single beetle was tested), was consistent in most of these levels of prey organization and, in a very general way, the plots of data describing various responses have tended to follow trends similar to the Type-II functional response curve of Holling, i.e. a decelerating rise to an upper asymptote or its reverse, viz., a decelerating decline to a lower asymptote, depending on the nature of the response. The results have conclusively demonstrated that Rodolia has the ability to distinguish between patches of prey in relation to prey density. The beetle uses this power of discrimination in killing prey and, more importantly, in distributing its eggs judiciously, so as to ensure better survival of its progeny. While it is persistent in its search for patches of lower prey densities (Chapter 8), it still spends its time efficienctly because it leaves patches of lower prey densities sooner than those of higher prey densities in search of more patches (Chapter 6.1 and 8).

Therefore, if a predator's response to spatial heterogeneity in the distribution of prey can impart any degree of stability to the dynamics of interacting predator-prey populations (Hassell, 1978b; Beddington et al., 1978; Putman and Wratten, 1984), the data gathered for Rodolia provide some explanation for the apparent stability in the field populations of Icerya. It would be interesting to know if the other natural enemies (the parasites) of the scale also possess attributes similar to that of the

beetle. Until such data are collected, we can only conclude that, though Rodolia may possess some of the attributes of an "ideal" predator, it may not necessarily be solely responsible for the stability in the scale population in both Australia and California.

Biologists interested in Optimal Foraging theory are studying the behaviour of predators closely in an effort to understand all those factors that influence the predator's decision to emigrate from a patch of prey. Such studies also provide an explanation for the mechanism by which predators respond to patchily distributed prey populations. It is also encouraging to note that biologists are realizing the importance of studying the behaviour of predators because unless we understand HOW the outcome is produced, it would be very difficult to devise proper techniques for the evaluation of the outcome of predator search.

With these ideas in mind, a concept of searching efficiency was developed by taking into account the series of steps that results in the attack of prey for evaluating a predator's response to patchiness in the distribution of prey. However, the concept is still in its infancy and demands further research so as to allow it to be applicable to a range of predator-prey systems and permit evaluation of predator effectiveness. The present study is, therefore, only the beginning!



## BIBLIOGRAPHY

## BIBLIOGRAPHY

- ABLES, J.R. and SHEPARD, M. (1976). Influence of temperature on oviposition by the parasite Spalangia endius and Muscidifurax raptor. Environ. Entomol., 5(3):511-513.
- AKINLOSOTU, T.A. (1973). The role of Diaeretiella rapae (McIntosh) in the control of the cabbage aphid. Unpublished Ph.D. thesis, University of London.
- AKRE, B.G. and JOHNSON, D.M. (1979). Switching and sigmoid functional response curves by damsel fly naiads with alternative prey available. J. Anim. Ecol., 48:703-720.
- ALLEN, D.C., KNIGHT, F.B. and FOLTZ, J.L. (1970). Invertebrate predators of the Jack-pine budworm, Choristoneura pinus, in Michigan. Ann. Entomol. Soc. Am., 63:59-64.
- AMOS, T.G. and WATERHOUSE, F.L. (1967). Phasic behaviour shown by two Carpophilus species (Coleoptera, Nitidulidae) in various humidity gradients and its ecological significance. Oikos, 18(2):345-350.
- ANDREWARTHA, H.G. and BIRCH, L.C. (1954). The distribution and abundance of animals. The University of Chicago Press, Chicago and London. pp. 782.
- ARTHUR, A.P. (1966). Associative learning in Itoplectis conquisitor (Say) (Hymenoptera : Ichneumonidae). Can. Ent., 98:213-223.
- BANKS, C.J. (1954). The searching behaviour of coccinellid larvae. Brit. J. Anim. Beh., 2:37-38.
- BANKS, C.J. (1957). The behaviour of individual coccinellid larvae on plants. Br. J. Anim. Behav., 5:12-24.
- BALAKOWSKY, A. (1932). Observations biologique sur l'adaptation de Novius cardinalis Muls. aux depens de Gueriniella serratulae F. (Contribution 'A L'etude des coccides de France; 6e note.) Rev. Pathol. Veg. Ent. Agr. Fr., 19:11-17.
- BARTLETT, B.R. (1978). Margarodidae. In C.P. Clausen (ed.). Introduced parasites and predators of Arthropod pests and weeds : a world review, pp. 132-135. USDA Agriculture Handbook No. 480.
- BARTLETT, B.R. and LAGACE, C.F. (1960). Interference with the biological control of cottony-cushion scale by insecticides and attempts to re-establish a favourable natural balance. Jour. Econ. Ent., 53(6):1055-58.

- BEDDINGTON, J.R., FREE, C.A. and LAWTON, J.H. (1978). Characteristics of natural enemies in models of biological control of insect pests. Nature (London), 273:513-519.
- BEGON, M. and MORTIMER, M. (1981). Population ecology, a unified study of animals and plants. Blackwell scientific Publications, Oxford, London. pp. 200.
- BELLOWS, T.S. Jr., and BIRLEY, M. (1981). Estimating developmental and mortality rates and stage recruitment from insect stage-frequency data. Res. Popul. Ecol., 23:232-244.
- BELLOWS, T.S. Jr., ORTIZ, M., OWENS, J.C. and HUDDLESTON, E.W. (1982). A model for analysing insect stage-frequency data when mortality varies with time. Res. Popul. Ecol., 24 (1):142-156.
- BENNETT, F.D. and HUGHES, I.W. (1959). Biological control of insect pests in Bermuda. Bull. Ent. Res., 50:423-436.
- BIEVER, K.D. (1971). Effect of temperature on the rate of search by Trichogramma and its potential application in field releases. Environ. Entomol., 1(2):194-197.
- BIRLEY, M. (1977). The estimation of insect density and instar survivorship functions from census data. J. Anim. Ecol., 46:467-510.
- BISHOP, G.R. and MAELZER, D.A. (1981). Methods of estimating survival-rates from insect population stage-frequency data. Proc. 3rd Australian Conf. Grassl. Ecol., Adelaide, 127-133.
- BODENHEIMER, F.S. (1934). Icerya purchasi Mask. und Novius cardinalis Muls. Z. ang. Ent., 19(4):514-543.
- BODENHEIMER, F.S. (1951). Citrus entomology in the middle east with special reference to Egypt, Iran, Iraq, Palestine, Syria and Turkey, Vitjevrij Dr. Junk. Gravenhage. pp. 663.
- BOLT, P.E. (1974). Temperature, humidity and host : effect on rate of search of Trichogramma evanescens and T. minutum auctt. (not Riley, 1871) (Hymenoptera: Trichogrammatidae). Ann. Ent. Soc. Am., 67(4):706-708.
- BOND, A.B. (1980). Optimal foraging in a uniform habitat : the search mechanism of the Green Lacewing. Anim. Behav., 28:10-19.
- BRECK, J.E. (1978). Sub-optimal foraging strategies for a patchy environment. Unpublished Ph.D. thesis, Michigan State University.

- BRYAN, K.M. and WRATTEN, S.D. (1984). The responses of polyphagous predators to prey spatial heterogeneity : aggregation by carabid and staphylinid beetles to their cereal aphid prey.  
Ecol. Ent., 9(3):251-259.
- BURNETT, T. (1951). Effects of temperature and host density on the rate of increase of an insect parasite.  
Am. Nat., 85:337-352.
- BURNETT, T. (1956). Effects of natural temperatures on oviposition of various numbers of an insect parasite (Hymenoptera : Chalcididae, Tenthredinidae).  
Ann. Ent. Soc. Am., 49:55-59.
- CADE, W. (1975). Acoustically orienting parasitoids : fly phonotaxis to cricket song.  
Science, 190:1312-1313.
- CAMOURS, F.B. and PAYNE, T.L. (1972). Response of Hydemia unica (Hymenoptera : Pteromalidae) to Dendroctonus frontalis (Coleoptera : Scolytidae) pheromones and a host-tree terpene.  
Ann. Ent. Soc. Am., 65:31-33.
- CARTER, M.C. and DIXON, A.F.G. (1982). Habitat quality and the foraging behaviour of coccinellid larvae.  
J. Anim. Ecol., 51:865-878.
- CHARNOV, E.L. (1976a). Optimal foraging, the marginal value theorem.  
Theor. Popul. Biol., 9:129-136.
- CHARNOV, E.L. (1976b). Optimal foraging : attack strategy of a mantid.  
Am. Nat., 110:141-151.
- CHESSON, J. (1982). Estimation and analysis of parasitoid search and attack parameters from field data.  
Environ. Entomol., 11(3):531-537.
- CLARKE, L.R. (1963). The influence of predation by Syrphus sp. on the numbers of Cardiaspina albitextura (Psyllidae).  
Aust. J. Zool., 11:470-487.
- CLAUSEN, C.P. (Ed.) (1978). Introduced Parasites and Predators of Arthropod Pests and Weeds : A World Review. USDA Handbook. 480. 545 pp.
- CODY, M.L. (1974). Optimization in ecology.  
Science, 183:1156-1164.
- COLBURN, R. and ASQUITH, D. (1970). A cage used to study the finding of a host by the ladybird beetle, Stethorus punctum.  
J. Econ. Entomol., 63:1376-1377.
- COOK, R.M. (1977). Searching behaviour of various insect predators and parasitoids. Unpublished D.Phil. thesis, University of Oxford.

- COOK, R.M. and COCKERELL, B.J. (1978). Predator ingestion rate and its bearing on feeding time and the theory of optimal diets. J. Anim. Ecol., 47:529-547.
- COOK, R.M. and HUBBARD, S.F. (1977). Adaptive searching strategies in insect parasites. J. Anim. Ecol., 46:115-125.
- COQUILLET, D.W. (1889). The imported Australian lady bird. Insect Life, II(3):70-74.
- COWIE, R.J. (1977). Optimal foraging in Great Tits (Parus major). Nature (London), 268:137-139.
- COWIE, R.J. and KREBS, J.R. (1979). Optimal foraging in patchy environments. In R.M. Anderson, B.D. Turner, and L.R. Taylor (eds.). The British Ecological Society Symposium, Vol. 20, Population dynamics, pp. 183-205. Oxford : Blackwell Scientific Publications.
- GRESSMAN, A.W. and DUMESTRE, J.O. (1930). The feeding rate of the Australian lady beetle, Rodolia cardinalis. Jour. Ag. Res., 41:197-203.
- CROZE, H. (1970). Searching image in carrion crows. Z. Tierpsychol., Beiheft 5.
- DeBACH, P. (1974). Biological control by natural enemies. Cambridge University Press. pp. 323.
- DeBACH, P. and BARTLET, B.R. (1964). Methods of colonization, recovery and evaluation. In P. DeBach (ed.). Biological control of insect pests and weeds, pp. 402-426. Chapman and Hall, London.
- DeBACH, P. and HUFFAKER, C. (1971). Experimental techniques for evaluation of the effectiveness of natural enemies. In C.B. Huffaker (ed.). Biological Control, pp. 113-139. Plenum Press, New York.
- DeBACH, P., HUFFAKER, C.B. and MacPHEE, A.W. (1976). Evaluation of the impact of natural enemies. In Huffaker, C.B. and Messenger, P.S. (eds.). Theory and practice of biological control. pp. 255-285. Academic Press, New York, San Francisco, London.
- 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.
- DOUTT, R.L. (1964a). Biological characteristics of entomophagous adults. In DeBach, P. (ed.). Biological control of insect pests and weeds. pp. 145-167. Chapman and Hall, London.
- DOUTT, R.L. (1964b). The historical development of biological control. In P. DeBach (ed.). Biological control of insect pests and weeds, pp. 21-42. Chapman and Hall, London.

- DOWELL, R.V., PUCKETT, D. and JOHNSON, M. (1981). Searching and ovipositional behaviour of Amitus hesperidum (Hymenoptera : Platygasteridae) and Encarsia opulaenta (Hymenoptera : Aphelinidae) parasitoids of the citrus blackfly (Homoptera : Aleyrodidae). Entomophaga, 26(3):233-239.
- DREISIG, H. (1981). The rate of predation and its temperature dependence in the tiger beetle, Cicindela hybrida. Oikos, 36:196-202.
- EL-SAADANY, G. and GOMA, A. (1974). Distribution and abundance of Icerya purchasi Mask. (Homoptera : Margarodidae) on Stercholia diversifolia in Egypt. Z. ang. Ent., 77(1):73-77.
- ELTON, C. (1938). Animal numbers and adaptation. In Beer, G.R. de (ed.). Evolution : essays on aspects of evolutionary biology, pp. 127-137. Oxford, Clarendon Press. pp 489, 557.
- EMLEM, J.M. (1966). The role of time and energy in food preference. Am. Nat., 100:611-617.
- EVANS, H.F. (1976). The searching behaviour of Anthocoris confusus in relation to prey density and plant surface topography. Ecol. Ent., 1(3):163-169.
- FLANDERS, S.E. (1947). Elements of host discovery exemplified by parasitic Hymenoptera. Ecology, 28(3):299-309.
- FLESHNER, C.A. (1950). Studies on the searching capacity of the larvae of three predators of the citrus red mite. Hilgardia, 20:233-265.
- FREE, C.A., BEDDINGTON, J.R. and LAWTON, J.H. (1977). On the inadequacy of simple models of mutual interference for parasitism and predation. J. Anim. Ecol., 46:543-554.
- FROGATT, W.W. (1902). Australian ladybird beetles. Agriculture Gaz. N.S.W. XIII, 1902. pp. 895-911.
- GEHAN, E.A. and SIDDIQUI, M.M. (1973). Simple regression methods for survival time studies. J. Am. Stat. Assoc., 68:848-856.
- GIBB, J.A. (1962). L. Tinbergen's hypothesis on the role of specific search images. Ibis, 104:106-111.
- GILBERT, N., GUTIERREZ, A.P., FRAZER, B.D. and JONES, R.E. (1976). Ecological relationships. W.H. Freeman & Co. Reading and San Francisco. pp. 156.

- GOSSARD, H.A. (1901). The cottony-cushion scale.  
Fla. Agr. Expt. Sta. Bull., 56:312-356.
- GREEN, R.F. (1984). Stopping rules for optimal foragers.  
Am. Nat., 123(1):30-43.
- GRESENS, S.E., COTHRAN, M.L. and THORP, J.H. (1982). The influence of temperature on the functional response of the Dragonfly, Celithemis fasciata (Odonata, Libellulidae).  
Oecologia, 53(3):281-284.
- HAFEZ, M. (1961). Seasonal fluctuations of population density of the cabbage aphid, Brevicoryne brassicae (L.) in the Netherlands and the role of its parasite, Aphidius (Diaeretiella) rapae (Curtis).  
Tijdschr. PlZiekt., 67:445-548.
- HAHN, G.E. and SHAPIRO, S.S. (1967). Statistical models in engineering. John Wiley & Sons, Inc. New York. pp. 355.
- HALE, L.D. (1970). Behaviour, distribution and population dynamics of the cottony-cushion scale Icerya purchasi in Desmodium fields in Hawaii.  
Ann. Ent. Soc. Amer., 63(4):1040-1047.
- HALL, R.W., EHLER, L.E. and BISABRI-ERSHADI, B. (1980). Rate of success in classical biological control of arthropods.  
Bull. Ent. Soc. Am., 26(2):111-114.
- HARVEY, P.H. and MACE, G.M. (1983). Foraging models and territory size.  
Nature (London), 305:14-15.
- HASELL, M.P. (1966). Evaluation of parasite or predator responses.  
J. Anim. Ecol., 35:65-75.
- HASELL, M.P. (1968). The behavioural response of a tachinid fly (Cyzenis albicans (Fall.)) to its host, the winter moth (Operophtera brumata (L.)).  
J. Anim. Ecol., 37:627-639.
- HASELL, M.P. (1971). Mutual interference between searching parasitoids.  
J. Anim. Ecol., 40:473-485.
- HASELL, M.P. (1978a). The dynamics of competition and predation. Edward Arnold, London. pp. 68.
- HASELL, M.P. (1978b). The dynamics of arthropod predator-prey systems. Princeton Univ. Press, Princeton, New Jersey. pp. 237.
- HASELL, M.P. (1980). Foraging strategies, population models and biological control : a case study.  
J. Anim. Ecol., 49:603-628.
- HASELL, M.P. (1982a). What is searching efficiency?  
Ann. Appl. Biol., 101(1):170-175.

- HASSELL, M.P. (1982b). Patterns of parasitism by insect parasitoids in patchy environments.  
Ecol. Ent., 7(4):365-378.
- HASSELL, M.P., LAWTON, J.H. and BEDDINGTON, J.R. (1976). The components of arthropod predation. I. The prey death-rate.  
J. Anim. Ecol., 45:135-164.
- HASSELL, M.P., LAWTON, J.H. and BEDDINGTON, J.R. (1977). Sigmoid functional responses by invertebrate predators and parasitoids.  
J. Anim. Ecol., 46:249-262.
- HASSELL, M.P. and MAY, R.M. (1973). Stability in insect host-parasite models.  
J. Anim. Ecol., 42:693-726.
- HASSELL, M.P. and MAY, R.M. (1974). Aggregation in predators and insect parasites and its effect on stability.  
J. Anim. Ecol., 43:567-594.
- HASSELL, M.P. and SOUTHWOOD, T.R.E. (1978). Foraging strategies of insects.  
Annu. Rev. Ecol. Syst., 9:75-98.
- HEADS, P.A. and LAWTON, J.H. (1983). Studies on the natural enemy complex of the holly leaf-miner -- the effects of scale on detection of aggregative responses and the implications for biological control.  
Oikos, 40(2):267-276.
- HEAP, M. (1980). A study of the biology of Icerya purchasi Maskell (Homoptera : Margarodidae) on two major hosts, Acacia baileyana and the citrus variety, Washington Navel orange. Honours Thesis, University of Adelaide. pp. 100.
- HILDREW, A.G. and TOWNSEND, C.R. (1977). The influence of substrate on the functional response of Plectroreimia conspersa larvae (Trichoptera : Polycentropodidae).  
Oecologia, 31:21-26.
- HISLOP, R.T.G. and PROKOPY, R.J. (1981). Mite predator responses to prey and predator emitted stimuli.  
J. Chem. Ecol., 7(5):895-904.
- HOGG, D.B. and NORDHEIM, E.V. (1983). Age-specific survivorship analysis of Heliothis spp. populations on cotton.  
Res. Popul. Ecol., 25(2):280-297.
- HOLLING, C.S. (1959). Some characteristics of simple types of predation and parasitism.  
Can. Ent., 91:385-398.
- HOLLING, C.S. (1966). The functional response of invertebrate predators to prey density.  
Mem. Ent. Soc. Can., 48:1-86.



- HOWELL, D.J. (1983). Optimization of behaviour : introduction and overview.  
Amer. Zool., 23(2):257-260.
- HOWELL, J.O. and BESHEAR, R.J. (1981). An illustrated redescription of Icerya purchasi.  
J. Georgia Entomol. Soc., 16(4):441-444.
- HUBBARD, S.F. and COOK, R.M. (1978). Optimal foraging by parasitoid wasps.  
J. Anim. Ecol., 47:593-604.
- HUFFAKER, C.B. (ed.) (1971). Biological control. Plenum Press, New York.  
pp. 551.
- HUFFAKER, C.B. and MESSENGER, P.S. (eds.) (1976). Theory and practice of biological control. Academic Press, New York, San Francisco, London.  
pp. 788.
- HUGHES, R.D. and WOOLCOCK, L.T. (1965). A modification of Johnson's method of rearing aphids for ecological studies.  
N. Z. J. agric. Res., 8:728-736.
- HUGHES-SCHRADER, S. (1930). Contributions to the life history of the Iceryne coccids, with special reference to parthenogenesis and hermaphroditism.  
Ann. Ent. Soc. Amer., 23(2):359-380.
- HURLBERT, S.H. (1984). Pseudoreplication and the design of ecological field experiments.  
Ecol. Monogr., 54(2):187-211.
- IWASA, Y., HIGASHI, M. and YAMAMURA, N. (1981). Prey distribution as a factor determining the choice of optimal foraging strategy.  
Am. Nat., 117:710-723.
- JANNONE, G. (1967). Coccid biocoenology on citrus and Pittosporum in Liguria and the consequences of the control of Icerya purchasi by Rodolia cardinalis in connection with the spread of Chloropulvindra floccifera.  
Entomologica, 85-138.
- JOHNSON, B.L. and BIRKS, P.R. (1960). Studies on wing polymorphism in aphids. 1. The developmental process involved in the production of different forms.  
Ent. exp. & appl., 3:326-339.

- KAMIL, A.C. (1983). Optimal foraging theory and the psychology of learning.  
Amer. Zool., 23(2):291-302.
- KAMIL, A.C. and SARGENT, T.D. (eds.) (1981). Foraging behaviour, ecological, ethological and psychological approaches, Garland STPM Press, New York.
- KAUSSARI, M. (1946). Coastal citrus pests (Iran).  
Ent. Phytopath. Appl. Teheran, 1:32-38.
- KEHAT, M. (1968). The feeding behaviour of Pharoscymnus numidicus (Coccinellidae), predator of the date palm scale, Parlatoria blanchardi.  
Entomol. Exp. Appl., 11:30-32.
- KIRITANI, K. and DEMPSTER, J.P. (1973). Different approaches to the quantitative evaluation of natural enemies.  
J. Appl. Ecol., 10:323-330.
- KIRITANI, K. and NAKASUJI, F. (1967). Estimation of the stage-specific survival rate in the insect population with overlapping stages.  
Res. Popul. Ecol., 9:143-152
- KREBS, J.R. (1973). Behavioural aspects of predation. In P.G. Bateson and P.H. Klopfer (eds.). Perspectives in ethology, Vol.I, pp. 73-111. New York : Plenum.
- KREBS, J.R. (1978). Optimal foraging : decision rules for predators. In J.R. Krebs and N.B. Davies (eds.). Behavioural ecology, an evolutionary approach. Sutherland, Mass. : Sinauer Associates.
- KREBS, J.R. (1979). Foraging strategies and their social significance. In P. Marler and J. Vandenberg (eds.). Social Behaviour and Communication. New York : Plenum.
- KREBS, J.R., KACELNIK, A. and TAYLOR, P. (1978). Test of optimal sampling by foraging Great Tits.  
Nature (London), 275:27-31.
- KREBS, J.R., RYAN, J.C. and CHARNOV, E.I. (1974). Hunting by expectation or optimal foraging? A study of patch use by Chikadees.  
Anim. Behav., 22:953-964.
- KREBS, J.R., STEPHENS, D.W. and SUTHERLAND, W.J. (1983). Perspectives in optimal foraging. In A.H. Brush and G.A. Clarke, Jr. (eds.). Perspectives in ornithology, pp. 165-216. Cambridge Univ. Press.
- KUWANA. I. (1922). Studies on Japanese Monophlebinae. II. The genus Icerya.  
Dept. Agric. Imp. Plant Quarant. Yokohama, 1-43. Sta. Bul. 2.

- LAING, J. (1937). Host-finding by insect parasites. I. Observations on the finding of hosts by Alysia munducator, Mormoniella vitripennis, and Trichogramma evanescens.  
J. Anim. Ecol., 6:298-317.
- LAWLESS, J.F. (1982). Statistical models and methods for lifetime data.  
John Wiley and Sons.
- LEGNER, E.F. (1969). Distribution pattern of hosts and parasitization by Spalangia drosophilae (Hymenoptera : Pteromalidae).  
Can. Ent., 101:551-557.
- LOTKA, A.J. (1925). Elements of Physical Biology, Williams and Wilkins, Baltimore. (Reissued as Elements of Mathematical Biology by Dover, 1956).
- MacARTHER, R.M. and PIANKA, E.R. (1966). On optimal use of a patchy environment.  
Am. Nat., 100:603-609.
- MANLY, B.F.J. (1974a). A comparison of methods for the analysis of insect stage-frequency data.  
Oecologia, 17:335-348.
- MANLY, B.F.J. (1974b). Estimation of stage-specific survival rates and other parameters for insect populations developing through several stages.  
Oecologia, 15:277-285.
- MANLY, B.F.J. (1976). Extensions to Kiritani and Nakasuji's method for analysing insect stage-frequency data.  
Res. Popul. Ecol., 17:191-199.
- MANLY, B.F.J. (1977). A further note on Kiritani and Nakasuji's model for the stage-frequency data including comments on the use of Tukey's jackknife technique for estimating variances.  
Res. Popul. Ecol., 18:177-186.
- MATSUKA, M. and WATANABE, M. (1980). Laboratory rearing of Vedalia beetles, Rodolia cardinalis.  
Bull. Fac. Agri., Tamagawa Univ. No. 20. pp. 1-8.
- MAY, R.M. (1978). Host-parasitoid systems in patchy environments : a phenomenological model.  
J. Anim. Ecol., 47(3):833-843.
- McARDLE, B.H. and LAWTON, J.H. (1979). Effects of prey-size and predator instar on the predation of Daphnia by Notonecta.  
Ecol. Ent., 4(3):267-275.
- McFARLAND, D.J. (1977). Decision making in animals.  
Nature (London), 269:15-21.

- McNAIR, J.N. (1982). Optimal giving up times and the marginal value theorem.  
Am. Nat., 119:511-529.
- McNEILL ALEXANDER, R. (1982). Optima for animals. pp. 112. Edward Arnold.
- MESSENGER, P.S. (1968). Bioclimatic studies of aphid parasite. I. Effects of temperature on functional response.  
Can. Ent., 100:728-741.
- MILLS, N.J. (1982). Satiation and the functional response : a test of a new model.  
Ecol. Ent., 7(3):305-315.
- MITCHELL, W.C. and MAU, R.F.L. (1971). Response of the female southern green stink bug and its parasite, Trichopoda pennipes, to male stink bug pheromones.  
J. Anim. Ecol., 64:856-859.
- MORAN, V.C., GUNN, B.H. and WALTER, G.H. (1982). Wind dispersal and settling of 1st instar crawlers of cochineal insect Dactylopius austrinus (Homoptera : Coccoidea : Dactylopiidae).  
Ecol. Ent., 7(4):409-420.
- MORRIS, R.F. (ed.) (1963). The population dynamics of epidemic spruce budworm populations.  
Mem. ent. Soc. Can., 31, 332 pp.
- MORRISON, G. and LEWIS, W.J. (1984). Inferring parasitoid searching behaviour from host mortality data : a note of caution.  
Environ. Entomol., 13(1):7-14.
- MORRISON, G., LEWIS, W.J. and NORDLUND, D.A. (1980). Spatial differences in Heliothis zea egg density and intensity of parasitism by Trichogramma spp. : an experimental analysis.  
Environ. Entomol., 9:75-85.
- MORRISON, G. and STRONG Jr., D.R. (1980). Spatial variations in host density and the intensity of parasitism : some empirical examples.  
Environ. Entomol., 9:149-152.
- MORRISON, G. and STRONG Jr., D.R. (1981). Spatial variations in egg density and the intensity of parasitism in a Neotropical crysometid (Cephaloleia consanguinea).  
Ecol. Ent., 6(1):55-61.
- MURDIE, G. and HASSELL, M.P. (1973). Food distribution, searching success and predator-prey models. In The mathematical theory of the dynamics of biological populations, pp. 87-101. Academic Press, London.
- MURDOCH, W.W. (1971). The developmental responses of predators to changes in prey density.  
Ecology, 52:132-137.

- MURDOCH, W.W. (1973). The functional response of predators.  
J. appl. Ecol., 14:335-341.
- MURDOCH, W.W. and OATEN, A. (1975). Predation and population stability.  
Adv. Ecol. Res., 9:2-132.
- NAKAMURA, K. (1974). A model of the functional response of a predator to prey density involving the hunger effect.  
Oecologia, 16:265-278.
- NAKAMUTA, K. (1982). Switchover in searching behaviour of Coccinella septempunctata L. (Coleoptera : Coccinellidae) caused by prey consumption.  
Appl. Ent. & Zool., 17(4):501-506.
- NAKAMUTA, K. (1983). Sequence of predatory behaviour of the ladybeetle, Coccinella septempunctata L. (Coleoptera : Coccinellidae) on the green peach aphid, Myzus persicae Sulz. (Homoptera : Aphididae).  
Appl. Ent. & Zool., 18(4):559-560.
- NAKAMUTA, K. (1984). Visual orientation of a lady beetle, Coccinella septempunctata (L.); (Coleoptera : Coccinellidae) towards its prey.  
Appl. Ent. & Zool., 19(1):82-86.
- NICHOLSON, A.J. (1933). The balance of animal populations.  
J. Anim. Ecol., 2:132-178.
- NICHOLSON, A.J. and BAILEY, V.A. (1935). The balance of animal populations. Part I.  
Proc. Zool. Soc. Lond., 1935, 551-598.
- NOYES, J.S. (1974). The biology of the leek moth, Acrolepia assectella (Zeller). Unpublished Ph.D. thesis, University of London.
- NUR, N. (1984). Fitness, population growth rate and natural selection.  
Oikos, 42(3):413-414.
- OWEN, D.F. and WIEGERT, R.G. (1982). Grasses and grazers : is there a mutualism  
Oikos, 38(2):258-259.
- PARKER, R.E. (1973). Introductory Statistics for Biology. Edward Arnold, London.
- PINDER III, J.E., WIENER, J.G. and SMITH, M.H. (1978). The Weibull distribution : a new method of summarizing survivorship data.  
Ecology, 59(1):175-179.
- PODOLER, H. (1981). Effects of variable temperatures on responses of Aphytis melinus and A. lingnanensis to host density.  
Phytoparasitica, 9(3):179-190.

- PODOLER, H. and MENDEL, Z. (1979). Analysis of a host-parasite (Ceratitis muscidifurax) relationship under laboratory conditions. Ecol. Ent., 4(1):45-59.
- POPPER, K. (1977). Unended quest, an intellectual autobiography. Fontanna/Collins. pp. 255.
- POUTIERS, R. (1930). Sur le comportement du Novius cardinalis vis-a-vis de certaines alcaloides. C. R. Soc. Biol., 103:1023-1025.
- PRIORE, R. (1963). Studio morfo-biologico sulla Rodolia cardinalis Muls. Boll. Lab. Entomol. Agric. "F. Silvestri", Portici, 21:62-198.
- PUTMAN, R.J. and WRATTEN, S.D. (1984). Principles of ecology. Croom Helm, London and Canberra. pp. 388.
- PUTMAN, W.L. (1955). Bionomics of Stethorus punctillum Weise (Coleoptera : Coccinellidae) in Ontario. Can. Ent., 87:9-33.
- PYKE, G. (1984). Optimal Foraging Theory : a critical review. Ann. Rev. Ecol. Syst., 15:523-575.
- PYKE, G.H., PULLIMAN, H.R. and CHARNOV, E.L. (1977). Optimal foraging : a selective review of theory and tests. Q. Rev. Biol., 52(2):137-154.
- QUAYLE, H.J. (1938). Insects of citrus and other sub-tropical fruits. Ithaca, New York : Comstock Pub. Co. pp. 538.
- QUEZADA, J.R. and DeBACH, P. (1973). Bioecological and population studies of the cottony-cushion scale, Icerya purchasi Mask., and its natural enemies, Rodolia cardinalis Mul. and Cryptochaetum iceryae Will. in Southern California. Hilgardia, 41(20):631-688.
- READ, D.P., FEENY, P.P., ROOT, R.B. (1970). Habitat selection by the aphid parasite Diaeretiella rapae (Hymenoptera : Braconidae) and hyperparasite Charips brassicae (Hymenoptera : Cynipidae). Can. Ent., 102:1567-1578.
- READSHAW, J.L. (1973). The numerical response of predators to prey density. J. Appl. Ecol., 10:342-351.
- ROBINSON, A.G. (1952). Notes on Stethorus punctum (Leg.) (Coleoptera : Coccinellidae), a predator of tetranychid mites in Manitoba. Rep. Entomol. Soc. Ontario, 83:24-26.
- ROGERS, D.J. (1972). Random search and insect population models. J. Anim. Ecol., 41:369-383.

- ROITBERG, B.D., van LENTEREN, J.C., van ALPHEN, J.J.M., GALIS, F. and PROKOPY, R.J. (1982). Foraging behaviour of Rhagoletis pomonella a parasite of hawthorn (Crataegus viridis) in nature. J. Anim. Ecol., 51(1):307-326.
- ROYAMA, T. (1970). Factors governing the hunting behaviour and selection of food by the Great Tit, Parus major. J. Anim. Ecol., 39:619-668.
- ROYAMA, T. (1971). A comparative study of models for predation and parasitism. Res. Popul. Ecol., supp.(1):1-91.
- RUESINK, W.G. (1975). Estimating time-varying survival of arthropod life stages from population density. Ecology, 56:244-247.
- SCHOENER, T.W. (1971). Theory of feeding strategies. Annu. Rev. Ecol. Syst., 11:369-404.
- SHIELD, E.J. and WATSON, T.F. (1980). Searching behaviour of female Orius tristicolor. Ann. Ent. Soc. Amer., 73(5):533-535.
- SIBLY, R. and McFARLAND, D. (1976). On the fitness of behaviour sequences. Am. Nat., 110:601-619.
- SMITH, J.M. (1978). Optimization theory in evolution. Annu. Rev. Ecol. Syst., 9:31-56.
- SMITH, J.N.M. and SWEETMAN, H.P.A. (1974). Food searching behaviour of titmice in patchy environments. Ecology, 55:1216-1232.
- SNEDECOR, G.W. and COCHRAN, W.G. (1968). Statistical Methods. The Iowa State University Press, Ames, Iowa, U.S.A. pp. 593.
- SOLOMON, M.E. (1949). The natural control of animal populations. J. Anim. Ecol., 18:1-35.
- SOPER, R.S., SHEWELL, G.E. and TYRRELL, D. (1976). Colcondamyia auditrix nov. sp. (Diptera : Sarcophagidae), a parasite which is attracted by the mating song of its host, Okanagona rimosa (Hymenoptera : Cicadidae). Can. Ent., 108:61-68.
- SOUTHWOOD, T.R.E. (1978). Ecological Methods, with particular reference to the study of insect populations. The English Language Book Society and Chapman and Hall. pp. 524.
- STAMP, N.E. (1982). Searching behaviour of parasitoids for web making caterpillars -- a test of optimal searching theory. J. Anim. Ecol., 51(2):387-396.

- STEEL, R.G.D. and TORRIE, J.H. (1981). Principles and procedures of statistics a biometrical approach. International Student Edition, McGraw Hill International Book Co. pp. 633.
- STENSETH, N.C. (1983). Grasses, grazers, mutualism and coevolution : a comment about hand waving in ecology.  
Oikos, 41:152-153.
- STENSETH, N.C. (1984). Fitness, population growth rate and evolution in plant-grazer systems : a reply to Nur.  
Oikos, 42(3):414-415.
- STORCH, R.H. (1976). Prey detection by fourth stage Coccinella transversoguttata larvae (Coleoptera : Coccinellidae).  
Anim. Behav., 24:690-693.
- STRENLICHT, M. (1973). Parasitic wasps attracted by the sex pheromones of their coccid hosts.  
Entomophaga, 18:339-343.
- STUBBS, M. (1980). Another look at prey detection by coccinellids.  
Ecol. Entomol., 5:179-182.
- SUBRAMANIAM, T.V. (1954-55). Control of the fluted scale in peninsular India.  
Ind. J. Ent., 16:391-415.
- SUBRAMANYAM, V.K. (1950). Homalotylus flaminus (Dalman), a parasite of the Rodolia grubs predatory on the fluted scale, Icerya purchasi Maskell.  
Ind. J. Ent., 12:103-106.
- THOMPSON, D.J. (1975). Towards a predator-prey model incorporating age structure : the effects of prey and predator size on the predation of Daphnia magna by Ischnura elegans.  
J. Anim. Ecol., 44:907-916.
- THOMPSON, W.R. (1924). La theorie mathematique de l'action des parasites entomophages et le facteur du hasard.  
Annls. Fac. Sci. Marseille, 2:69-89.
- TINBERGEN, N., IMPEKOVEN, M. and FRANCK, D. (1967). An experiment on spacing-out as a defence against predation.  
Behaviour, 28:307-321.
- TOWNSEND, C.R. and HILDREW, A.G. (1980). Foraging in a patchy environment by a predatory net spinning-caddis larvae : a test of optimal foraging theory.  
Oecologia (Berlin), 47:219-221.
- USHER, M.B. and WILLIAMSON, M.H. (eds.) (1974). Ecological stability. Chapman and Hall, London. pp. 196.



- van ALPHEN, J.J.M. (1980). Aspects of the foraging behaviour of Tetrastichus asparagi Crawford and Tetrastichus sp., gregarious egg parasitoids of the asparagus beetles Crioceris asparagi and C. duodeimpunctata. I. Host-species selection, host-stage selection and host discrimination. Netherlands J. Zool., 30:307-325.
- van ALPHEN, J.J.M. and GALIS, F. (1983). Patch time allocation and parasitization efficiency of Asobara tabida, a larval parasitoid of Drosophila. J. Anim. Ecol., 52(3):937-952.
- van den BOSCH, R. and MESSENGER, P.S. (1973). Biological control. Intext Education Publishing, New York, pp. 180.
- van LENTEREN, J.C. (1980). Evaluation of control capabilities of natural enemies : Does art have to become science Netherlands J. Zool., 30(2):369-381.
- van LENTEREN, J.C., and BAKKER, K. (1976). Functional responses in invertebrates. Netherlands J. Zool., 26:567-572.
- van LENTEREN, J.C. and BAKKER, K. (1978). Behavioral aspects of the functional responses of a parasite (Pseudeucoila bochei Weld.) to its host (Drosophila melanogaster). Netherlands J. Zool., 28(2):213-233.
- van STRAALLEN, N.M. (1982). Demographic analysis of arthropod populations using a continuous stage-variable. J. Anim. Ecol., 51:769-783.
- VOLTERRA, V. (1926). Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. Mem. Acad. Lincei., 2:31-113. (Translation in : CHAPMAN, R.N. 1931. Animal Ecology, pp. 409-448. McGraw-Hill, New York.)
- WAAGE, J.K. (1979). Foraging for patchily-distributed hosts by the parasitoid, Nemeritis canescens. J. Anim. Ecol., 48: 353-371.
- WAAGE, J.K. (1983). Aggregation in field parasitoid populations : foraging time allocation by a population of Diadegma (Hymenoptera : Ichneumonidae). Ecol. Ent., 8(4):447-453.
- WASELOH, R.M. (1973). Relationships of natural field populations to gypsy moth abundance. Ann. Ent. Soc. Am., 66:853-856.
- WAY, M.J. (1973). Objectives, methods and scope of integrated control. In Geier, P.W., Clark, L.R., Anderson, D.J. and Nix, H.A. (eds.). Insects : studies in population management. Ecol. Soc. Austr. Memoirs, 1:1-17.

- WHITE, T.C.R. (1968). Hatching of eggs of Cardiaspina densitexta (Homoptera : Psyllidae) in relation to light and temperature.  
J. Insect Physiol., 14:1847-1859.
- WILLARD, J.R. (1973). Wandering time of the crawlers of California red scale Aonidiella aurantii (Mask.) (Homoptera : Diaspididae) on citrus.  
Aust. J. Zool., 21:217-229.
- WILLARD, J.R. (1976). Leaf disc method for rearing California red scale, Aonidiella aurantii (Maskell) (Homoptera : Diaspididae).  
J. Aust. ent. Soc., 15:7-11.
- WOLCOTT, G.N. and SEIN, F. Jr. (1933). A year's experience with the cottony-cushion scale in Puerto Rico.  
J. P. R. Dep. Agr., 17:199-221.
- WRATTEN, S.D. (1973). The effectiveness of the coccinellid beetle Adalia bipunctata (L.), as a predator of the lime aphid, Eucallipterus tiliiae (L.).  
J. Anim. Ecol., 42:785-802.
- WYLIE, H.G. (1958). Factors that affect host finding by Nasonia vitripennis (Walk.) (Hymenoptera : Pteromalidae).  
Can. Ent., 90:597-608.
- YEARGAN, K.V. and LATHEEF, M.A. (1976). Host-parasitoid density relationships between Hypera postica (Coleoptera : Curculionidae) and Bathyplectes curculionis (Hymenoptera : Ichneumonidae).  
J. Kansas Entomol. Soc., 49(4):551-556.
- ZACH, R. and SMITH, J.N.M. (1981). Optimal foraging in Wild birds In A.L. Kamil and T.D. Sargent (eds.). Foraging behaviour, ecological, ethological and psychological approaches, pp. 95-109. New York : Garland STPM Press.

## APPENDICES

Appendix Table 1

LIST OF SPECIES REPRESENTED BY THE GENUS ICERYA

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1. Icerya aegyptiaca (Douglas)
  2. I. callitri (Froggatt)
  3. I. koebelei Maskell
  4. I. montserratensis Riley & Howard
  5. I. palmeri Riley & Howard
  6. I. purchasi (Maskell)
  7. I. rileyi Cockerell
  8. I. rosae
  9. I. seychellarum (Westwood)
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Appendix Table 2

LIST OF HOST PLANTS OF I. purchasi RECORDED IN ADELAIDE

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SCIENTIFIC NAMES (COMMON NAMES)	FAMILY
1. <u>Acacia baileyana</u> (Cootamundra wattle)	Leguminosae
2. <u>A. iteaphylla</u> (Willow-leaved wattle)	Leguminosae
3. <u>A. durus</u>	Leguminosae
4. <u>Albizia lophantha</u> (Willd.) (Cape Wattle)	Leguminosae
5. <u>Armoracia rusticana</u> (Horseradish)	Cruciferae
6. <u>Casuarina</u> spp. (Sheoak)	Casuarinaceae
7. <u>Citrus limon</u> (Lemon)	Rutaceae
8. <u>C. sinensis</u> (Orange)	Rutaceae
9. <u>Fortunella</u> spp. (Cumquat)	Rutaceae
10. <u>Grevillea</u> spp.	Proteaceae
11. <u>Hypericum</u> spp.	Guttiferae
12. <u>Kennedia nigricans</u> (Black-orall Pea)	Leguminosae
13. <u>Nandina domestica</u> (Sacred or Heavenly Bamboo)	Berberidaceae
14. <u>Pittosporum tobira</u> (Tobera)	Pittosporaceae
15. <u>P. phylliraeoides</u> Dc. (Butterbush)	Pittosporaceae
16. <u>Prunus armeniaca</u> (Apricot)	Rosaceae
17. <u>Rosa</u> spp. (Rose)	Rosaceae
18. <u>Rosmarinus officinalis</u> L. (Rosemary)	Labiatae
19. <u>Sonchus oleraceus</u> (Common Sowthistle)	Compositae
20. <u>Spartium juceum</u> (Spanish broom)	Leguminosae

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Appendix Table 3

LIST OF NATURAL ENEMIES ATTACKING Icerya purchasi

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SCIENTIFIC NAMES	FAMILY
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PREDATORS

ORDER COLEOPTERA

1. Rodolia cardinalis (Mulsant) (vedalia beetle) Coccinellidae
2. R. iceryae Coccinellidae
3. R. koebelei Coccinellidae
4. R. pumila (Weise) (in Australia) Coccinellidae
5. Leis conformis (Boisd.) (found feeding on eggs) Coccinellidae

ORDER NEUROPTERA

1. Crysopa spp. (Green Lace Wing) Chrysopidae

PARASITES

ORDER DIPTERA

1. Cryptochaetum iceryae Will. (in U.S.A. & Aust.) Agromyzidae
2. Syneura cocciphila Coq. (in Puerto Rico) Phoridae
3. S. infrapospita Borgm. & Schm. (in Brazil) Phoridae

ORDER HYMENOPTERA

1. Brethesiella latifrons Timb. Encyrtidae
2. Coccophagus scutellaris Dalm. (in Tenerife) Aphelinidae
3. Euryschia spp. (in Australia) Aphelinidae
4. Ophelosia crawfordi Riley (in U.S.A. & Aust.) Pteromalidae

HYPERPARASITES

ORDER HYMENOPTERA

1. Cheiloneurus pulvinariae Doz. (in Argentina) Encyrtidae  
(parasite of Cryptochaetum iceryae)
2. Homalotylus flaminus (Dalman) (in India) Encyrtidae  
(parasite of Rodolia cardinalis larvae)

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Appendix Table 4

METEOROLOGICAL DATA COMPRISING OF MONTHLY MEANS OF TEMPERATURE, RELATIVE HUMIDITY, RAINFALL, AND WIND SPEED FOR THE 1982 AND 1983, AND THE MONTHS CONSTITUTING THE FOUR SEASONS.

YEAR	MONTH	TEMPERATURE ( $^{\circ}$ C)			REL. HUM. (%)	RAINFALL (mm)	WIND SPEED (km/h)
		MIN.	MAX.	MEAN			
1982	JANUARY	19.0	30.2	24.6	50.3	24.6	151.7
	FEBRUARY	17.5	28.7	22.9	54.2	7.0	135.6
	MARCH	16.2	26.1	21.2	56.6	54.2	124.2
	APRIL	13.9	21.5	17.7	62.1	81.2	92.1
	MAY	11.4	17.4	14.5	71.4	63.2	102.3
	JUNE	7.2	14.2	10.8	76.3	62.6	95.2
	JULY	7.3	13.8	10.6	70.4	38.6	99.7
	AUGUST	10.2	19.0	14.6	57.0	24.6	106.7
	SEPTEMBER	9.6	17.6	13.6	60.6	32.0	123.8
	OCTOBER	11.3	20.4	15.8	55.5	16.0	134.6
	NOVEMBER	15.1	27.0	21.1	43.9	3.4	126.4
	DECEMBER	15.4	27.3	21.3	51.2	13.2	130.5
1983	JANUARY	15.4	27.4	21.4	53.4	22.4	141.9
	FEBRUARY	19.5	31.5	25.5	46.8	1.8	128.5
	MARCH	16.0	25.3	20.6	64.9	105.6	126.1
	APRIL	12.2	19.2	15.7	63.3	99.0	127.4
	MAY	11.0	17.8	14.4	74.5	76.6	107.6
	JUNE	8.5	15.4	11.9	75.3	34.0	95.1
	JULY	7.7	13.5	10.6	80.1	127.6	131.4
	AUGUST	9.4	16.3	12.8	69.3	90.6	127.9
	SEPTEMBER	10.1	17.6	13.8	69.0	77.0	149.9
	OCTOBER	11.4	21.0	16.2	60.0	56.0	123.8
	NOVEMBER	13.6	24.0	18.8	55.3	10.6	160.9
	DECEMBER	16.0	27.8	21.9	49.5	20.0	136.5

SEASONS

MONTHS

- |           |                                   |
|-----------|-----------------------------------|
| 1. SUMMER | DECEMBER, JANUARY, AND FEBRUARY.  |
| 2. AUTUMN | MARCH, APRIL, AND MAY.            |
| 3. WINTER | JUNE, JULY, AND AUGUST.           |
| 4. SPRING | SEPTEMBER, OCTOBER, AND NOVEMBER. |

Appendix Table 5

NUMBERS OF SCALES COLLECTED IN PRELIMINARY SAMPLING IN JULY, 1981  
ON TREE (A) AND TREE (B)

SAMPLE NUMBER	STRATA	TREE (A)				TREE (B)					
		R1	R2	R3	SUM	R1	R2	R3	R4	SUM	
<u>LOWER LEVEL</u>											
1	OUTER	E	17	1	1	19	1	5	5	3	14
2	SECTION	S	3	0	0	3	1	1	3	3	8
3		W	9	0	2	11	4	0	5	2	11
4		N	2	3	2	7	2	1	0	0	3
5	INNER	E	14	1	8	23	2	28	51	50	131
6	SECTION	S	8	13	1	22	14	13	23	34	84
7		W	3	2	3	8	14	11	6	30	61
8		N	10	3	12	25	35	108	12	9	164
<u>MIDDLE LEVEL</u>											
9	OUTER	E	1	19	55	75	5	5	3	0	13
10	SECTION	S	2	0	1	3	0	4	2	0	6
11		W	0	37	2	39	0	0	2	0	2
12		N	3	11	5	19	1	2	2	0	5
13	INNER	E	13	15	32	60	2	10	7	16	35
14	SECTION	S	3	17	15	35	20	5	3	6	34
15		W	2	8	1	11	0	0	0	1	1
16		N	1	3	12	16	0	1	4	1	6
<u>UPPER LEVEL</u>											
17	OUTER	E	3	1	13	17					
18	SECTION	S	1	2	5	8					
19		W	0	1	0	1					
20		N	0	10	2	12					
21	INNER	E	7	4	37	48					
22	SECTION	S	3	0	3	6					
23		W	3	4	1	8					
24		N	2	6	3	11					

R1, R2, R3, R4, ARE REPLICATES WITHIN STRATA  
N, S, E, and W REPRESENT NORTH, SOUTH, EAST, AND WEST RESPECTIVELY



Appendix Table 6

SUMMARY OF THE POPULATION ESTIMATES OF SCALES OVER TWO YEARS FROM JULY, 1981 TO JUNE, 1983 ON TREE (A) AND TREE (B) (SAMPLE SIZE 16)

YEAR	MONTH	TREE (A)					TREE (B)				
		1st	2nd	3rd	Ad	SUM	1st	2nd	3rd	Ad	SUM
1981	JULY*	88	237	103	59	487	88	265	154	63	570
	AUGUST	0	16	36	40	92	20	37	44	40	141
	SEPT.	0	13	7	44	64	0	8	28	37	73
	OCT.	1	0	1	83	85	0	0	0	12	12
	NOV.	2	0	0	0	2	15	2	0	5	22
	DEC.	1	4	0	0	5	0	1	0	0	1
1982	JAN.	0	0	1	0	1	0	0	0	1	1
	FEB.	0	0	0	2	2	0	0	0	3	3
	MARCH	1	0	0	1	2	0	0	0	1	1
	APRIL	9	3	0	0	12	1	2	0	0	3
	MAY	38	28	7	4	77	3	3	2	1	9
	JUNE	39	23	11	10	83	4	0	1	2	7
	JULY	21	22	14	4	61	12	2	2	2	18
	AUGUST	2	10	3	8	23	0	3	1	2	6
	SEPT.	0	7	6	21	34	0	4	7	6	17
	OCT.	1	0	3	3	7	1	0	3	9	13
	NOV.	11	0	0	0	11	12	4	0	0	16
	DEC.	2	6	2	0	10	2	6	2	0	10
1983	JAN.	0	0	0	5	5	0	0	4	3	7
	FEB.	0	0	1	7	8	0	0	0	10	10
	MARCH	0	0	0	14	14	12	0	0	6	18
	APRIL	38	15	0	3	56	37	33	1	10	81
	MAY	22	107	11	4	144	7	55	29	3	94
	JUNE	169	99	66	19	353	15	12	15	2	44

1st, 2nd, 3rd represent the three instars

Ad = adults

\* = sample size 72 for Tree (A) and 64 for Tree (B) for July, 1981.

Appendix Table 7

SUMMARY OF THE POPULATION ESTIMATES OF NATURAL ENEMIES OVER TWO YEARS FROM JULY, 1981 TO JUNE, 1983 ON TREE (A) AND TREE (B) (SAMPLE SIZE 16)

YEAR	MONTH	TREE (A)				TREE (B)			
		ROD	PAR	GLW	SUM	ROD	PAR	GLW	SUM
1981	JULY*	0	-	-	0	0	-	-	0
	AUGUST	0	0	-	0	0	13	-	13
	SEPT.	1	11	-	12	4	27	-	31
	OCT.	6	21	1	28	11	5	0	16
	NOV.	0	0	0	0	9	1	8	18
	DEC.	0	0	3	3	0	0	0	0
	1982	JAN.	0	0	0	0	0	0	0
FEB.		0	0	0	0	0	0	0	0
MARCH		0	0	0	0	0	0	0	0
APRIL		0	0	0	0	0	0	0	0
MAY		0	0	0	0	0	0	1	1
JUNE		0	0	0	0	0	0	0	0
JULY		0	0	0	0	0	0	0	0
AUGUST		0	1	1	2	0	0	0	0
SEPT.		0	1	0	1	0	0	0	0
OCT.		0	0	0	0	8	0	0	8
NOV.		2	0	0	2	3	0	0	3
DEC.		0	0	1	1	0	0	0	0
1983	JAN.	0	0	0	0	0	0	0	0
	FEB.	0	0	0	0	0	0	0	0
	MARCH	1	0	0	1	0	0	0	0
	APRIL	1	1	0	2	0	0	0	0
	MAY	1	0	0	1	0	0	0	0
	JUNE	2	0	0	2	1	0	0	1

ROD = Rodolia cardinalis

PAR = PARASITES (Cryptochaetum iceryae and Euryschia spp.)

GLW = Green Lace Wing (Chrysopa spp.)

\* = sample size 72 for Tree (A) and 64 for Tree (B) for July, 1981.

(-) = NO OBSERVATION MADE

Appendix Table 8A

NUMBERS OF SCALES SURVIVING AND NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH OF THE THREE REPLICATES OF EACH OF THE UNCAGED, OPEN-CAGED AND CAGED TREATMENTS IN THE NATURAL ENEMY EXCLUSION EXPERIMENT. (THE ABBREVIATIONS USED IN THE TABLE ARE GIVEN BELOW THE TABLE)

MONTHLY COHORT SET : APRIL

INTRODUCTION DATE : 24 April, 1982

WEEK	DATE	INSECT	UNCAGED				OPEN CAGED				CAGED			
			R1	R2	R3	SUM	R1	R2	R3	SUM	R1	R2	R3	SUM
0	24/4	CS	70	70	70	210	70	70	70	210	70	70	70	210
2	8/5	Pr-1	70	70	70	210	70	70	70	210	70	70	70	210
4	22/5	Pr-1	68	66	70	204	70	70	70	210	70	70	70	210
6	4/6	Pr-1	65	66	68	199	70	70	69	209	70	70	70	210
8	18/6	Pr-1	58	65	66	189	68	70	69	207	70	70	70	210
10	4/7	Pr-1	48	47	55	150	66	57	64	187	66	32	52	150
		Pr-2	10	6	5	21	0	8	4	12	4	35	12	51
		SUM	58	53	60	171	66	65	68	199	70	67	64	201
12	18/7	Pr-1	40	15	22	77	50	15	27	92	23	5	35	63
		Pr-2	18	36	20	74	15	45	36	96	37	61	24	122
		SUM	58	51	42	151	65	60	63	188	60	66	59	185
14	30/7	Pr-1	4	5	3	12	16	3	12	31	8	0	3	11
		Pr-2	48	44	38	130	43	56	48	147	52	66	56	174
		SUM	52	49	41	142	59	59	60	178	60	66	59	185
16	13/8	Pr-1	3	1	3	7	2	0	4	6	3	1	0	4
		Pr-2	47	33	31	111	57	58	52	167	53	58	58	169
		SUM	50	34	34	118	59	58	56	173	56	59	58	173
18	27/8	Pr-2	26	24	23	73	57	34	42	133	35	4	31	70
		Pr-3	14	2	1	17	2	15	8	25	13	22	11	46
		Pr-M	0	0	0	0	0	0	0	0	3	21	7	31
		SUM	40	26	24	90	59	49	50	158	51	47	49	147
20	10/9	Pr-2	4	12	6	22	36	8	13	57	11	2	10	23
		Pr-3	17	7	6	30	13	28	27	68	23	20	17	60
		Pr-M	0	0	0	0	0	0	0	0	13	3	7	23
		SUM	21	19	12	52	49	36	40	125	47	25	34	106
22	24/9	Pr-3	14	5	6	25	16	15	27	58	22	4	21	47
		Pr-M	0	0	0	0	0	0	0	0	4	0	0	4
		Ad	6	1	1	8	8	15	1	24	1	11	4	16
		SUM	20	6	7	33	24	30	28	82	27	15	25	67
24	8/10	Pr-3	3	1	1	5	15	5	8	28	4	1	4	9
		Ad	17	3	3	23	9	20	16	45	20	14	13	47
		SUM	20	4	4	28	24	25	24	73	24	15	17	56
26	22/10	Pr-3	2	0	0	2	5	0	0	5	1	0	1	2
		Ad	11	3	3	17	17	22	24	63	23	15	16	54
		SUM	13	3	3	19	22	22	24	68	24	15	17	56
28	5/11	Ad	5	0	3	8	22	15	24	61	23	15	16	54
PARASITES EMERGED			0	0	0	0	0	0	0	0	0	0	0	0

R1, R2, R3 ARE THE THREE REPLICATES  
 CS = CRAWLERS SETTLED  
 Pr-1 = 1st INSTAR SCALE  
 Pr-2 = 2nd INSTAR SCALE

Pr-3 = 3rd INSTAR SCALE  
 Pr-M = 3rd INSTAR SCALE (MALE)  
 Ad = ADULT SCALE

Appendix Table 8B

NUMBERS OF SCALES SURVIVING AND NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH OF THE THREE REPLICATES OF EACH OF THE UNCAGED, OPEN-CAGED AND CAGED TREATMENTS IN THE NATURAL ENEMY EXCLUSION EXPERIMENT. (THE ABBREVIATIONS USED IN THE TABLE ARE GIVEN BELOW THE TABLE)

MONTHLY COHORT SET : MAY

INTRODUCTION DATE : 25, May 1982

WEEK	DATE	INSECT	UNCAGED				OPEN CAGED				CAGED			
			R1	R2	R3	SUM	R1	R2	R3	SUM	R1	R2	R3	SUM
0	25/5	CS	78	45	58	181	55	65	74	194	42	67	65	174
2	4/6	Pr-1	78	45	58	181	55	65	74	194	42	67	65	174
4	18/6	Pr-1	72	44	57	173	55	65	72	192	42	67	65	174
6	2/7	Pr-1	60	39	54	153	55	63	71	189	42	67	65	174
8	16/7	Pr-1	40	22	40	102	53	57	66	176	42	60	65	167
10	30/7	Pr-1	36	22	36	94	53	55	65	173	41	60	65	166
12	13/8	Pr-1	35	22	36	93	53	46	65	164	41	58	62	161
14	27/8	Pr-1	16	6	16	38	3	1	6	10	8	6	12	26
		Pr-2	18	11	18	47	50	41	58	149	31	48	50	129
		SUM	34	17	34	85	53	42	64	159	39	54	62	155
16	10/9	Pr-1	2	0	4	6	1	0	2	3	0	1	2	3
		Pr-2	29	16	30	75	48	41	62	151	39	53	60	152
		SUM	31	16	34	81	49	41	64	154	39	54	62	155
18	24/9	Pr-2	30	9	30	69	23	15	50	88	37	48	52	137
		Pr-3	0	0	0	0	23	10	7	40	1	4	8	13
		SUM	30	9	30	69	46	25	57	128	38	52	60	150
20	8/10	Pr-2	14	3	18	35	0	1	6	7	8	8	7	23
		Pr-3	10	3	10	23	41	17	44	102	26	40	45	111
		Pr-M	0	0	0	0	0	0	0	0	2	1	2	5
		SUM	24	6	28	58	41	17	50	109	36	49	54	139
22	22/10	Pr-2	1	0	3	4	0	0	2	2	2	2	1	5
		Pr-3	23	6	21	50	40	13	40	93	28	45	53	126
		SUM	24	6	24	54	40	13	42	95	30	47	54	131
24	5/11	Pr-3	2	1	6	9	3	1	7	11	27	40	51	118
		Ad	3	0	3	6	10	1	0	11	3	6	3	12
		SUM	5	1	9	15	13	2	7	22	30	46	54	130
26	19/11	Pr-3	0	0	0	0	0	0	0	0	2	4	2	8
		Ad	1	0	1	2	5	0	0	5	28	42	52	122
		SUM	1	0	1	2	5	0	0	5	30	46	54	130
28	3/12	Ad	1	0	1	2	4	0	0	4	29	46	52	127
PARASITES EMERGED			2	0	3	5	9	0	3	12	0	0	0	0

R1, R2, R3 ARE THE THREE REPLICATES  
 CS = CRAWLERS SETTLED  
 Pr-1 = 1st INSTAR SCALE  
 Pr-2 = 2nd INSTAR SCALE

Pr-3 = 3rd INSTAR SCALE  
 Pr-M = 3rd INSTAR SCALE (MALE)  
 Ad = ADULT SCALE

Appendix Table 8C

NUMBERS OF SCALES SURVIVING AND NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH OF THE THREE REPLICATES OF EACH OF THE UNCAGED, OPEN-CAGED AND CAGED TREATMENTS IN THE NATURAL ENEMY EXCLUSION EXPERIMENT. (THE ABBREVIATIONS USED IN THE TABLE ARE GIVEN BELOW THE TABLE)

MONTHLY COHORT SET : JUNE

INTRODUCTION DATE : 25 June, 1982

WEEK	DATE	INSECT	UNCAGED				OPEN CAGED				CAGED			
			R1	R2	R3	SUM	R1	R2	R3	SUM	R1	R2	R3	SUM
0	25/6	CS	69	70	63	202	75	80	60	215	62	58	53	173
2	2/7	Pr-1	69	70	63	202	75	80	60	215	62	58	53	173
4	16/7	Pr-1	69	70	63	202	75	80	60	215	62	58	53	173
6	30/7	Pr-1	54	50	45	149	67	68	42	177	56	47	53	156
8	13/8	Pr-1	51	48	45	144	63	50	39	152	54	46	52	152
10	27/8	Pr-1	40	37	44	121	58	40	23	121	41	38	40	119
		Pr-2	4	8	1	13	1	6	13	20	6	8	10	24
		SUM	44	45	45	134	59	46	36	141	47	46	50	143
		GLW	0	0	0	0	1	0	0	1	0	0	0	0
12	10/9	Pr-1	10	6	28	44	8	6	7	21	9	7	11	27
		Pr-2	28	23	14	65	42	32	29	103	33	31	26	90
		SUM	38	29	42	109	50	38	36	124	42	38	37	117
14	24/9	Pr-2	28	10	36	74	21	27	20	68	41	37	32	110
16	8/10	Pr-2	14	6	35	55	19	15	13	47	28	28	23	79
		Pr-3	4	4	0	8	1	6	6	13	13	9	6	28
		SUM	18	10	35	63	20	21	19	60	41	37	29	107
		GLW	1	0	0	1	0	0	1	1	0	0	0	0
18	22/10	Pr-2	0	0	13	13	3	3	2	8	5	2	9	16
		Pr-3	12	11	13	36	17	16	15	48	36	33	11	80
		SUM	12	11	26	49	20	19	17	56	41	35	20	96
		GLW	0	0	0	0	0	0	1	1	0	0	0	0
20	5/11	Pr-3	0	1	12	13	8	2	6	16	16	12	9	37
		Ad	3	2	0	5	3	3	1	7	18	18	5	41
		SUM	3	3	12	18	11	5	7	23	34	30	14	78
22	19/11	Pr-3	0	0	1	1	0	0	0	0	4	1	2	7
		Ad	0	1	2	3	5	3	0	8	30	29	11	70
		SUM	0	1	3	4	5	3	0	8	34	30	13	77
24	3/12	Ad	0	1	0	1	2	2	0	4	34	30	13	77
PARASITES EMERGED			2	2	4	8	3	0	5	8	0	0	0	0

R1, R2, R3 ARE THE THREE REPLICATES  
 CS = CRAWLERS SETTLED  
 Pr-1 = 1st INSTAR SCALE  
 Pr-2 = 2nd INSTAR SCALE

Pr-3 = 3rd INSTAR SCALE  
 Ad = ADULT SCALE  
 GLW = Green lace wing

Appendix Table 8D

NUMBERS OF SCALES SURVIVING AND NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH OF THE THREE REPLICATES OF EACH OF THE UNCAGED, OPEN-CAGED AND CAGED TREATMENTS IN THE NATURAL ENEMY EXCLUSION EXPERIMENT. (THE ABBREVIATIONS USED IN THE TABLE ARE GIVEN BELOW THE TABLE)

MONTHLY COHORT SET : JULY

INTRODUCTION DATE : 29 July, 1982

WEEK	DATE	INSECT	UNCAGED				OPEN CAGED				CAGED			
			R1	R2	R3	SUM	R1	R2	R3	SUM	R1	R2	R3	SUM
0	29/7	CS	66	88	84	232	66	75	71	212	60	64	86	210
2	13/8	Pr-1	60	88	84	232	66	75	71	212	60	64	86	210
4	27/8	Pr-1 GLW	56 1	88 0	84 0	228 1	64 0	70 0	57 1	191 1	60 0	64 0	86 0	210 0
6	10/9	Pr-2 GLW	56 0	34 1	55 0	145 1	55 0	56 0	57 0	168 0	57 0	64 0	81 0	202 0
8	24/9	Pr-1 Pr-2 SUM	6 30 36	4 20 24	0 4 4	10 54 64	5 34 39	4 36 40	9 28 37	18 98 116	9 33 42	4 58 62	8 62 70	21 153 174
10	8/10	Pr-1 Pr-2 SUM	0 31 31	0 19 19	0 2 2	0 52 52	0 29 29	3 37 40	2 29 31	5 95 100	1 38 39	0 60 60	0 70 70	1 168 169
12	22/10	Pr-2 Pr-3 SUM	21 10 31	7 6 13	1 0 1	29 16 45	21 6 27	27 13 40	24 4 28	72 23 95	28 8 36	43 18 61	54 15 69	125 41 166
14	5/11	Pr-3	17	10	0	27	22	23	18	63	36	56	64	156
16	19/11	Pr-3 Ad SUM ROD	3 3 6 0	3 1 4 0	0 0 0 0	6 4 10 0	4 10 14 0	3 11 14 0	0 3 3 7	7 24 31 7	6 30 36 0	23 32 55 0	23 41 64 0	52 103 155 0
18	3/12	Pr-3 Ad SUM ROD	0 4 4 0	0 0 0 0	0 0 0 0	0 4 4 0	0 6 6 0	1 7 8 0	0 1 1 1	1 14 15 1	0 34 34 0	10 42 52 0	5 45 50 0	15 121 136 0
20	17/12	Ad	4	0	0	4	6	7	0	13	33	47	48	128
PARASITES EMERGED			2	1	3	6	0	6	2	8	0	0	0	0

R1, R2, R3 ARE THE THREE REPLICATES  
 CS = CRAWLERS SETTLED  
 Pr-1 = 1st INSTAR SCALE  
 Pr-2 = 2nd INSTAR SCALE  
 Pr-3 = 3rd INSTAR SCALE

Ad = ADULT SCALE  
 ROD = Rodolia cardinalis  
 GLW = Green lace wing

Appendix Table 8E

NUMBERS OF SCALES SURVIVING AND NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH OF THE THREE REPLICATES OF EACH OF THE UNCAGED, OPEN-CAGED AND CAGED TREATMENTS IN THE NATURAL ENEMY EXCLUSION EXPERIMENT. (THE ABBREVIATIONS USED IN THE TABLE ARE GIVEN BELOW THE TABLE)

MONTHLY COHORT SET : AUGUST

INTRODUCTION DATE : 27 August, 1982

WEEK	DATE	INSECT	UNCAGED				OPEN CAGED				CAGED			
			R1	R2	R3	SUM	R1	R2	R3	SUM	R1	R2	R3	SUM
0	27/8	CS	70	70	70	210	70	70	70	210	70	70	70	210
2	10/9	Pr-1	70	70	70	210	70	70	70	210	70	70	70	210
4	24/9	Pr-1	52	58	26	136	56	70	68	194	68	67	67	202
6	8/10	Pr-1	48	58	25	131	47	70	64	181	68	66	67	201
		GLW	0	0	0	0	0	0	1	1	0	0	0	0
		ROD	0	0	0	0	2	0	0	2	0	0	0	0
8	22/10	Pr-1	4	3	2	9	3	11	19	33	10	24	22	56
		Pr-2	9	37	15	61	23	57	28	108	40	32	38	110
		SUM	13	40	17	70	26	68	47	141	50	56	60	166
		ROD	0	0	0	0	3	0	0	3	0	0	0	0
10	5/11	Pr-2	9	16	2	27	1	41	35	77	43	48	50	141
		Pr-3	1	23	4	28	0	7	1	8	6	2	0	8
		SUM	10	39	6	55	1	48	36	85	49	50	50	149
12	19/11	Pr-2	0	0	0	0	0	1	0	1	0	5	5	10
		Pr-3	8	31	4	43	1	20	13	34	49	40	42	131
		SUM	8	31	4	43	1	21	13	35	49	45	47	141
14	3/12	Pr-3	1	0	1	2	0	0	3	3	15	14	12	41
		Ad	4	16	2	22	0	14	6	20	33	26	34	93
		SUM	5	16	3	24	0	14	9	23	48	40	46	134
16	17/12	Pr-3	0	0	0	0	0	0	0	0	0	7	4	11
		Ad	4	5	0	9	0	9	1	10	48	29	41	118
		SUM	4	5	0	9	0	9	1	10	48	36	45	129
18	31/12	Ad	2	5	0	7	0	4	1	5	44	32	39	115
PARASITES EMERGED			0	7	2	9	0	5	3	8	0	0	0	0

R1, R2, R3 ARE THE THREE REPLICATES  
 CS = CRAWLERS SETTLED  
 Pr-1 = 1st INSTAR SCALE  
 Pr-2 = 2nd INSTAR SCALE  
 Pr-3 = 3rd INSTAR SCALE

Ad = ADULT SCALE  
 ROD = Rodolia cardinalis  
 GLW = Green lace wing

Appendix Table 8F

NUMBERS OF SCALES SURVIVING AND NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH OF THE THREE REPLICATES OF EACH OF THE UNCAGED, OPEN-CAGED AND CAGED TREATMENTS IN THE NATURAL ENEMY EXCLUSION EXPERIMENT. (THE ABBREVIATIONS USED IN THE TABLE ARE GIVEN BELOW THE TABLE)

MONTHLY COHORT SET : SEPTEMBER

INTRODUCTION DATE : 25 September, 1982

WEEK	DATE	INSECT	UNCAGED				OPEN CAGED				CAGED			
			R1	R2	R3	SUM	R1	R2	R3	SUM	R1	R2	R3	SUM
0	25/9	CS	70	70	70	210	70	70	70	210	70	70	70	210
2	8/10	Pr-1	70	70	70	210	70	70	70	210	70	70	70	210
4	22/10	Pr-1	53	50	70	210	70	70	70	210	70	70	70	210
6	5/11	Pr-1	5	2	4	11	2	3	3	8	4	2	2	8
		Pr-2	43	36	40	119	42	40	45	127	62	68	64	194
		SUM	48	38	44	130	44	43	48	135	66	70	66	202
8	19/11	Pr-2	23	20	24	67	29	26	25	80	26	43	20	89
		Pr-3	9	5	7	21	14	1	5	20	38	23	27	88
		SUM	32	25	31	88	43	27	30	100	64	66	47	177
10	2/12	Pr-2	3	1	0	4	0	0	0	0	2	5	3	10
		Pr-3	8	12	14	34	14	6	4	24	43	42	33	118
		SUM	11	13	14	38	14	6	4	24	45	47	36	128
12	17/12	Pr-2	2	0	0	2	0	0	0	0	0	4	6	10
		Pr-3	1	1	1	3	1	0	1	2	27	30	17	74
		Ad	1	3	4	8	9	3	2	14	0	0	0	0
		SUM	4	4	5	13	10	3	3	16	27	34	23	84
14	31/12	Pr-3	1	0	0	1	0	0	0	0	17	22	12	51
		Ad	2	1	2	5	3	1	1	5	12	10	10	32
		SUM	3	1	2	6	3	1	1	5	27	34	22	83
16	14/1	Ad	1	0	2	3	0	1	0	1	25	32	18	75
PARASITES EMERGED			6	2	2	10	4	3	1	8	0	0	0	0

R1, R2, R3 ARE THE THREE REPLICATES  
 CS = CRAWLERS SETTLED  
 Pr-1 = 1st INSTAR SCALE  
 Pr-2 = 2nd INSTAR SCALE

Pr-3 = 3rd INSTAR SCALE  
 Ad = ADULT SCALE



Appendix Table 8G

NUMBERS OF SCALES SURVIVING AND NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH OF THE THREE REPLICATES OF EACH OF THE UNCAGED, OPEN-CAGED AND CAGED TREATMENTS IN THE NATURAL ENEMY EXCLUSION EXPERIMENT. (THE ABBREVIATIONS USED IN THE TABLE ARE GIVEN BELOW THE TABLE)

MONTHLY COHORT SET : OCTOBER

INTRODUCTION DATE : 25 October, 1982

WEEK	DATE	INSECT	UNCAGED				OPEN CAGED				CAGED			
			R1	R2	R3	SUM	R1	R2	R3	SUM	R1	R2	R3	SUM
0	25/10	CS	70	70	70	210	70	70	70	210	70	70	70	210
2	5/11	Pr-1	70	70	70	210	70	70	70	210	70	70	70	210
4	19/11	Pr-1	32	17	23	72	40	16	22	78	35	46	44	125
		Pr-2	30	1	4	35	30	30	9	69	30	24	24	78
		SUM	62	18	27	107	70	46	31	147	65	70	68	203
		ROD	0	0	4	4	0	0	0	0	0	0	0	0
6	3/12	Pr-2	25	11	9	45	51	20	20	91	57	64	63	184
		Pr-3	2	0	0	2	4	2	0	6	8	6	5	19
		SUM	27	11	9	47	55	22	20	97	65	70	68	203
8	17/12	Pr-2	3	6	3	12	0	1	6	7	2	17	10	29
		Pr-3	10	5	6	19	23	5	12	40	60	52	58	170
		SUM	13	11	7	31	23	6	18	47	62	69	68	199
10	31/12	Pr-3	3	6	3	12	8	5	5	18	11	16	10	37
		Ad	0	1	0	1	0	1	2	3	48	50	51	149
		SUM	3	7	3	13	8	6	7	21	59	66	61	186
12	14/1	Pr-3	0	1	0	1	1	0	2	3	7	15	8	30
		Ad	0	1	0	1	0	3	3	6	48	49	50	147
		SUM	0	2	0	2	1	3	5	9	55	64	58	177
14	28/1	Ad	0	0	0	0	1	2	3	6	52	63	56	171
PARASITES EMERGED			1	2	2	5	3	1	2	6	0	0	0	0

R1, R2, R3 ARE THE THREE REPLICATES  
 CS = CRAWLERS SETTLED  
 Pr-1 = 1st INSTAR SCALE  
 Pr-2 = 2nd INSTAR SCALE

Pr-3 = 3rd INSTAR SCALE  
 Ad = ADULT SCALE  
 ROD = Rodolia cardinalis

Appendix Table 8H

NUMBERS OF SCALES SURVIVING AND NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH OF THE THREE REPLICATES OF EACH OF THE UNCAGED, OPEN-CAGED AND CAGED TREATMENTS IN THE NATURAL ENEMY EXCLUSION EXPERIMENT. (THE ABBREVIATIONS USED IN THE TABLE ARE GIVEN BELOW THE TABLE)

MONTHLY COHORT SET : NOVEMBER

INTRODUCTION DATE : 25 November, 1982

WEEK	DATE	INSECT	UNCAGED				OPEN CAGED				CAGED			
			R1	R2	R3	SUM	R1	R2	R3	SUM	R1	R2	R3	SUM
0	25/11	CS	70	70	70	210	70	70	70	210	70	70	70	210
2	3/12	Pr-1	68	53	66	187	70	70	70	210	70	70	70	210
4	17/12	Pr-1	61	21	54	136	69	70	70	209	70	70	61	201
6	31/12	Pr-1	6	3	3	12	4	10	5	19	9	6	3	18
		Pr-2	33	13	32	78	29	20	39	88	51	54	40	145
		Pr-3	0	0	0	0	0	0	2	2	6	4	10	20
		SUM	39	16	35	90	33	30	46	109	66	64	53	183
8	14/1	Pr-1	0	0	0	0	5	1	1	7	5	0	6	11
		Pr-2	12	7	4	23	1	1	3	5	10	10	12	32
		Pr-3	7	4	9	20	11	3	15	29	43	54	30	129
		Pr-M	0	0	0	0	0	0	0	0	0	0	2	2
		SUM	19	11	13	43	17	5	19	41	58	64	50	172
10	28/1	Pr-3	3	3	3	9	3	1	6	10	18	18	8	44
		Ad	1	2	1	4	3	0	2	5	33	39	32	104
		SUM	4	5	4	13	6	1	8	15	51	57	40	148
		Pr-3	0	2	0	2	1	0	0	1	8	10	3	21
12	11/2	Ad	3	1	1	5	5	0	3	8	39	46	32	117
		SUM	3	3	1	7	6	0	3	9	47	56	35	138
		Ad	3	1	1	5	4	0	3	7	47	54	34	135
14	25/2	Ad	3	1	1	5	4	0	3	7	47	54	34	135
PARASITES EMERGED			0	2	0	2	1	0	2	3	0	0	0	0

R1, R2, R3 ARE THE THREE REPLICATES  
 CS = CRAWLERS SETTLED  
 Pr-1 = 1st INSTAR SCALE  
 Pr-2 = 2nd INSTAR SCALE

Pr-3 = 3rd INSTAR SCALE  
 Pr-M = 3rd INSTAR SCALE (MALE)  
 Ad = ADULT SCALE

Appendix Table 8I

NUMBERS OF SCALES SURVIVING AND NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH OF THE THREE REPLICATES OF EACH OF THE UNCAGED, OPEN-CAGED AND CAGED TREATMENTS IN THE NATURAL ENEMY EXCLUSION EXPERIMENT. (THE ABBREVIATIONS USED IN THE TABLE ARE GIVEN BELOW THE TABLE)

MONTHLY COHORT SET : DECEMBER

INTRODUCTION DATE : 25 December, 1982

WEEK	DATE	INSECT	UNCAGED				OPEN CAGED				CAGED			
			R1	R2	R3	SUM	R1	R2	R3	SUM	R1	R2	R3	SUM
0	25/12	CS	60	70	70	200	70	70	68	208	70	70	63	203
2	31/12	Pr-1	60	68	65	193	69	68	65	202	65	70	63	198
4	14/1	Pr-1	60	63	58	181	67	66	60	193	58	68	62	188
6	28/1	Pr-1	20	3	0	23	6	7	5	18	4	8	6	18
		Pr-2	5	2	0	7	42	38	34	114	45	48	45	138
		SUM	25	5	0	30	48	45	39	132	49	56	51	156
8	11/2	Pr-2	10	0	0	10	31	23	28	82	19	30	27	76
		Pr-3	0	0	0	0	10	12	11	33	18	20	5	43
		SUM	10	0	0	10	41	35	39	115	37	50	32	119
10	25/2	Pr-2	4	0	0	4	4	6	7	17	2	0	0	2
		Pr-3	0	0	0	0	32	15	14	61	30	44	20	94
		Pr-M	0	0	0	0	0	0	0	0	3	0	0	3
		SUM	4	0	0	4	36	21	21	78	35	44	20	99
12	11/3	Pr-3	1	0	0	1	0	7	2	9	7	8	2	17
		Pr-M	0	0	0	0	0	0	0	0	0	0	1	1
		Ad	1	0	0	1	30	13	9	52	23	34	13	70
		SUM	2	0	0	2	30	20	11	61	30	42	16	88
14	25/3	Pr-3	0	0	0	0	0	4	1	5	0	2	2	4
		Ad	1	0	0	1	22	14	7	43	28	39	14	81
		SUM	1	0	0	1	22	18	8	48	28	41	16	85
16	8/4	Ad	0	0	0	0	22	14	8	44	28	41	14	83
PARASITES EMERGED			1	0	0	1	0	1	0	1	0	0	0	0

R1, R2, R3 ARE THE THREE REPLICATES  
 CS = CRAWLERS SETTLED  
 Pr-1 = 1st INSTAR SCALE  
 Pr-2 = 2nd INSTAR SCALE

Pr-3 = 3rd INSTAR SCALE  
 Pr-M = 3rd INSTAR SCALE (MALE)  
 Ad = ADULT SCALE

Appendix Table 8J

NUMBERS OF SCALES SURVIVING AND NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH OF THE THREE REPLICATES OF EACH OF THE UNCAGED, OPEN-CAGED AND CAGED TREATMENTS IN THE NATURAL ENEMY EXCLUSION EXPERIMENT. (THE ABBREVIATIONS USED IN THE TABLE ARE GIVEN BELOW THE TABLE)

MONTHLY COHORT SET : JANUARY

INTRODUCTION DATE : 26 January, 1982

WEEK	DATE	INSECT	UNCAGED				OPEN CAGED				CAGED			
			R1	R2	R3	SUM	R1	R2	R3	SUM	R1	R2	R3	SUM
0	26/1	CS	70	70	70	210	70	70	70	210	70	70	68	208
2	11/2	Pr-1	18	48	38	104	30	64	30	124	67	70	66	203
4	25/2	Pr-1	3	6	1	10	4	2	4	10	7	23	3	33
		Pr-2	6	25	14	45	16	32	13	61	44	40	40	124
		SUM	9	31	15	55	20	34	17	71	51	63	43	157
6	11/3	Pr-2	2	7	4	13	6	12	9	27	31	45	21	97
		Pr-3	3	15	6	24	8	18	1	27	19	16	16	51
		SUM	5	22	10	37	14	30	10	54	50	61	37	148
8	25/3	Pr-3	3	10	10	23	7	28	8	43	44	48	33	125
		Ad	0	0	0	0	5	2	0	7	6	5	4	15
		SUM	3	10	10	23	12	30	8	50	50	53	37	140
		ROD	0	5	0	5	0	0	0	0	0	0	0	0
10	8/4	Pr-3	0	1	4	5	3	12	5	20	36	40	27	103
		Ad	0	0	1	1	8	13	2	23	11	13	10	34
		SUM	0	1	5	6	11	25	7	43	47	53	37	137
		ROD	0	0	0	0	1	0	0	1	0	0	0	0
12	22/4	Pr-3	0	1	2	3	3	9	4	16	35	38	26	99
		Ad	0	0	1	1	3	11	2	16	11	12	11	34
		SUM	0	1	3	4	6	20	6	32	46	50	37	133
14	6/5	Pr-3	0	0	0	0	1	1	2	4	9	12	6	27
		Ad	0	0	0	0	3	17	4	24	36	36	31	103
		SUM	0	0	0	0	4	18	6	28	45	48	37	130
		ROD	0	0	0	0	0	4	0	4	0	0	0	0
16	20/5	Pr-3	0	0	0	0	0	0	0	0	3	5	2	10
		Ad	0	0	0	0	4	15	6	25	40	43	35	118
		SUM	0	0	0	0	4	15	6	25	43	48	37	128
18	3/6	Ad	0	0	0	0	2	13	5	20	43	48	36	127
		ROD	0	0	0	0	0	1	0	1	0	0	0	0
PARASITES EMERGED			0	0	0	0	0	2	0	2	0	0	0	0

R1, R2, R3 ARE THE THREE REPLICATES  
 CS = CRAWLERS SETTLED  
 Pr-1 = 1st INSTAR SCALE  
 Pr-2 = 2nd INSTAR SCALE

Pr-3 = 3rd INSTAR SCALE  
 Ad = ADULT SCALE  
 ROD = Rodolia cardinalis

Appendix Table 8K

NUMBERS OF SCALES SURVIVING AND NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH OF THE THREE REPLICATES OF EACH OF THE UNCAGED, OPEN-CAGED AND CAGED TREATMENTS IN THE NATURAL ENEMY EXCLUSION EXPERIMENT. (THE ABBREVIATIONS USED IN THE TABLE ARE GIVEN BELOW THE TABLE)

MONTHLY COHORT SET : FEBRUARY

INTRODUCTION DATE : 26 February, 1982

WEEK	DATE	INSECT	UNCAGED				OPEN CAGED				CAGED			
			R1	R2	R3	SUM	R1	R2	R3	SUM	R1	R2	R3	SUM
0	26/2	CS	61	78	46	185	50	74	88	212	87	59	79	225
2	11/3	Pr-1	55	77	46	178	49	70	84	203	80	49	79	208
		ROD	0	2	0	2	0	0	0	0	0	0	0	0
4	25/3	Pr-1	2	2	7	11	3	0	8	11	6	6	12	24
		Pr-2	13	22	23	58	29	17	64	110	69	38	56	163
		SUM	15	24	30	69	32	17	72	121	75	44	68	187
		ROD	1	0	0	1	0	1	0	1	0	0	0	0
6	8/4	Pr-2	9	18	26	53	26	17	70	113	61	34	64	159
		ROD	0	0	0	0	0	1	0	1	0	0	0	0
8	22/4	Pr-2	1	10	10	21	10	2	28	40	20	26	40	86
		Pr-3	3	5	7	15	7	14	34	55	32	8	20	60
		SUM	4	15	17	36	17	16	62	95	52	34	60	146
10	6/5	Pr-2	1	1	2	4	3	0	4	7	4	4	6	14
		Pr-3	1	11	11	23	10	14	42	66	46	28	53	127
		SUM	2	12	13	27	13	14	46	73	50	32	59	141
		ROD	0	0	0	0	0	0	3	3	0	0	0	0
12	20/5	Pr-3	2	8	9	19	10	12	31	53	37	32	53	122
		Ad	0	0	0	0	0	1	0	1	9	0	0	9
		SUM	2	8	9	19	10	13	31	54	46	32	53	131
		ROD	0	2	0	2	0	0	2	2	0	0	0	0
14	3/6	Pr-3	2	1	6	9	5	2	18	25	21	13	31	65
		Ad	0	0	0	0	0	10	4	14	24	14	22	60
		SUM	2	1	6	9	5	12	22	39	45	27	53	125
		ROD	0	2	0	2	0	5	2	7	0	0	0	0
16	17/6	Pr-3	2	0	6	8	5	3	2	10	12	8	15	35
		Ad	0	0	0	0	0	0	0	0	32	19	38	89
		SUM	2	0	6	8	5	3	2	10	44	27	53	124
		ROD	0	0	0	0	0	3	0	3	0	0	0	0
18	1/7	Pr-3	2	0	5	7	2	0	2	4	6	3	8	17
		Ad	0	0	0	0	0	0	0	0	36	24	45	105
		SUM	2	0	5	7	2	0	2	4	42	27	53	122
20	15/7	Pr-3	0	0	0	0	0	0	2	2	0	1	2	3
		Ad	0	0	0	0	0	0	0	0	41	26	51	118
		SUM	0	0	0	0	0	0	2	2	41	27	53	121
22	29/7	Ad	0	0	0	0	0	0	0	0	40	27	51	118
PARASITES EMERGED			0	1	0	1	0	0	1	1	0	0	0	0

R1, R2, R3 ARE THE THREE REPLICATES  
 CS = CRAWLERS SETTLED  
 Pr-1 = 1st INSTAR SCALE  
 Pr-2 = 2nd INSTAR SCALE

Pr-3 = 3rd INSTAR SCALE  
 Ad = ADULT SCALE  
 ROD = Rodolia cardinalis

Appendix Table 8L

NUMBERS OF SCALES SURVIVING AND NATURAL ENEMIES OBSERVED AT FORTNIGHTLY INTERVALS IN EACH OF THE THREE REPLICATES OF EACH OF THE UNCAGED, OPEN-CAGED AND CAGED TREATMENTS IN THE NATURAL ENEMY EXCLUSION EXPERIMENT. (THE ABBREVIATIONS USED IN THE TABLE ARE GIVEN BELOW THE TABLE)

MONTHLY COHORT SET : MARCH

INTRODUCTION DATE : 25 March, 1982

WEEK	DATE	INSECT	UNCAGED				OPEN CAGED				CAGED			
			R1	R2	R3	SUM	R1	R2	R3	SUM	R1	R2	R3	SUM
0	25/3	CS	70	70	70	210	70	70	70	210	70	70	70	210
2	8/4	Pr-1	70	68	22	160	52	50	34	136	70	70	70	210
4	22/4	Pr-1	69	62	10	141	51	23	28	102	66	69	69	204
6	6/5	Pr-1	32	25	5	62	34	12	9	55	52	58	58	168
		Pr-2	5	3	0	8	4	6	1	11	12	7	10	29
		SUM	37	28	5	70	38	18	10	66	64	65	68	197
		ROD	0	0	0	0	0	0	1	1	0	0	0	0
8	20/5	Pr-1	2	0	-*	2	2	0	0	2	6	8	7	21
		Pr-2	15	8	-	23	9	9	4	22	56	56	59	171
		SUM	17	8	-	25	11	9	4	24	62	64	66	192
10	3/6	Pr-2	13	6	-	19	8	5	2	15	60	64	64	188
12	17/6	Pr-2	12	5	-	17	8	5	2	15	60	64	64	188
		ROD	0	0	-	0	0	2	0	2	0	0	0	0
14	1/7	Pr-2	12	5	-	17	7	5	2	14	53	64	64	181
16	15/7	Pr-2	11	2	-	13	2	3	2	7	43	56	57	156
		Pr-3	1	2	-	3	3	0	0	3	8	8	5	21
		SUM	12	4	-	16	5	3	2	10	51	64	62	177
18	29/7	Pr-2	6	0	-	6	2	3	2	7	25	29	22	76
		Pr-3	2	2	-	4	3	0	0	3	26	31	36	93
		SUM	8	2	-	10	5	3	2	10	51	60	58	169
20	12/8	Pr-2	2	0	-	2	0	2	2	4	4	7	10	21
		Pr-3	3	1	-	4	5	0	0	5	47	49	43	139
		SUM	5	1	-	6	5	2	2	9	51	56	53	160
22	26/8	Pr-2	1	0	-	1	0	1	0	1	2	2	3	7
		Pr-3	4	1	-	5	5	1	2	8	49	53	49	151
		SUM	5	1	-	6	5	2	2	9	51	55	52	158
24	2/9	Pr-3	2	1	-	3	4	1	1	6	47	42	39	128
		Ad	1	0	-	1	1	0	0	1	4	12	10	26
		SUM	3	1	-	4	5	1	1	7	51	54	49	154
26	16/9	Pr-3	0	1	-	1	4	0	1	5	40	6	2	48
		Ad	1	0	-	1	1	0	0	1	10	46	43	99
		SUM	1	1	-	2	5	0	1	6	50	52	45	147
		ROD	5	0	-	5	0	0	0	0	0	0	0	0
28	30/9	Ad	0	1	-	1	5	0	1	6	48	51	45	144
PARASITES EMERGED			0	0	-	0	0	0	0	0	0	0	0	0

\* ALL INSECTS DIED AS A RESULT OF BREAKING OF THE TWIG.

R1, R2, R3 ARE THE THREE REPLICATES

CS = CRAWLERS SETTLED

Pr-1 = 1st INSTAR SCALE

Pr-2 = 2nd INSTAR SCALE

Pr-3 = 3rd INSTAR SCALE

Ad = ADULT SCALE

ROD = Rodolia cardinalis

Appendix Table 9

ESTIMATES OF STAGE SPECIFIC SURVIVAL RATES FOR COHORTS OF SCALES  
IN THE NATURAL ENEMY EXCLUSION EXPERIMENT USING MANLY'S MODEL

MONTH	STAGE SPECIFIC SURVIVAL RATES $\pm$ STANDARD ERRORS		
	UNCAGED	OPEN-CAGED	CAGED
<u>1st INSTAR SCALES</u>			
1. APRIL	0.3103 $\pm$ 0.0215	0.4207 $\pm$ 0.0220	0.4248 $\pm$ 0.0240
2. MAY	0.2874 $\pm$ 0.0324	0.3471 $\pm$ 0.0360	0.4785 $\pm$ 0.0356
3. JUNE	0.2296 $\pm$ 0.0258	0.2510 $\pm$ 0.0376	0.4268 $\pm$ 0.0289
4. JULY	0.1808 $\pm$ 0.0306	0.3330 $\pm$ 0.0485	0.5500 $\pm$ 0.0497
5. AUGUST	0.2162 $\pm$ 0.0526	0.2397 $\pm$ 0.0568	0.4695 $\pm$ 0.0562
6. SEPTEMBER	0.3119 $\pm$ 0.0748	0.3039 $\pm$ 0.0748	0.5433 $\pm$ 0.0730
7. OCTOBER	0.2226 $\pm$ 0.0474	0.3547 $\pm$ 0.0710	0.6697 $\pm$ 0.0561
8. NOVEMBER	0.2410 $\pm$ 0.0785	0.2153 $\pm$ 0.0938	0.5670 $\pm$ 0.0735
9. DECEMBER	0.0472 $\pm$ 0.0114	0.4772 $\pm$ 0.0664	0.5321 $\pm$ 0.0608
10. JANUARY	0.2557 $\pm$ 0.0978	0.4178 $\pm$ 0.1025	0.6917 $\pm$ 0.0658
11. FEBRUARY	0.3912 $\pm$ 0.0815	0.5487 $\pm$ 0.0850	0.7535 $\pm$ 0.0561
12. MARCH	0.2161 $\pm$ 0.0273	0.2097 $\pm$ 0.0412	0.6965 $\pm$ 0.0317
<u>2nd INSTAR SCALES</u>			
1. APRIL	0.2385 $\pm$ 0.0254	0.3812 $\pm$ 0.0285	0.3549 $\pm$ 0.0306
2. MAY	0.4143 $\pm$ 0.0810	0.3976 $\pm$ 0.0647	0.5843 $\pm$ 0.0578
3. JUNE	0.2334 $\pm$ 0.0673	0.2722 $\pm$ 0.0789	0.5152 $\pm$ 0.0508
4. JULY	0.2969 $\pm$ 0.0660	0.3537 $\pm$ 0.0847	0.5800 $\pm$ 0.0603
5. AUGUST	0.5417 $\pm$ 0.1334	0.2874 $\pm$ 0.1095	0.6645 $\pm$ 0.0907
6. SEPTEMBER	0.2809 $\pm$ 0.0984	0.2390 $\pm$ 0.0805	0.5911 $\pm$ 0.1070
7. OCTOBER	0.2813 $\pm$ 0.0847	0.3293 $\pm$ 0.1033	0.7130 $\pm$ 0.0966
8. NOVEMBER	0.3082 $\pm$ 0.1333	0.4000 $\pm$ 0.2159	0.7624 $\pm$ 0.1188
9. DECEMBER	0.1250 $\pm$ 0.0423	0.5370 $\pm$ 0.0898	0.5790 $\pm$ 0.1037
10. JANUARY	0.5126 $\pm$ 0.1513	0.6667 $\pm$ 0.1035	0.7929 $\pm$ 0.0532
11. FEBRUARY	0.4138 $\pm$ 0.0559	0.4600 $\pm$ 0.0592	0.6874 $\pm$ 0.0422
12. MARCH	0.1783 $\pm$ 0.0164	0.2836 $\pm$ 0.0363	0.4550 $\pm$ 0.0321
<u>3rd INSTAR SCALES</u>			
1. APRIL	0.4148 $\pm$ 0.0540	0.5119 $\pm$ 0.0478	0.5104 $\pm$ 0.0514
2. MAY	0.4938 $\pm$ 0.1603	0.0611 $\pm$ 0.0277	0.4003 $\pm$ 0.0881
3. JUNE	0.1343 $\pm$ 0.0597	0.1630 $\pm$ 0.0660	0.5529 $\pm$ 0.0822
4. JULY	0.1404 $\pm$ 0.0500	0.3517 $\pm$ 0.1281	0.5714 $\pm$ 0.1022
5. AUGUST	0.2981 $\pm$ 0.1266	0.4000 $\pm$ 0.1739	0.6306 $\pm$ 0.1305
6. SEPTEMBER	0.2133 $\pm$ 0.0780	0.2923 $\pm$ 0.1235	0.2443 $\pm$ 0.0865
7. OCTOBER	0.0556 $\pm$ 0.0244	0.1829 $\pm$ 0.0645	0.6459 $\pm$ 0.1330
8. NOVEMBER	0.3111 $\pm$ 0.0967	0.3226 $\pm$ 0.1193	0.6268 $\pm$ 0.1090
9. DECEMBER	0.6667 $\pm$ 0.1925	0.5628 $\pm$ 0.1030	0.5969 $\pm$ 0.0994
10. JANUARY	0.0984 $\pm$ 0.0515	0.3977 $\pm$ 0.0739	0.5095 $\pm$ 0.0506
11. FEBRUARY	0.1563 $\pm$ 0.0280	0.0652 $\pm$ 0.0494	0.5377 $\pm$ 0.0344
12. MARCH	0.1304 $\pm$ 0.0237	0.2105 $\pm$ 0.1042	0.3168 $\pm$ 0.0664

Appendix Table 10A

MEAN NUMBERS OF CRAWLERS PRODUCED PER ADULT SCALE PER WEEK IN CAGES  
AT LOCATION (1) (SHADE HOUSE) AND LOCATION (2) (OPEN).

EXPT. DATE	LOCATION (1) (SHADE HOUSE)				LOCATION (2) (OPEN)				
	R1*	R2	R3	MEAN $\pm$ S.E.	R1	R2	R3	MEAN $\pm$ S.E.	
(1)	24/1	17.0	11.3	26.3	18.2 $\pm$ 4.4	27.3	42.0	38.3	35.9 $\pm$ 4.4
	31/1	70.7	80.0	79.0	76.6 $\pm$ 3.0	19.3	5.0	5.7	10.0 $\pm$ 4.7
	7/2	14.0	13.0	43.0	23.3 $\pm$ 9.8	1.7	1.7	0.0	1.1 $\pm$ 0.6
(2)	25/4	1.3	1.3	2.0	1.6 $\pm$ 0.2	11.0	7.3	5.3	7.9 $\pm$ 1.7
	2/5	11.0	2.0	3.7	5.6 $\pm$ 2.8	4.0	27.7	5.0	12.2 $\pm$ 7.7
	9/5	18.7	20.0	21.7	20.1 $\pm$ 0.9	6.0	24.7	3.3	11.3 $\pm$ 6.7
(3)	30/5	16.0	35.3	37.7	29.7 $\pm$ 6.7	18.0	24.3	11.3	17.9 $\pm$ 3.8
	6/6	49.0	50.7	63.3	54.3 $\pm$ 4.5	25.3	21.3	9.7	18.8 $\pm$ 4.7
	13/6	29.0	35.0	34.7	32.9 $\pm$ 2.0	30.0	20.0	10.5	20.2 $\pm$ 5.6
	20/6	14.7	23.3	25.3	21.1 $\pm$ 3.3	10.0	10.0	8.0	9.3 $\pm$ 0.7
	27/6	19.0	43.7	41.0	34.6 $\pm$ 7.8	22.0	11.5	9.0	14.2 $\pm$ 4.0
	4/7	20.7	14.3	24.3	19.8 $\pm$ 2.9	3.5	9.0	2.0	4.8 $\pm$ 2.1
	11/7	7.3	28.0	20.0	18.4 $\pm$ 6.0	7.0	6.0	4.0	5.7 $\pm$ 0.9
	18/7	16.7	24.0	24.7	21.8 $\pm$ 2.6	3.5	5.0	3.0	3.8 $\pm$ 0.6
(4)	8/8	25.3	17.3	56.7	33.1 $\pm$ 12.0	46.7	21.7	43.7	37.3 $\pm$ 7.9
	15/8	34.7	14.0	39.0	29.2 $\pm$ 7.7	56.7	25.0	60.3	47.3 $\pm$ 11.2
	22/8	21.3	9.3	28.3	19.7 $\pm$ 5.6	16.0	12.3	27.0	18.4 $\pm$ 4.4
	29/8	26.0	12.3	56.5	31.6 $\pm$ 13.1	21.7	30.0	28.7	26.8 $\pm$ 2.6
	5/9	15.0	7.7	21.0	14.6 $\pm$ 3.9	24.0	39.0	35.0	32.7 $\pm$ 4.5
	12/9	24.3	15.3	20.0	19.9 $\pm$ 2.6	36.3	33.3	28.0	32.6 $\pm$ 2.4
	19/9	23.3	30.0	10.0	21.1 $\pm$ 5.9	37.0	36.0	37.7	36.9 $\pm$ 0.5
26/9	16.0	29.0	9.0	18.0 $\pm$ 5.9	42.5	34.7	38.3	38.5 $\pm$ 2.3	

\* R1, R2, R3 are the three replicates



Appendix Table 10B

MEAN NUMBERS OF CRAWLERS SETTLED PER ADULT SCALE PER WEEK AT LOCATION (1)  
(SHADE HOUSE) AND LOCATION (2) (OPEN).

EXPT. DATE	LOCATION (1) (SHADE HOUSE)				LOCATION (2) (OPEN)			
	R1*	R2	R3	MEAN $\pm$ S.E.	R1	R2	R3	MEAN $\pm$ S.E.
(1) 24/1	4.5	2.3	1.3	2.7 $\pm$ 0.9	2.7	3.0	3.7	3.1 $\pm$ 0.3
(1) 31/1	35.0	33.7	34.3	34.3 $\pm$ 0.4	10.0	15.0	8.7	11.2 $\pm$ 1.9
(1) 7/2	14.5	14.0	18.7	15.7 $\pm$ 1.5	4.0	10.7	4.3	6.3 $\pm$ 2.2
(2) 25/4	3.3	2.5	5.7	3.8 $\pm$ 1.0	2.7	3.7	2.0	2.8 $\pm$ 0.5
(2) 2/5	0.7	1.0	2.0	1.2 $\pm$ 0.4	1.3	3.7	4.3	3.1 $\pm$ 0.9
(2) 9/5	3.7	3.0	5.0	3.9 $\pm$ 0.6	1.0	2.0	0.3	1.1 $\pm$ 0.5
(3) 30/5	3.0	3.3	6.0	4.1 $\pm$ 1.0	2.7	4.7	0.7	2.7 $\pm$ 1.2
(3) 6/6	4.7	4.3	5.7	4.9 $\pm$ 0.4	7.0	3.7	1.0	3.9 $\pm$ 1.7
(3) 13/6	1.7	2.7	1.7	2.0 $\pm$ 0.3	3.3	4.0	1.7	3.0 $\pm$ 0.7
(3) 20/6	2.0	2.3	5.0	3.1 $\pm$ 1.0	2.3	2.7	1.3	2.1 $\pm$ 0.4
(3) 27/6	3.3	3.3	2.7	3.1 $\pm$ 0.2	1.3	1.3	0.7	1.1 $\pm$ 0.2
(3) 4/7	3.3	4.0	4.3	3.9 $\pm$ 0.3	0.7	0.7	0.3	0.6 $\pm$ 0.1
(3) 11/7	3.3	4.0	5.7	4.3 $\pm$ 0.7	0.7	0.7	0.7	0.7 $\pm$ 0.0
(3) 18/7	2.7	4.3	5.0	4.0 $\pm$ 0.7	0.7	0.3	0.7	0.6 $\pm$ 0.1
(4) 8/8	7.3	4.0	7.3	6.2 $\pm$ 1.1	2.3	2.0	3.3	2.6 $\pm$ 0.4
(4) 15/8	3.3	1.7	3.0	2.7 $\pm$ 0.5	5.3	2.7	3.3	3.8 $\pm$ 0.8
(4) 22/8	3.3	3.3	4.7	3.8 $\pm$ 0.5	0.7	0.7	2.7	1.3 $\pm$ 0.7
(4) 29/8	3.0	2.0	1.7	2.2 $\pm$ 0.4	0.3	0.3	0.7	0.4 $\pm$ 0.1
(4) 5/9	2.3	5.0	1.7	3.0 $\pm$ 1.0	0.3	0.3	0.3	0.3 $\pm$ 0.0
(4) 12/9	2.3	1.5	1.0	1.6 $\pm$ 0.4	0.7	1.3	1.0	1.0 $\pm$ 0.2
(4) 19/9	6.0	7.0	4.3	5.8 $\pm$ 0.8	0.3	0.7	1.0	0.7 $\pm$ 0.2
(4) 26/9	6.0	1.5	3.7	3.7 $\pm$ 1.3	1.0	0.0	1.0	0.7 $\pm$ 0.3

\* R1, R2, R3 are the three replicates

APPENDIX TABLE 11

RAW DATA WITH MEANS  $\pm$  S.E. FOR PREY EATEN AND EGGS LAID EITHER ABOVE, UNDER OR AWAY FROM SCALES ON PATCHES OF DIFFERENT PREY DENSITIES. THE DATA ARE FOR EACH OF THE FIVE DAYS FOR EACH OF THREE BEETLES (REPLICATES) FOR EXPERIMENT DESCRIBED IN CHAPTER (6.1). THE DESCRIPTIONS OF THE ABBREVIATIONS IN THE TABLE ARE GIVEN BELOW THE TABLE.

PREY DENS.	DAYS	BEETLE (1)					BEETLE (2)					BEETLE (3)					RESPONSE PER DAY
		(1)		(2)		(3)	(1)		(2)		(3)	(1)		(2)		(3)	MEAN $\pm$ S.E. (3x5=15)
		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	
	REPS	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	
(0)	ET	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	EU	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	EA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	TOT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	SED	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	1E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	2E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	3E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	>3E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	NET	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
(1)	ET	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	0.07 $\pm$ 0.07
	EU	-	-	-	-	-	1	-	-	2	-	-	-	2	-	-	0.47 $\pm$ 0.22
	EA	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	0.07 $\pm$ 0.07
	TOT	-	-	-	-	-	1	-	1	2	-	-	-	3	-	-	0.60 $\pm$ 0.29
	SED	-	-	-	-	-	1	-	1	1	-	-	-	1	-	-	0.40 $\pm$ 0.19
	1E	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	0.27 $\pm$ 0.15
	2E	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	0.13 $\pm$ 0.09
	3E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	>3E	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	NET	-	-	-	-	- 1 1	-	-	- 1	- 1	-	-	-	-	-	1	0.40 $\pm$ 0.16
(2)	ET	-	-	-	-	-	-	-	3	-	-	2	-	-	-	-	0.33 $\pm$ 0.23
	EU	-	-	-	-	3 1 - -	-	-	2 2 1	-	-	8 - - -	-	3	-	9 -	2.27 $\pm$ 0.76
	EA	-	-	-	-	-	-	-	-	4 -	1 - - 1	-	-	-	-	-	0
	TOT	-	-	-	-	3 1 - -	-	-	2 5 1	-	-	10 - - -	-	3	-	8 -	2.60 $\pm$ 0.90
	SED	-	-	-	-	2 1 - -	-	-	1 2 1	-	-	1 - - -	-	1	-	2 -	1.00 $\pm$ 0.34
	1E	-	-	-	-	1 1 - -	-	-	- - 1	-	-	-	-	-	-	1 -	0.47 $\pm$ 0.19
	2E	-	-	-	-	1 - - -	-	-	- 1 -	-	-	-	-	-	-	-	0.20 $\pm$ 0.15
	3E	-	-	-	-	-	-	-	- 1 -	-	-	-	-	1	-	-	0.20 $\pm$ 0.11
	>3E	-	-	-	-	-	-	-	-	1 -	-	1 - - -	-	-	-	1 -	0.13 $\pm$ 0.09
	NET	-	-	-	-	-	1 - - -	-	1 - - -	1 1 - -	-	-	-	-	-	- 1 -	0.33 $\pm$ 0.16

ET = EGGS LAID ABOVE SCALES  
 EU = EGGS LAID UNDER SCALES  
 EA = EGGS LAID AWAY FROM SCALES

TOT = TOTAL EGGS LAID  
 SED = SCALES WITH EGGS  
 1E = SCALES WITH 1 EGG  
 2E = SCALES WITH 2 EGGS

3E = SCALES WITH 3 EGGS  
 >3E = SCALES WITH >3 EGGS  
 NET = PREY EATEN  
 - = ZEROES

(CONTINUED)

APPENDIX TABLE 11 (CONTINUED)

RAW DATA WITH MEANS  $\pm$  S.E. FOR PREY EATEN AND EGGS LAID EITHER ABOVE, UNDER OR AWAY FROM SCALES ON PATCHES OF DIFFERENT PREY DENSITIES. THE DATA ARE FOR EACH OF THE FIVE DAYS FOR EACH OF THREE BEETLES (REPLICATES) FOR EXPERIMENT DESCRIBED IN CHAPTER (6.1). THE DESCRIPTIONS OF THE ABBREVIATIONS IN THE TABLE ARE GIVEN BELOW THE TABLE.

PREY DENS.	DAYS	BEETLE (1)					BEETLE (2)					BEETLE (3)					RESPONSE PER DAY			
		(1)	(2)	(3)	(4)	(5)	(1)	(2)	(3)	(4)	(5)	(1)	(2)	(3)	(4)	(5)	MEAN $\pm$ S.E.			
		REPS	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	(3x5=15)		
(4)	ET	---	---	---	---	3	---	---	4 - 5 -	---	- 2 2 -	1	---	---	---	---	3	1.33 $\pm$ 0.65		
	EU	---	---	---	2	4 2 - 3	---	---	2	---	- 1 - - 5 2 -	2	---	---	---	---	8	2.07 $\pm$ 0.83		
	EA	---	---	---	---	---	---	---	---	---	---	---	---	2	---	---	---	0.27 $\pm$ 0.18		
	TOT	---	---	---	2	- 3 4 2 - 3	---	---	4 4 - 5 -	---	- 1 - - 7 4 -	3	---	---	2	---	---	11	3.67 $\pm$ 1.11	
	SED	---	---	---	1	- 2 3 1 - 2	---	---	1 3 - 2 -	---	- 1 - - 4 2 -	2	---	---	---	---	---	4	1.87 $\pm$ 0.60	
	1E	---	---	---	---	1 2 - - 1	---	---	2 - - - 1 -	---	- 1 - - 2 1 -	1	---	---	---	---	---	1	0.80 $\pm$ 0.28	
	2E	---	---	---	1	- 1 1 - 1	---	---	1 - 1 -	---	- 1 - - 1 1 -	1	---	---	---	---	---	1	0.73 $\pm$ 0.25	
	3E	---	---	---	---	---	---	---	---	---	- 1 - - 1 1 -	---	---	---	---	---	---	1	0.27 $\pm$ 0.15	
>3E	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	1	0.07 $\pm$ 0.07		
NET	---	---	---	1	- - 1	---	---	---	---	---	---	---	---	---	---	---	---	0.13 $\pm$ 0.13		
(8)	ET	---	---	---	---	---	5 1	---	---	---	---	- - 3 3	---	---	---	2	---	---	0.93 $\pm$ 0.55	
	EU	---	---	---	---	- 7 6 2	8	---	- 1	---	5	---	- 4 3 9	---	---	1	8 12	---	7	4.93 $\pm$ 1.78
	EA	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	0	
	TOT	---	---	---	- 7 6 2	13 1	---	- 1	---	6	---	- 4 6 12	---	---	1	- 10 12	---	7	5.87 $\pm$ 2.14	
	SED	---	---	---	---	- 4 4 2	7 1	---	- 1	---	4	---	- 3 4 5	---	---	1	- 4 5	---	4	3.27 $\pm$ 1.12
	1E	---	---	---	---	- 2 2 2	3 1	---	- 1	---	2	---	- 2 3 1	---	---	1	---	---	2	1.47 $\pm$ 0.56
	2E	---	---	---	---	- 1 2 -	2	---	---	---	2	---	- 1 - 2	---	---	---	2 1	---	1	0.93 $\pm$ 0.33
	3E	---	---	---	---	- 1 - -	2	---	---	---	---	---	- 1 1	---	---	---	2 2	---	1	0.67 $\pm$ 0.30
>3E	---	---	---	---	---	---	---	---	---	---	---	- - 1	---	---	---	1	---	---	0.13 $\pm$ 0.09	
NET	---	---	---	1	- - 1 1	- 2	---	---	---	---	---	- 1 1 2	---	---	1	1	---	---	0.73 $\pm$ 0.30	
(16)	ET	---	---	---	---	---	---	---	3 7 - 1	---	- 1 - 2	---	---	---	---	---	---	0.93 $\pm$ 0.75		
	EU	---	---	---	5	- 4	---	---	1 1 3 - 3	---	- 1 2 2 - 4 8 3	---	---	---	8	---	5 4 2 - -	3.80 $\pm$ 1.11		
	EA	---	---	---	---	1	---	---	1 - -	---	- 1 2 - - 1 1	---	---	---	---	---	---	0.53 $\pm$ 0.24		
	TOT	---	---	---	6	- 1 - 4	---	---	2 - 5 10 - 4	---	- 3 4 4 - 4 9 4	---	---	---	8	---	5 4 2 - -	5.27 $\pm$ 1.60		
	SED	---	---	---	3	- 3	---	---	1 - 4 5 - 3	---	- 2 1 3 - 3 3 3	---	---	---	5	---	3 3 2 - -	3.13 $\pm$ 0.96		
	1E	---	---	---	1	- 2	---	---	1 - 4 3 - 2	---	- 2 - 2 - 2 1 3	---	---	---	3	---	2 2 - -	2.07 $\pm$ 0.70		
	2E	---	---	---	1	- 1	---	---	1 - 1 - 1	---	- 1 1 - 1 -	---	---	---	1	---	1 - - -	0.67 $\pm$ 0.19		
	3E	---	---	---	1	- 1	---	---	---	---	- 1 -	---	---	---	1	---	1 - - -	0.27 $\pm$ 0.12		
>3E	---	---	---	---	---	---	---	---	---	- 1 -	---	---	---	---	---	---	0.13 $\pm$ 0.09			
NET	---	---	1	- - 4 -	1 1 - -	---	---	1 1 - -	---	- 1 - - 1 -	---	---	---	---	---	- 1 - 1	0.93 $\pm$ 0.30			

ET = EGGS LAID ABOVE SCALES  
 EU = EGGS LAID UNDER SCALES  
 EA = EGGS LAID AWAY FROM SCALES

TOT = TOTAL EGGS LAID  
 SED = SCALES WITH EGGS  
 1E = SCALES WITH 1 EGG  
 2E = SCALES WITH 2 EGGS

3E = SCALES WITH 3 EGGS  
 >3E = SCALES WITH >3 EGGS  
 NET = PREY EATEN  
 - = ZEROES

Appendix Table 12

SUB-PATCHES ATTENDED BY EACH OF THREE BEETLES (REPLICATES) FOR EATING PREY, LAYING EGGS, AND TOTAL SUB-PATCHES ATTENDED PER DAY IN THE EXPERIMENT DESCRIBED IN CHAPTER (6.1).

DAY	PREY DENS.	BEETLE (1)					BEETLE (2)					BEETLE (3)				
		PPE A	PEL A	A	TPA B	C	PPE A	PEL A	A	TPA B	C	PPE A	PEL A	A	TPA B	C
(1)	1	0	0	0	0.000	0.00	0	2	2	0.400	0.50	0	0	0	0.000	0.00
	2	0	0	0	0.000	0.00	1	0	1	0.200	0.25	0	1	1	0.500	0.25
	4	0	0	0	0.000	0.00	0	0	0	0.000	0.00	0	1	1	0.500	0.25
	8	0	0	0	0.000	0.00	1	2	2	0.400	0.50	0	0	0	0.000	0.00
	16	0	0	0	0.000	0.00	0	0	0	0.000	0.00	0	0	0	0.000	0.00
	SUM	0	0	0			2	4	5			0	2	2		
(2)	1	0	0	0	0.000	0.00	1	0	1	0.143	0.25	0	0	0	0.000	0.00
	2	0	0	0	0.000	0.00	0	3	3	0.429	0.75	0	0	0	0.000	0.00
	4	0	0	0	0.000	0.00	0	1	1	0.143	0.25	0	0	0	0.000	0.00
	8	0	0	0	0.000	0.00	0	1	1	0.143	0.25	1	1	1	1.000	0.25
	16	1	0	1	1.000	0.25	0	1	1	0.143	0.25	0	0	0	0.000	0.00
	SUM	1	0	1			1	6	7			1	1	1		
(3)	1	0	0	0	0.000	0.00	1	2	3	0.333	0.75	0	1	1	0.167	0.25
	2	0	0	0	0.000	0.00	1	0	1	0.111	0.25	0	1	1	0.167	0.25
	4	0	0	0	0.000	0.00	0	2	2	0.222	0.50	0	1	1	0.167	0.25
	8	1	0	1	0.500	0.25	0	0	0	0.000	0.00	1	2	2	0.333	0.50
	16	1	1	1	0.500	0.25	2	3	3	0.333	0.75	0	1	1	0.167	0.25
	SUM	2	1	2			4	7	9			1	6	6		
(4)	1	0	0	0	0.000	0.00	0	0	0	0.000	0.00	1	0	1	0.500	0.25
	2	0	0	0	0.000	0.00	2	1	3	0.375	0.75	0	0	0	0.000	0.00
	4	2	2	2	0.667	0.50	0	1	1	0.125	0.25	0	0	0	0.000	0.00
	8	0	0	0	0.000	0.00	0	1	1	0.125	0.25	0	0	0	0.000	0.00
	16	0	1	1	0.333	0.25	1	3	3	0.375	0.75	1	1	1	0.500	0.25
	SUM	2	3	3			3	6	8			2	1	2		
(5)	1	2	0	2	0.167	0.25	1	1	2	0.167	0.50	0	0	0	0.000	0.00
	2	0	2	2	0.167	0.25	0	2	2	0.167	0.50	1	1	1	0.167	0.25
	4	0	3	3	0.250	0.75	0	2	2	0.167	0.50	0	1	1	0.167	0.25
	8	2	3	3	0.250	0.75	3	3	3	0.250	0.75	0	1	1	0.167	0.25
	16	2	1	2	0.167	0.50	1	3	3	0.250	0.75	2	2	3	0.500	0.75
	SUM	6	9	12			5	11	12			3	5	6		

PREY DENS.	MEANS ± S.E. (N=15)	
	COL. (B)	COL. (C)
1	0.125 ± 0.04	0.183 ± 0.06
2	0.152 ± 0.04	0.230 ± 0.07
4	0.161 ± 0.05	0.230 ± 0.06
8	0.211 ± 0.07	0.250 ± 0.07
16	0.285 ± 0.07	0.330 ± 0.08

LEGEND

PPE = Patches at which prey eaten  
 PEL = Patches at which eggs laid  
 TPA = Total patches ATTENDED  
 A = Numbers  
 B = Proportions of the SUM (TPA)  
 C = Proportions of total patches of the same prey density PRESENT (=4)

Appendix Table 13

TIME SPENT, AND PERCENTAGE OF TOTAL TIME SPENT BY EACH OF THREE BEETLES ON PATCHES OF DIFFERENT PREY DENSITIES IN THE EXPERIMENT DESCRIBED IN CHAPTER (6.1)

PREY DENS.	TIME SPENT ( $\times 10^{-2}$ sec)				% OF TOTAL TIME OBSERVED (TTOB)			
	B1*	B2	B3	MEAN $\pm$ S.E.	B1	B2	B3	MEAN $\pm$ S.E.
0	1.2	2.4	0	1.20 $\pm$ 0.69	0.8	1.7	0	0.84 $\pm$ 0.49
1	4.2	6.6	0	3.60 $\pm$ 1.93	2.9	4.6	0	2.50 $\pm$ 1.34
2	6.6	3.6	0	3.40 $\pm$ 1.91	4.6	2.5	0	2.37 $\pm$ 1.33
4	3.0	16.2	20.4	13.20 $\pm$ 5.24	2.1	11.3	19.3	10.34 $\pm$ 5.47
8	34.2	37.2	28.2	33.20 $\pm$ 2.65	23.8	25.8	26.7	25.43 $\pm$ 0.86
16	26.4	29.4	55.2	37.00 $\pm$ 9.14	18.3	20.4	52.3	30.34 $\pm$ 10.99
TSAP	68.4	48.6	1.8	39.60 $\pm$ 19.75	47.5	33.8	1.7	27.67 $\pm$ 13.57
TTOB	144.0	144.0	105.6					

\* = B1, B2, and B3 represent the three beetles (replicates)

TSAP = time spent away from patches, i.e. on walls or roof of the searching arena

TTOB = total time observed

Appendix Table 14A

NUMBERS OF FLIGHTS PER 5 min (INDEX OF ACTIVITY) MADE  
BY UNSTARVED AND STARVED BEETLES IN FOUR OBSERVATIONS  
AT 15 min INTERVALS AT 1000 h AND 1600 h AT 25° C.

DAY TIME	OBSERV. NUMBER	UNSTARVED BEETLES				STARVED BEETLES				
		B1	B2	B3	FLIGHTS / 5 MIN MEAN ± S.E.	B1	B2	B3	FLIGHTS / 5 MIN MEANS ± S.E.	
1	1000	1	0	0	0		0	0	0	
		2	0	0	0		0	0	0	
		3	0	0	0		0	0	0	
		4	0	0	0		0	0	0	
		SUM	0	0	0	0	0	0	0	0
	1600	1	0	0	0		4	23	3	
		2	0	0	0		6	14	0	
		3	0	0	0		0	52	2	
4		0	0	0		4	16	1		
	SUM	0	0	0	0	14	105	7	10.42 ± 4.32	
2	1000	1	0	7	1		0	0	1	
		2	0	6	4		0	0	0	
		3	0	3	2		0	0	1	
		4	0	7	0		0	0	0	
		SUM	0	23	7	2.50 ± 0.82	0	0	2	0.17 ± 0.11
	1600	1	11	21	2		4	36	3	
		2	26	0	10		1	0	3	
		3	14	0	0		3	7	0	
4		0	0	5		6	9	1		
	SUM	51	21	17	7.42 ± 2.62	14	52	7	6.08 ± 2.84	
3	1000	1	0	0	0		0	19	4	
		2	0	0	0		0	21	6	
		3	0	0	0		0	16	0	
		4	0	0	0		0	27	5	
		SUM	0	0	0	0	0	83	15	8.17 ± 2.84
	1600	1	24	0	3		6	11	0	
		2	54	5	10		4	34	0	
		3	45	8	5		13	10	9	
4		61	5	6		6	7	5		
	SUM	184	18	24	18.83 ± 6.32	29	62	14	8.75 ± 2.57	
4	1000	1	0	4	0		4	16	0	
		2	0	2	0		0	11	0	
		3	0	2	0		0	13	0	
		4	0	6	0		2	31	0	
		SUM	0	14	0	1.17 ± 0.58	6	71	0	6.42 ± 2.8
	1600	1	0	24	5		0	11	0	
		2	10	21	4		0	4	0	
		3	3	0	0		2	4	0	
4		12	0	8		6	2	0		
	SUM	25	45	17	7.25 ± 2.37	8	21	0	2.42 ± 0.98	
5	1000	1	0	8	4		2	11	D	
		2	0	3	9		9	5	E	
		3	0	5	8		0	8	A	
		4	0	11	6		6	17	D	
		SUM	0	27	27	4.50 ± 1.15	17	41		7.25 ± 1.89
	1600	1	0	0	0		7	4	-	
		2	0	0	0		5	0	-	
		3	0	0	0		5	0	-	
4		0	0	0		3	0	-		
	SUM	0	0	0	0	20	4		3.00 ± 0.96	
6	1000	1	0	11	2		0	D	-	
		2	0	5	4		0	E	-	
		3	0	0	7		0	A	-	
		4	0	0	0		0	D	-	
		SUM	0	16	13	2.42 ± 1.05	0			0
	1600	1	14	21	0		D	-	-	
		2	0	21	0		E	-	-	
		3	0	16	7		A	-	-	
4		0	33	12		D	-	-		
	SUM	14	91	19	10.33 ± 3.18					

Appendix Table 14B

NUMBERS OF FLIGHTS PER 5 min (INDEX OF ACTIVITY) MADE  
BY UNSTARVED AND STARVED BEETLES IN FOUR OBSERVATIONS  
AT 15 min INTERVALS AT 1000 h AND 1600 h AT 30° C.

DAY TIME	OBSERV. NUMBER	UNSTARVED BEETLES				STARVED BEETLES			
		B1	B2	B3	FLIGHTS / 5 MIN MEAN ± S.E.	B1	B2	B3	FLIGHTS / 5 MIN MEANS ± S.E.
1 1000	1	1	7	5		19	24	0	
	2	0	16	0		8	6	13	
	3	3	7	2		15	2	0	
	4	6	0	6		0	7	6	
	SUM	10	30	13	4.42 ± 1.32	42	39	19	8.33 ± 2.28
1600	1	0	0	3		19	15	0	
	2	0	0	1		28	9	0	
	3	0	0	0		30	21	10	
	4	7	0	0		73	0	32	
	SUM	7	0	4	0.92 ± 0.61	140	45	42	19.75 ± 5.88
2 1000	1	3	8	10		24	0	0	
	2	27	34	7		25	2	10	
	3	0	10	12		17	4	6	
	4	12	51	14		14	4	0	
	SUM	42	103	43	15.67 ± 4.22	80	10	16	8.83 ± 2.64
1600	1	0	0	0		68	27	0	
	2	0	7	0		57	24	0	
	3	0	0	4		4	28	19	
	4	0	51	9		34	0	5	
	SUM	0	58	13	5.92 ± 4.20	163	79	24	22.17 ± 6.53
3 1000	1	0	49	2		10	0	0	
	2	0	29	0		4	29	21	
	3	13	27	6		8	3	2	
	4	0	0	8		10	30	14	
	SUM	13	105	16	11.17 ± 4.56	32	62	37	10.92 ± 3.07
1600	1	1	0	4		1	19	12	
	2	0	16	7		4	11	16	
	3	9	0	0		0	15	19	
	4	3	0	2		1	10	22	
	SUM	13	16	13	3.50 ± 1.43	6	55	69	10.83 ± 2.24
4 1000	1	0	0	2		D	0	0	
	2	0	0	10		E	0	0	
	3	6	9	12		A	0	7	
	4	12	44	0		D	0	12	
	SUM	18	53	24	7.92 ± 3.58		0	19	2.38 ± 1.63
1600	1	9	0	7		-	D	4	
	2	5	0	6		-	E	0	
	3	0	0	0		-	A	3	
	4	2	10	0		-	D	1	
	SUM	16	10	13	3.25 ± 1.13			8	2.00 ± 0.91
5 1000	1	0	0	7		-	-	D	
	2	0	0	0		-	-	E	
	3	5	0	3		-	-	A	
	4	8	8	0		-	-	D	
	SUM	13	8	10	2.58 ± 1.00				
1600	1	0	0	0					
	2	2	0	0					
	3	0	0	0					
	4	6	0	0					
	SUM	8	0	0	0.67 ± 0.51				

RAW DATA WITH MEANS  $\pm$  S.E. FOR THE NUMBERS OF PREY EATEN AND EGGS LAID EITHER ABOVE, UNDER OR AWAY FROM SCALES ON SUB-PATCHES OF DIFFERENT PREY DENSITIES PLACED AT DIFFERENT HEIGHTS. THE DATA ARE FOR EACH OF FOUR DAYS FOR EACH OF THREE BEETLES (REPLICATES) IN SEARCHING EFFICIENCY EXPERIMENT No. (1). THE DASHES IN THE TABLE DENOTE ZEROES. THE DESCRIPTIONS OF THE ABBREVIATIONS IN THE TABLE ARE GIVEN BELOW THE TABLE.

PREY DENS	BEETLE (1)												BEETLE (2)												BEETLE (3)												MEAN $\pm$ S.E. PER BEETLE PER DAY (3x4=12)																																	
	(1)			(2)			(3)			(4)			(1)			(2)			(3)			(4)																																																
	DAYS	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7																																									
(2)	SPPOS	c	a	c	d	c	c	d	c	a	c	d	c	c	d	c	a	c	d	c	c	d	c	a	c	d	c	c	d	b	c	d	c	d	b	a	b	c	d	c	d	b	a	b	c	d	c	d	b	a	b	c	d	c	d	b	a	0												
	ET																																																									3.08 $\pm$ 0.54												
	EU	-	-	3	-	-	1	-	1	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	-	-	2	-	-	-	-	4	-	-	-	-	3	-	-	-	-	2	-	-	1.83 $\pm$ 0.30																				
	EA																																											1.00 $\pm$ 0.25																										
	TOT	-	-	3	-	-	1	-	1	-	-	1	-	-	-	-	2	-	-	-	-	4	-	-	-	-	2	-	-	-	-	4	-	-	-	-	2	-	-	-	-	2	-	-	0.50 $\pm$ 0.20																									
	SED	-	-	2	-	-	1	-	1	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	-	-	2	-	-	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	0.25 $\pm$ 0.13																									
	1E	-	-	1	-	-	1	-	1	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	-	-	2	-	-	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	0.08 $\pm$ 0.08																									
	2E	-	-	1	-	-	1	-	1	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	1.33 $\pm$ 0.31																									
	3E																																																																					
	>3E																																																																					
	NET	2	-	-	-	1	-	-	-	-	-	2	-	-	-	-	-	1	-	-	-	-	-	2	-	-	-	-	-	1	-	-	-	-	-	2	-	-	-	-	-	1	-	-																										
(4)	SPPOS	a	d	a	c	a	b	a	a	d	a	c	a	b	a	a	d	a	b	a	c	d	a	d	a	b	a	c	d	d	b	d	c	c	b	a	d	b	d	c	c	b	a	0.25 $\pm$ 0.13																										
	ET																																											6.58 $\pm$ 1.46																										
	EU	2	-	-	1	-	-	-	-	-	4	-	-	-	1	-	-	4	-	-	1	-	-	4	-	-	4	-	3	6	4	-	-	-	-	2	1	-	-	-	-	2	1	-	-	-	-	2	1	-	-	0.08 $\pm$ 0.08																		
	EA																																											5.92 $\pm$ 1.57																										
	TOT	2	-	-	1	-	-	-	-	-	4	-	-	-	1	-	-	4	-	-	1	-	-	4	-	-	4	-	3	6	5	-	-	-	-	2	1	-	-	-	-	2	1	-	-	4.17 $\pm$ 0.79																								
	SED	1	-	-	1	-	-	-	-	-	3	-	-	-	1	-	-	2	1	-	-	1	-	-	2	1	-	-	2	-	2	3	3	-	-	-	-	2	1	-	-	-	-	2	1	-	-	2.08 $\pm$ 0.43																						
	1E	-	-	1	-	-	1	-	1	-	-	1	-	-	1	-	-	1	-	-	1	-	-	1	-	-	1	-	4	-	-	1	-	-	2	-	1	-	-	2	-	1	-	-	1.83 $\pm$ 0.55																									
	2E	1	-	-	1	-	-	-	1	-	-	1	-	-	1	-	-	2	-	-	1	-	-	1	-	-	2	-	1	3	-	-	-	-	-	-	1	-	-	-	-	1	-	-	0.17 $\pm$ 0.11																									
	3E																																											0.08 $\pm$ 0.08																										
	>3E																																																																					
	NET	-	-	1	-	-	-	-	-	-	1	-	-	-	2	-	-	1	-	-	2	-	-	1	-	-	2	-	1	1	-	-	2	-	-	-	-	1	-	-	-	-	1	-	-	2.08 $\pm$ 0.60																								
(8)	SPPOS	b	b	d	b	d	d	b	b	b	d	b	d	d	b	b	b	d	b	d	d	b	d	b	b	a	b	d	c	d	b	b	a	b	d	c	a	c	a	d	b	a	d	a	c	a	d	b	a	d	a	c	a	d	b	a	d	1.17 $\pm$ 0.66												
	ET	-	-	3	-	-	5	-	1	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	-	-	2	-	-	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	9.87 $\pm$ 1.25																				
	EU	-	-	4	-	-	2	-	1	1	-	5	2	-	-	2	-	4	-	3	-	-	4	-	1	-	-	-	4	-	3	1	-	-	2	-	-	4	-	-	-	-	5	-	2	-	-	-	1	-	-	10.00 $\pm$ 1.38																		
	EA																																											5.92 $\pm$ 0.69																										
	TOT	-	-	7	-	-	8	-	2	1	-	5	3	-	-	2	-	4	-	3	-	-	4	-	1	-	-	-	4	-	3	1	-	-	3	-	3	1	-	-	1	-	1	-	-	5.00 $\pm$ 0.60																								
	SED	-	-	2	-	-	7	-	2	1	-	4	3	-	-	2	-	2	-	3	-	-	4	-	1	-	-	-	4	-	1	3	-	-	2	-	-	4	-	-	2	-	4	-	-	1.33 $\pm$ 0.38																								
	1E	-	-	-	-	-	7	-	2	1	-	3	3	-	-	2	-	3	-	4	-	-	4	-	1	-	-	-	4	-	1	1	-	-	2	-	-	4	-	-	2	-	3	-	2	-	0.33 $\pm$ 0.19																							
	2E	-	-	1	-	-	1	-	1	-	-	2	-	-	2	-	-	2	-	-	-	2	-	-	1	-	-	2	-	1	-	1	-	-	1	-	-	1	-	-	1	-	-	1	-	-	0.25 $\pm$ 0.13																							
	3E	-	-	1	-	-	1	-	1	-	-	1	-	-	1	-	-	1	-	-	-	1	-	-	1	-	-	1	-	1	-	1	-	-	1	-	-	1	-	-	1	-	-	1	-	-	0.25 $\pm$ 0.13																							
	>3E	-	-	1	-	-	1	-	1	-	-	1	-	-	1	-	-	1	-	-	-	1	-	-	1	-	-	1	-	1	-	1	-	-	1	-	-	1	-	-	1	-	-	1	-	-	0.25 $\pm$ 0.13																							
	NET	-	-	1	-	-	3	-	-	-	-	3	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	3	-	-	2.58 $\pm$ 0.48																								
(16)	SPPOS	d	c	b	a	b	a	b	a	c	a	d	c	a	b	d	c	b	a	b	a	c	a	d	c	a	b	c	a	c	d	c	a	b	c	a	c	d	c	a	b	c	a	b	b	a	d	c	c	a	b	b	a	d	c	c	a	b	b	a	d	c	c	a	b	b	a	d	c	3.92 $\pm$ 1.14
	ET																																											11.58 $\pm$ 1.32																										
	EU	-	-	3	-	-	3	-	5	-	-	2	4	-	3	-	-	4	1	4	-	-	3	-	-	4	1	-	-	7	9	-	3	-	-	1	1	6	-	5	-	-	2	5	-	3	2	-	-	15.75 $\pm$ 1.78																				
	EA																																											11.67 $\pm$ 1.23																										
	TOT	-	-	3	-	-	9	-	5	-	-	12	6	-	6	4	7	-	-	3	-	-	6	4	7	-	-	6	4	7	-	-	3	-	-	3	-	-	3	-	-	3	-	-	9.33 $\pm$ 0.96																									
	SED	-	-	3	-	-	3	-	5	-	-	8	5	-	5	4	5	-	-	3	-	-	5	4	5	-	-	5	4	5	-	-	3	-	-	3	-	-	3	-	-	3	-	-	3.00 $\pm$ 0.70																									
	1E	-	-	3	-	-	3	-	5	-	-	8	5	-	5	4	5	-	-	3	-	-	5	-	-	4	4	3	-	-	3	-	-	3	-	-	3	-	-	3	-	-	0.08 $\pm$ 0.08																											
	2E	-	-	3	-	-	3	-	5	-	-	8	5	-	5	4	5	-	-	3	-	-	5	-	-	4	4	3	-	-	3	-	-	3	-	-	3	-	-	3	-	-	0.25 $\pm$ 0.18																											
	3E	-	-	3	-	-	3	-	5	-	-	8	5	-	5	4	5	-	-	3	-	-	5	-	-	4	4	3	-	-	3	-	-	3	-	-	3	-	-	3	-	-	2.83 $\pm$ 0.74																											
	>3E	-	-	3	-	-	3	-	5	-	-	8	5	-	5	4	5	-	-	3	-	-	5	-	-	4	4	3	-	-	3	-	-	3	-	-	3	-	-	3	-	-																												
	NET	-	-	1	-	-	3	-	-	-	-	2	1	-	-	-	-	-	2	1	-	-	-	-	-																																													





RAW DATA WITH MEANS  $\pm$  S.E. FOR THE NUMBERS OF PREY EATEN AND EGGS LAID EITHER ABOVE, UNDER OR AWAY FROM SCALES ON SUB-PATCHES OF DIFFERENT PREY DENSITIES PLACED AT DIFFERENT HEIGHTS. THE DATA ARE FOR EACH OF FOUR DAYS FOR EACH OF THREE BEETLES (REPLICATES) IN SEARCHING EFFICIENCY EXPERIMENT No. (3). THE DASHES IN THE TABLE DENOTE ZEROES. THE DESCRIPTIONS OF THE ABBREVIATIONS IN THE TABLE ARE GIVEN BELOW THE TABLE.

PREY DENS	BEETLE (1)				BEETLE (2)				BEETLE (3)				MEAN $\pm$ S.E. PER BEETLE PER DAY (3x4=12)		
	DAYS	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)	(1)	(2)	(3)		(4)	
	REPS	1 2 3 4 5 6 7	1 2 3 4 5 6 7	1 2 3 4 5 6 7	1 2 3 4 5 6 7	1 2 3 4 5 6 7	1 2 3 4 5 6 7	1 2 3 4 5 6 7	1 2 3 4 5 6 7	1 2 3 4 5 6 7	1 2 3 4 5 6 7	1 2 3 4 5 6 7		1 2 3 4 5 6 7	
(2)	SPPOS	d c b a b d c	d c b a b d c	d c b a b d c	d c b a b d c	b a d c d a c	b a d c d a c	b a d c d a c	b a d c d a c	a b b a d c c	a b b a d c c	a b b a d c c	a b b a d c c	0.17 $\pm$ 0.17	
	ET	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	1.50 $\pm$ 0.58	
	EU	-----	-----1-----	-----	-----2-----	-----	-----	-----	-----	-----	-----	-----	-----	0	
	EA	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	1.67 $\pm$ 0.67	
	TOT	-----	-----1-----	-----	-----2-----	-----	-----	-----	-----	-----	-----	-----	-----	0.92 $\pm$ 0.31	
	SED	-----	-----1-----	-----	-----2-----	-----	-----	-----	-----	-----	-----	-----	-----	0.50 $\pm$ 0.20	
	1E	-----	-----1-----	-----	-----2-----	-----	-----	-----	-----	-----	-----	-----	-----	0.17 $\pm$ 0.11	
	2E	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	0.17 $\pm$ 0.11	
	3E	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	0.17 $\pm$ 0.11	
	>3E	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	0.08 $\pm$ 0.08	
NET	-----2-----	-----1-----	-----	-----	-----1-----	-----	-----	-----	-----	-----11-----	-----	-----	0.50 $\pm$ 0.23		
(4)	SPPOS	a b a c d c d	a b a c d c d	a b a c d c d	a b a c d c d	c d b d a b a	c d b d a b a	c d b d a b a	c d b d a b a	d a c c b a d	d a c c b a d	d a c c b a d	d a c c b a d	0	
	ET	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	4.50 $\pm$ 0.44	
	EU	-----2-----	-----3-1-----	-----	-----1-4-----	-----3-2-----	-----1-6-----	-----3-1-1-----	-----5-----	-----2-----	-----6-----	-----3-2-----	-----2-1-1-----	-----1-1-4-----	0
	EA	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	4.50 $\pm$ 0.44	
	TOT	-----2-----	-----3-1-----	-----	-----1-4-----	-----3-2-----	-----1-6-----	-----3-1-1-----	-----5-----	-----2-----	-----6-----	-----3-2-----	-----2-1-1-----	-----1-1-4-----	3.08 $\pm$ 0.34
	SED	-----2-----	-----3-1-----	-----	-----1-3-----	-----2-2-----	-----1-3-----	-----3-1-1-----	-----2-----	-----1-----	-----2-----	-----2-1-----	-----2-1-----	-----1-2-----	1.83 $\pm$ 0.47
	1E	-----2-----	-----3-1-----	-----	-----1-2-----	-----1-----	-----1-1-----	-----3-1-1-----	-----1-----	-----1-----	-----2-----	-----2-1-----	-----2-1-----	-----1-----	0.92 $\pm$ 0.23
	2E	-----	-----	-----	-----1-1-----	-----1-1-----	-----1-----	-----1-----	-----1-----	-----1-----	-----1-----	-----1-1-----	-----1-----	-----2-----	0.17 $\pm$ 0.11
	3E	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	0.08 $\pm$ 0.08	
	>3E	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	0.08 $\pm$ 0.08	
NET	-----1-----	-----1-----	-----	-----2-----	-----2-----	-----3-----	-----1-2-----	-----1-----	-----3-----	-----	-----	-----	-----1-2-----	1.83 $\pm$ 0.35	
(8)	SPPOS	b d c d c a a	b d c d c a a	b d c d c a a	b d c d c a a	d b a b c c d	d b a b c c d	d b a b c c d	d b a b c c d	b d a d c d b	b d a d c d b	b d a d c d b	b d a d c d b	0	
	ET	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	9.08 $\pm$ 1.63	
	EU	5-----4-----	-----2-10-----	-----	-----6-----2-----	-----5-----7-----	-----2-----	-----11-----	-----10-----	-----2-1-6-----	-----6-9-----	-----2-----	-----4-9-8-----	-----	0
	EA	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	9.08 $\pm$ 1.63	
	TOT	5-----4-----	-----2-10-----	-----	-----6-----2-----	-----5-----7-----	-----2-----	-----11-----	-----10-----	-----2-1-6-----	-----6-9-----	-----2-----	-----4-9-8-----	-----	5.92 $\pm$ 0.91
	SED	4-----3-----	-----2-6-----	-----	-----5-----2-----	-----4-----5-----	-----2-----	-----5-----	-----5-----	-----2-1-3-----	-----4-5-----	-----2-----	-----2-4-4-----	-----	3.33 $\pm$ 0.56
	1E	3-----2-----	-----2-3-----	-----	-----4-----2-----	-----3-----3-----	-----2-----	-----2-----	-----2-----	-----2-1-1-----	-----2-2-----	-----2-----	-----1-1-----	-----	2.08 $\pm$ 0.56
	2E	1-----1-----	-----2-----	-----	-----1-----2-----	-----1-----2-----	-----	-----3-----	-----2-----	-----1-----	-----2-3-----	-----	-----4-2-----	-----	0.42 $\pm$ 0.15
	3E	-----	-----1-----	-----	-----	-----	-----	-----1-----	-----	-----	-----	-----	-----1-1-----	-----	0
	>3E	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	0	
NET	2-----	-----2-----	-----	-----1-2-2-----	-----2-----	-----4-----	-----1-----	-----2-----	-----1-2-1-----	-----1-1-----	-----3-----	-----1-1-----	-----1-----	2.58 $\pm$ 0.36	
(16)	SPPOS	c a d b a b c	c a d b a b c	c a d b a b c	c a d b a b c	a c c a b d b	a c c a b d b	a c c a b d b	a c c a b d b	c c d b a b a	c c d b a b a	c c d b a b a	c c d b a b a	0	
	ET	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	11.58 $\pm$ 1.28	
	EU	-----4-8-----	-----2-5-----	-----	-----12-3-2-----	-----9-----2-----	-----4-9-4-----	-----10-----2-----	-----4-5-----	-----5-----6-----	-----3-6-----	-----7-4-1-3-3-----	-----2-----	-----7-3-----2-----	0
	EA	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	11.58 $\pm$ 1.26	
	TOT	-----4-8-----	-----2-5-----	-----	-----12-3-2-----	-----9-----2-----	-----4-9-4-----	-----10-----2-----	-----4-5-----	-----5-----5-----	-----3-6-----	-----7-4-1-3-3-----	-----2-----	-----7-3-----2-----	9.58 $\pm$ 1.13
	SED	-----4-6-----	-----2-5-----	-----	-----8-3-2-----	-----5-----2-----	-----2-8-3-----	-----7-----2-----	-----3-6-----	-----3-----5-----	-----3-5-----	-----7-4-1-3-3-----	-----2-----	-----5-3-----2-----	7.83 $\pm$ 1.10
	1E	-----4-4-----	-----2-4-----	-----	-----5-3-2-----	-----4-----2-----	-----7-2-----	-----5-----2-----	-----2-6-----	-----1-----4-----	-----3-4-----	-----7-4-1-3-3-----	-----2-----	-----3-3-----2-----	1.50 $\pm$ 0.34
	2E	-----2-----	-----1-----	-----	-----2-----	-----1-----	-----2-1-1-----	-----1-----	-----1-----	-----2-----1-----	-----1-----	-----	-----	-----2-----	0.25 $\pm$ 0.13
	3E	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	0	
	>3E	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	0	
NET	-----1-2-----	-----2-3-----	-----	-----2-1-1-----	-----3-----1-----	-----4-----	-----1-4-----	-----2-3-----	-----3-----	-----2-----	-----1-1-1-----	-----2-----	-----2-1-1-3-----	3.75 $\pm$ 0.37	

SPPOS = Vertical position of sub-patches in a patch.  
REPS = Patches 1 to 7

a = Top most sub-patch  
b = Second from top sub-patch  
c = Third from top sub-patch  
d = Bottom sub-patch

ET = EGGS LAID ABOVE SCALES  
EU = EGGS LAID UNDER SCALES  
EA = EGGS LAID AWAY FROM SCALES  
TOT = TOTAL EGGS LAID

SED = SCALES WITH EGGS  
1E = SCALES WITH 1 EGG  
2E = SCALES WITH 2 EGGS

3E = SCALES WITH 3 EGGS  
>3E = SCALES WITH >3 EGGS  
NET = PREY EATEN



Appendix Table 16

NUMBER OF SUB-PATCHES AT DIFFERENT HEIGHTS WHICH WERE ATTENDED BY EACH OF THREE BEETLES (REPLICATES) IN EACH OF FOUR DAYS IN EACH OF THE SEARCHING EFFICIENCY EXPERIMENTS (1), (2), (3), & (4)

(A) EXPERIMENT (1)

S/PATCH POSITION	REP.(1)					REP.(2)					REP.(3)					TOTAL
	DAYS					DAYS					DAYS					
	1	2	3	4	SUM	1	2	3	4	SUM	1	2	3	4	SUM	
TOP	1	1	4	1	7	3	2	1	4	10	0	3	1	4	8	25
2nd TOP	2	3	2	4	11	2	4	3	4	13	3	2	2	2	9	33
3rd TOP	5	3	2	4	14	1	3	3	5	12	2	3	3	3	11	37
BOTTOM	1	2	3	4	10	2	3	4	3	12	1	2	3	1	7	29

(B) EXPERIMENT (2)

S/PATCH POSITION	REP.(1)					REP.(2)					REP.(3)					TOTAL
	DAYS					DAYS					DAYS					
	1	2	3	4	SUM	1	2	3	4	SUM	1	2	3	4	SUM	
TOP	2	2	1	0	5	4	5	4	2	15	2	5	4	5	16	36
2nd TOP	2	3	1	1	7	3	4	4	5	16	1	2	3	3	9	32
3rd TOP	4	2	2	3	11	3	3	3	3	12	1	1	1	1	4	27
BOTTOM	2	2	1	3	8	3	3	3	1	10	3	2	1	0	6	24

(C) EXPERIMENT (3)

S/PATCH POSITION	REP.(1)					REP.(2)					REP.(3)					TOTAL
	DAYS					DAYS					DAYS					
	1	2	3	4	SUM	1	2	3	4	SUM	1	2	3	4	SUM	
TOP	3	2	3	3	11	5	2	4	1	12	1	2	0	1	4	27
2nd TOP	2	2	2	0	6	2	3	0	1	6	2	2	3	2	9	21
3rd TOP	0	2	3	1	6	0	2	0	3	5	2	2	1	3	8	19
BOTTOM	1	1	1	2	5	0	0	2	2	4	3	2	4	1	10	19

(D) EXPERIMENT (4)

S/PATCH POSITION	REP.(1)					REP.(2)					REP.(3)					TOTAL
	DAYS					DAYS					DAYS					
	1	2	3	4	SUM	1	2	3	4	SUM	1	2	3	4	SUM	
TOP	3	2	4	4	13	2	1	2	1	6	2	2	1	1	6	25
2nd TOP	2	1	1	0	4	1	3	1	5	10	1	3	1	1	6	20
3rd TOP	2	1	3	1	7	1	3	2	1	7	2	2	3	1	8	22
BOTTOM	1	3	1	4	9	1	4	5	4	14	1	1	4	1	7	30

Appendix Table 17A

NUMBER OF PREY EATEN, EGGS LAID AND  
SUB-PATCHES ATTENDED FOR THIS PURPOSE  
SEARCHING EFFICIENCY EXPERIMENT (1)

ITEM	DAY	R1	R2	R3	MEANS $\pm$ S.E.
PREY EATEN	1	6	9	7	7.33 $\pm$ 0.88
	2	7	14	13	11.33 $\pm$ 2.19
	3	9	7	5	7.00 $\pm$ 1.16
	4	8	12	9	9.67 $\pm$ 1.20
EGGS LAID	1	25	48	26	33.00 $\pm$ 7.51
	2	26	45	33	34.67 $\pm$ 5.55
	3	40	33	45	39.33 $\pm$ 3.48
	4	30	51	32	37.67 $\pm$ 6.69
# S/PATCH PREY EATEN	1	5	6	4	5.00 $\pm$ 0.58
	2	4	8	7	6.33 $\pm$ 1.20
	3	6	5	4	5.00 $\pm$ 0.58
	4	6	8	4	6.00 $\pm$ 1.16
@ S/PATCH EGGS LAID	1	7	7	5	6.33 $\pm$ 0.67
	2	8	12	8	9.33 $\pm$ 1.33
	3	10	10	9	9.67 $\pm$ 0.33
	4	9	15	10	11.33 $\pm$ 1.86
* TOTAL S/PATCH ATTENDED	1	9	8	6	7.67 $\pm$ 0.88
	2	9	12	10	10.33 $\pm$ 0.88
	3	11	11	9	10.33 $\pm$ 0.67
	4	13	16	10	13.00 $\pm$ 1.73

\* is NOT equal to # + @ (see text)

Appendix Table 17B

NUMBER OF PREY EATEN, EGGS LAID AND  
SUB-PATCHES ATTENDED FOR THIS PURPOSE  
SEARCHING EFFICIENCY EXPERIMENT (2)

ITEM	DAY	R1	R2	R3	MEANS $\pm$ S.E.
PREY EATEN	1	7	8	10	8.33 $\pm$ 0.88
	2	6	11	9	8.66 $\pm$ 1.45
	3	7	12	12	10.33 $\pm$ 1.67
	4	6	10	11	9.00 $\pm$ 1.53
EGGS LAID	1	44	49	36	43.00 $\pm$ 3.79
	2	22	46	47	38.33 $\pm$ 8.17
	3	36	50	44	43.33 $\pm$ 4.06
	4	24	43	45	37.33 $\pm$ 6.69
# S/PATCH PREY EATEN	1	5	7	5	5.67 $\pm$ 0.67
	2	4	8	6	6.00 $\pm$ 1.15
	3	3	9	7	6.33 $\pm$ 1.76
	4	3	6	7	5.33 $\pm$ 1.20
@ S/PATCH EGGS LAID	1	9	12	5	8.67 $\pm$ 2.03
	2	8	15	9	10.67 $\pm$ 2.19
	3	5	12	7	8.00 $\pm$ 2.08
	4	5	8	7	6.67 $\pm$ 0.88
* TOTAL S/PATCH ATTENDED	1	10	13	7	10.00 $\pm$ 1.73
	2	9	15	10	11.33 $\pm$ 1.86
	3	5	15	9	9.67 $\pm$ 2.91
	4	7	11	9	9.00 $\pm$ 1.56

\* is NOT equal to # + @ (see text)

Appendix Table 17C

NUMBER OF PREY EATEN, EGGS LAID AND  
SUB-PATCHES ATTENDED FOR THIS PURPOSE  
SEARCHING EFFICIENCY EXPERIMENT (3)

ITEM	DAY	R1	R2	R3	MEANS $\pm$ S.E.
PREY EATEN	1	8	12	6	8.67 $\pm$ 1.76
	2	9	10	9	9.33 $\pm$ 0.33
	3	10	8	5	7.67 $\pm$ 1.45
	4	8	10	10	9.33 $\pm$ 0.67
EGGS LAID	1	23	26	34	27.67 $\pm$ 3.28
	2	25	28	25	26.00 $\pm$ 1.00
	3	32	26	31	29.67 $\pm$ 1.86
	4	28	27	17	24.00 $\pm$ 3.51
# S/PATCH PREY EATEN	1	5	4	5	4.67 $\pm$ 0.33
	2	5	5	6	5.33 $\pm$ 0.33
	3	6	4	4	4.67 $\pm$ 0.67
	4	4	5	6	5.00 $\pm$ 0.58
@ S/PATCH EGGS LAID	1	5	6	7	6.00 $\pm$ 0.58
	2	7	6	8	7.00 $\pm$ 0.58
	3	8	5	8	7.00 $\pm$ 1.00
	4	6	7	5	6.00 $\pm$ 0.58
* TOTAL S/PATCH ATTENDED	1	6	7	8	7.00 $\pm$ 0.58
	2	7	7	8	7.33 $\pm$ 0.33
	3	9	6	8	7.33 $\pm$ 0.88
	4	6	7	7	6.67 $\pm$ 0.33

\* is NOT equal to # + @ (see text)

Appendix Table 17D

NUMBER OF PREY EATEN, EGGS LAID AND  
SUB-PATCHES ATTENDED FOR THIS PURPOSE  
SEARCHING EFFICIENCY EXPERIMENT (4)

ITEM	DAY	R1	R2	R3	MEANS $\pm$ S.E.
PREY EATEN	1	7	6	8	7.00 $\pm$ 0.58
	2	9	10	10	9.67 $\pm$ 0.33
	3	10	8	9	9.00 $\pm$ 0.58
	4	11	8	10	9.67 $\pm$ 0.88
EGGS LAID	1	20	18	21	19.67 $\pm$ 0.88
	2	27	26	28	27.00 $\pm$ 0.58
	3	29	24	30	27.67 $\pm$ 1.86
	4	32	39	28	33.00 $\pm$ 3.21
# S/PATCH PREY EATEN	1	4	5	4	4.33 $\pm$ 0.33
	2	4	5	5	4.67 $\pm$ 0.33
	3	6	5	6	5.67 $\pm$ 0.33
	4	7	6	3	5.33 $\pm$ 1.20
@ S/PATCH EGGS LAID	1	8	3	5	5.33 $\pm$ 1.45
	2	6	8	7	7.00 $\pm$ 0.58
	3	9	8	7	8.00 $\pm$ 0.58
	4	8	9	4	7.00 $\pm$ 1.53
* TOTAL S/PATCH ATTENDED	1	8	5	6	6.33 $\pm$ 0.88
	2	7	11	8	8.67 $\pm$ 1.20
	3	9	10	9	9.33 $\pm$ 0.33
	4	9	11	4	8.00 $\pm$ 2.08

\* is NOT equal to # + @ (see text)

Appendix Table 18A

SUB-PATCHES ATTENDED (SPATT) BY THE BEETLE FOR EATING PREY (SPPE), LAYING EGGS (SPEL), AND TOTAL SUB-PATCHES ATTENDED (TSPA) PER DAY IN SEARCHING EFFICIENCY EXPERIMENT (1)  
(PREY DENS = PREY DENSITY PER SUB-PATCH; B1, B2, & B3 ARE THE THREE BEETLES)

DAY	PREY DENS	SPATT FOR EATING PREY (SPPE)				SPATT FOR LAYING EGGS (SPEL)				TOTAL SPATT (TSPA)			
		B1	B2	B3	MEAN ± S.E.	B1	B2	B3	MEAN ± S.E.	B1	B2	B3	MEAN ± S.E.
(1)	2	2	0	1		2	1	1		3	1	1	
	4	1	3	2		2	2	1		2	3	2	
	8	1	2	0		2	2	1		2	2	1	
	16	1	1	1		1	2	2		2	2	2	
	SUM	5	6	4		7	7	5		9	8	6	
(2)	2	2	1	1		2	2	1		3	2	2	
	4	1	2	1		1	3	2		1	3	2	
	8	1	3	1		4	4	2		4	4	2	
	16	0	2	4		1	3	3		1	3	4	
	SUM	4	8	7		8	12	8		9	12	10	
(3)	2	0	1	0		1	1	0		1	2	0	
	4	4	1	1		3	1	4		4	1	4	
	8	1	2	2		3	4	2		3	4	2	
	16	1	1	1		3	4	3		3	4	3	
	SUM	6	5	4		10	10	9		11	11	9	
(4)	2	1	1	1		2	2	2		3	2	2	
	4	0	4	0		1	5	?		1	5	2	
	8	3	2	1		2	4	2		5	5	2	
	16	2	1	2		4	4	4		4	4	4	
	SUM	6	8	4		9	15	10		13	16	10	
TOTALS	2	5	3	3	3.67 ± 0.67	7	6	4	5.67 ± 0.88	10	7	5	7.33 ± 1.45
OVER	4	6	10	4	6.67 ± 1.76	7	11	9	9.00 ± 1.16	8	12	10	10.00 ± 1.16
4 DAYS	8	6	9	4	6.33 ± 1.45	11	14	7	10.67 ± 2.03	14	15	7	12.00 ± 2.52
16	4	5	8	5.67 ± 1.20	9	13	12	11.33 ± 1.20	10	13	13	12.00 ± 1.00	
SUM	21	27	19	22.33 ± 2.40	34	44	32	36.67 ± 3.71	42	47	35	41.33 ± 3.48	
PROPORTIONS OF THE SUM FROM TOTALS OVER 4 DAYS FOR EACH OF THE FOUR PREY DENSITIES													
2	.24	.11	.16	0.17 ± 0.04	.21	.14	.13	0.16 ± 0.03	.24	.15	.14	0.18 ± 0.03	
4	.29	.37	.21	0.29 ± 0.05	.21	.25	.28	0.25 ± 0.02	.19	.26	.29	0.24 ± 0.03	
8	.29	.33	.21	0.28 ± 0.04	.32	.32	.22	0.29 ± 0.03	.33	.32	.20	0.28 ± 0.04	
16	.19	.19	.42	0.27 ± 0.08	.27	.30	.38	0.31 ± 0.03	.24	.28	.37	0.30 ± 0.04	

Appendix Table 18B

SUB-PATCHES ATTENDED (SPATT) BY THE BEETLE FOR EATING PREY (SPPE), LAYING EGGS (SPEL), AND TOTAL SUB-PATCHES ATTENDED (TSPA) PER DAY IN SEARCHING EFFICIENCY EXPERIMENT (2)  
(PREY DENS = PREY DENSITY PER SUB-PATCH; B1, B2, & B3 ARE THE THREE BEETLES)

DAY	PREY DENS	SPATT FOR EATING PREY (SPPE)				SPATT FOR LAYING EGGS (SPEL)				TOTAL SPATT (TSPA)			
		B1	B2	B3	MEAN ± S.E.	B1	B2	B3	MEAN ± S.E.	B1	B2	B3	MEAN ± S.E.
(1)	1	1	0	2		0	0	1		1	0	3	
	3	0	1	0		2	4	1		2	4	1	
	12	3	2	1		5	5	1		5	5	1	
	20	1	4	2		2	3	2		2	4	2	
	SUM	5	7	5		9	12	5		10	13	7	
(2)	1	1	1	1		1	4	0		2	4	1	
	3	1	1	2		2	3	3		2	3	3	
	12	2	3	3		4	4	4		4	4	4	
	20	0	3	0		1	4	2		1	4	2	
	SUM	4	8	6		8	15	9		9	15	10	
(3)	1	0	1	1		0	2	1		0	3	1	
	3	3	4	3		1	3	2		1	4	3	
	12	1	1	2		2	3	2		2	3	3	
	20	2	3	1		2	4	2		2	5	2	
	SUM	3	9	7		5	12	7		5	15	9	
(4)	1	1	3	0		1	0	0		2	3	0	
	3	0	0	3		1	2	1		1	2	3	
	12	1	2	2		1	4	2		2	4	2	
	20	1	1	2		2	2	4		2	2	4	
	SUM	3	6	7		5	8	7		7	11	9	
TOTALS	1	3	5	4	4.00 ± 0.58	2	6	2	3.33 ± 1.33	5	10	5	6.67 ± 1.67
OVER	3	1	6	8	5.00 ± 2.08	6	12	7	8.33 ± 1.86	6	13	10	9.67 ± 2.03
4 DAYS	12	7	8	8	7.67 ± 0.33	12	16	9	12.33 ± 2.03	13	16	10	13.00 ± 1.73
	20	4	11	5	6.67 ± 2.19	7	13	10	10.00 ± 1.73	7	15	10	10.67 ± 2.33
SUM		15	30	25	23.33 ± 4.41	27	47	28	34.00 ± 6.51	31	54	35	40.00 ± 7.10
PROPORTIONS OF THE SUM FROM TOTALS OVER 4 DAYS FOR EACH OF THE FOUR PREY DENSITIES													
1	.20	.17	.16	0.18 ± 0.01	.07	.13	.07	0.09 ± 0.02	.16	.19	.14	0.16 ± 0.01	
3	.07	.20	.32	0.20 ± 0.07	.22	.26	.25	0.24 ± 0.01	.19	.24	.29	0.24 ± 0.03	
12	.47	.27	.32	0.35 ± 0.06	.44	.34	.32	0.37 ± 0.04	.42	.30	.29	0.33 ± 0.04	
20	.27	.37	.20	0.28 ± 0.05	.26	.28	.36	0.30 ± 0.03	.23	.28	.29	0.26 ± 0.02	



Appendix Table 18C

SUB-PATCHES ATTENDED (SPATT) BY THE BEETLE FOR EATING PREY (SPPE), LAYING EGGS (SPEL), AND TOTAL SUB-PATCHES ATTENDED (TSPA) PER DAY IN SEARCHING EFFICIENCY EXPERIMENT (3)  
(PREY DENS = PREY DENSITY PER SUB-PATCH; B1, B2, & B3 ARE THE THREE BEETLES)

DAY	PREY DENS	SPATT FOR EATING PREY (SPPE)				SPATT FOR LAYING EGGS (SPEL)				TOTAL SPATT (TSPA)			
		B1	B2	B3	MEAN ± S.E.	B1	B2	B3	MEAN ± S.E.	B1	B2	B3	MEAN ± S.E.
(1)	2	1	1	2		0	0	2		1	1	3	
	4	1	1	0		1	2	1		1	2	1	
	8	1	1	2		2	1	2		2	1	2	
	16	2	1	1		2	3	2		2	3	2	
	SUM	5	4	5		5	6	7		6	7	8	
(2)	2	1	0	0		1	0	0		1	0	0	
	4	1	2	2		2	3	2		2	3	2	
	8	1	1	1		2	1	1		2	2	1	
	16	2	2	3		2	2	5		2	2	5	
	SUM	5	5	6		7	6	8		7	7	8	
(3)	2	0	0	0		1	1	2		1	1	2	
	4	1	1	0		2	1	2		2	1	2	
	8	3	1	3		2	1	3		3	2	3	
	16	2	2	1		3	2	1		3	2	1	
	SUM	6	4	4		8	5	8		9	6	8	
(4)	2	0	0	0		0	1	0		0	1	0	
	4	1	1	2		2	1	2		2	1	2	
	8	3	3	1		2	3	0		2	3	1	
	16	2	1	3		2	2	3		2	2	4	
	SUM	4	5	6		6	7	5		6	7	7	
TOTALS	2	2	1	2	1.67 ± 0.33	2	2	4	2.67 ± 0.67	3	3	5	3.67 ± 0.67
OVER	4	4	5	4	4.33 ± 0.33	7	7	7	7.00 ± 0.00	7	7	7	7.00 ± 0.00
4 DAYS	8	6	6	7	6.33 ± 0.33	8	6	6	6.67 ± 0.67	9	8	7	8.00 ± 0.58
16	8	6	8	8	7.33 ± 0.67	9	9	11	9.67 ± 0.67	9	9	12	10.00 ± 1.00
SUM	20	18	21	21	19.67 ± 0.88	26	24	28	26.00 ± 1.16	28	27	31	28.67 ± 1.20
PROPORTIONS OF THE SUM FROM TOTALS OVER 4 DAYS FOR EACH OF THE FOUR PREY DENSITIES													
2	.10	.06	.10	0.08 ± 0.01	.08	.08	.14	0.10 ± 0.02	.11	.11	.16	0.13 ± 0.02	
4	.20	.28	.19	0.22 ± 0.03	.27	.29	.25	0.27 ± 0.01	.25	.26	.23	0.25 ± 0.01	
8	.30	.33	.33	0.32 ± 0.01	.31	.25	.21	0.26 ± 0.03	.32	.30	.23	0.28 ± 0.03	
16	.40	.33	.38	0.37 ± 0.02	.35	.38	.39	0.37 ± 0.01	.32	.33	.39	0.35 ± 0.02	

Appendix Table 18D

SUB-PATCHES ATTENDED (SPATT) BY THE BEETLE FOR EATING PREY (SPPE), LAYING EGGS (SPEL), AND TOTAL SUB-PATCHES ATTENDED (TSPA) PER DAY IN SEARCHING EFFICIENCY EXPERIMENT (4)  
(PREY DENS = PREY DENSITY PER SUB-PATCH; B1, B2, & B3 ARE THE THREE BEETLES)

DAY	PREY DENS	SPATT FOR EATING PREY (SPPE)				SPATT FOR LAYING EGGS (SPEL)				TOTAL SPATT (TSPA)			
		B1	B2	B3	MEAN ± S.E.	B1	B2	B3	MEAN ± S.E.	B1	B2	B3	MEAN ± S.E.
(1)	2	1	1	1		1	0	0		1	1	1	
	4	1	0	1		2	0	1		2	0	1	
	8	1	2	1		3	2	2		3	2	2	
	16	1	2	1		2	1	2		2	2	2	
	SUM	4	5	4		8	3	5		8	5	6	
(2)	2	0	3	0		0	0	0		0	3	0	
	4	2	1	1		1	3	1		2	3	2	
	8	1	0	2		2	3	3		2	3	3	
	16	1	1	2		3	2	3		3	2	3	
	SUM	4	5	5		6	8	7		7	11	8	
(3)	2	1	2	1		1	3	1		1	5	1	
	4	1	1	1		2	2	1		2	2	2	
	8	2	2	2		3	2	2		3	2	3	
	16	2	0	2		3	1	3		3	1	3	
	SUM	6	5	6		9	8	7		9	10	9	
(4)	2	2	2	0		2	2	0		2	3	0	
	4	2	2	1		2	2	1		2	3	1	
	8	2	1	0		2	3	1		3	3	1	
	16	1	1	2		2	2	2		2	2	2	
	SUM	7	6	3		8	9	4		8	11	4	
TOTALS	2	4	8	2	4.67 ± 1.67	4	5	1	3.33 ± 1.20	4	12	2	6.00 ± 3.06
OVER	4	6	4	4	4.67 ± 0.67	7	7	4	6.00 ± 1.00	8	8	6	7.33 ± 0.67
4 DAYS	8	6	5	5	5.33 ± 0.33	10	10	8	9.33 ± 0.67	11	10	9	10.00 ± 0.58
16	5	4	7	7	5.33 ± 0.33	10	6	10	8.67 ± 1.33	10	7	10	9.00 ± 1.00
SUM		21	21	18	20.00 ± 1.00	31	28	23	27.33 ± 2.33	33	37	27	32.33 ± 2.91
PROPORTIONS OF THE SUM FROM TOTALS OVER 4 DAYS FOR EACH OF THE FOUR PREY DENSITIES													
2	.19	.38	.11	0.23 ± 0.08	.13	.18	.04	0.12 ± 0.04	.12	.32	.07	0.17 ± 0.08	
4	.29	.19	.22	0.23 ± 0.03	.23	.25	.17	0.22 ± 0.02	.24	.22	.22	0.23 ± 0.01	
8	.29	.24	.28	0.27 ± 0.02	.32	.36	.35	0.34 ± 0.01	.33	.27	.33	0.31 ± 0.02	
16	.24	.19	.39	0.27 ± 0.06	.32	.21	.44	0.32 ± 0.06	.30	.19	.37	0.29 ± 0.05	

Appendix Table 19

THE PROPORTION OF SUB-PATCHES ATTENDED FROM THOSE OF A PARTICULAR PREY DENSITY PRESENT (7 PER DAY), AND ESTIMATES OF PATCH FINDING EFFICIENCY (PFE) BASED ON THE VOLUME OF THE SEARCHING ARENA FROM SEARCHING EFFICIENCY EXPERIMENTS 1, 2, 3, AND 4.  
(B1, B2, AND B3 represent the 3 beetles)

EXPT.	PREY DENS.	PROP. OF S/PATCHES ATTENDED			MEAN $\pm$ S.E.	PFE ( $\times 10^{-2}$ )			
		B1	B2	B3		B1	B2	B3	MEAN $\pm$ S.E.
(1)	2	.36	.25	.18	0.26 $\pm$ 0.05	3.60	2.53	1.80	2.64 $\pm$ 0.50
	4	.29	.43	.36	0.36 $\pm$ 0.04	2.88	4.33	3.60	3.60 $\pm$ 0.42
	8	.50	.54	.25	0.43 $\pm$ 0.09	5.05	5.40	2.53	4.80 $\pm$ 0.12
	16	.36	.46	.46	0.43 $\pm$ 0.04	3.60	4.68	4.68	4.32 $\pm$ 0.36
(2)	1	.18	.36	.18	0.24 $\pm$ 0.06	1.80	3.60	1.80	2.40 $\pm$ 0.60
	3	.21	.46	.36	0.35 $\pm$ 0.07	2.15	4.68	3.60	3.48 $\pm$ 0.73
	12	.46	.57	.36	0.46 $\pm$ 0.06	4.68	5.75	3.60	4.68 $\pm$ 0.62
	20	.25	.54	.36	0.38 $\pm$ 0.08	2.53	5.40	3.60	3.84 $\pm$ 0.84
(3)	2	.11	.11	.18	0.13 $\pm$ 0.02	1.08	1.08	1.80	1.32 $\pm$ 0.24
	4	.25	.25	.25	0.25 $\pm$ 0	2.53	1.08	2.53	2.04 $\pm$ 0.48
	8	.32	.29	.25	0.29 $\pm$ 0.02	3.25	2.88	2.53	2.89 $\pm$ 0.21
	16	.32	.32	.43	0.36 $\pm$ 0.04	2.53	5.40	3.60	3.84 $\pm$ 0.84
(4)	2	.14	.43	.07	0.21 $\pm$ 0.11	0.36	1.08	0.18	0.54 $\pm$ 0.28
	4	.29	.29	.21	0.26 $\pm$ 0.02	0.72	0.72	0.54	0.66 $\pm$ 0.06
	8	.39	.36	.32	0.36 $\pm$ 0.02	0.99	0.90	0.81	0.90 $\pm$ 0.05
	16	.36	.25	.36	0.32 $\pm$ 0.04	0.90	0.63	0.90	0.81 $\pm$ 0.09

Expts. (1), (2), & (3) --- Searching Arena Volume : (1.5 x 1.5 x 1.1 m)  
Expt. (4) --- Searching Arena Volume : ( 3 x 3 x 1.1 m)

Appendix Table 20

ESTIMATES OF THE PROBABILITY OF A PARTICULAR PREY ON AN ATTENDED SUB-PATCH BEING EATEN ( $P_n$ ), AND THE PROBABILITY OF SUB-PATCH WITH "n" PREY BEING DISCOVERED ( $\beta_n$ ) BY THE BEETLE FROM CHESSON'S BINOMIAL MODEL FOR EACH OF SEARCHING EFFICIENCY EXPERIMENT 1, 2, 3, AND 4.

(B1, B2, AND B3 represnt the three beetles)

(\* = Chesson's model produced erroneous results)

(# = Chesson's model could not be fitted to the data)

EXPT.	PREY DENS.	$P_n$			MEAN $\pm$ S.E.	$\beta_n$			MEAN $\pm$ S.E.
		B1	B2	B3		B1	B2	B3	
(1)	2	.57	.80	.50	0.62 $\pm$ 0.09	.22	.11	.14	0.16 $\pm$ 0.03
	4	.19	.17	*	0.18 $\pm$ 0.01	.38	.67	*	0.52 $\pm$ 0.18
	8	.12	.15	.17	0.15 $\pm$ 0.01	.33	.44	.19	0.32 $\pm$ 0.07
	16	.06	.09	.13	0.09 $\pm$ 0.02	.23	.26	.32	0.26 $\pm$ 0.03
(2)	1	#	#	#		#	#	#	
	3	*	.15	.22	0.19 $\pm$ 0.03	*	.55	.55	0.55 $\pm$ 0
	12	.14	*	.13	0.13 $\pm$ 0.01	.30	*	.36	0.33 $\pm$ 0.03
	20	.08	.08	.12	0.09 $\pm$ 0.01	.17	.50	.19	0.29 $\pm$ 0.10
(3)	2	.67	*	*	0.67	.08	*	*	0.08
	4	.28	.46	.27	0.33 $\pm$ 0.06	.20	.20	.20	0.20 $\pm$ 0
	8	.19	.19	.07	0.15 $\pm$ 0.04	.27	.27	.55	0.36 $\pm$ 0.09
	16	.09	.17	.07	0.11 $\pm$ 0.03	.36	.23	.42	0.34 $\pm$ 0.06
(4)	2	*	.77	.67	0.72 $\pm$ 0.05	*	.30	.08	0.19 $\pm$ 0.11
	4	.51	*	.46	0.48 $\pm$ 0.03	.23	*	.16	0.19 $\pm$ 0.04
	8	.15	.05	.25	0.15 $\pm$ 0.06	.29	.51	.20	0.33 $\pm$ 0.09
	16	.10	.12	.12	0.11 $\pm$ 0.01	.22	.16	.29	0.22 $\pm$ 0.04

Appendix Table 21

THE NUMBERS OF PREY EATEN (P.E.), EGGS LAID (E.L.), SUB-PATCHES ATTENDED FOR EATING PREY (SPPE), SUB-PATCHES ATTENDED FOR LAYING EGGS (SPEL), THE TOTAL SUB-PATCHES ATTENDED (TSPA), AND ESTIMATES OF PATCH FINDING EFFICIENCY (PFE) FOR EACH OF THE THREE BEETLES FOR SUB-PATCHES OF FOUR PREY DENSITIES IN SEARCHING EFFICIENCY EXPERIMENT (5).

PREY DENS.	ITEM	BET.(1)	BET.(2)	BET.(3)	MEAN $\pm$ S.E.
(2)	P.E.	3	6	4	4.33 $\pm$ 0.88
	E.L.	13	14	11	12.67 $\pm$ 0.88
	SPPE	2	3	4	3.00 $\pm$ 0.58
	SPEL	5	7	6	6.00 $\pm$ 0.58
	TSPA	6	9	8	7.67 $\pm$ 0.88
	PFE	0.087	0.13	0.115	0.111 $\pm$ 0.013
	(4)	P.E.	6	7	3
E.L.		15	14	15	14.67 $\pm$ 0.33
SPPE		3	3	2	2.67 $\pm$ 0.33
SPEL		4	3	4	3.67 $\pm$ 0.33
TSPA		5	5	4	4.67 $\pm$ 0.33
PFE		0.072	0.072	0.058	0.067 $\pm$ 0.005
(8)		P.E.	4	7	6
	E.L.	12	14	10	12.00 $\pm$ 1.16
	SPPE	2	3	1	2.00 $\pm$ 0.58
	SPEL	2	4	2	2.67 $\pm$ 0.67
	TSPA	2	4	2	2.67 $\pm$ 0.67
	PFE	0.029	0.058	0.029	0.039 $\pm$ 0.01
	(16)	P.E.	9	4	6
E.L.		19	20	18	19.00 $\pm$ 0.58
SPPE		3	2	2	2.33 $\pm$ 0.33
SPEL		4	3	3	3.33 $\pm$ 0.33
TSPA		4	3	3	3.33 $\pm$ 0.33
PFE		0.058	0.043	0.043	0.048 $\pm$ 0.005

Patch Finding Efficiency (per beetle per cu m per day) estimated on the basis of (28) Total sub-patches present (see text)