

SEARCHING BEHAVIOUR OF POLYPHAGOUS PREDATORS

BY

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ABSTRACT

In reviewing the literature, particular attention is paid to the functional response, preference and the effects of prey aggregation, which provide the theme of this work. The problems of abstracting the parameters of the Random Predator Equation are examined and an alternative least squares approach suggested. Models which vary these parameters are considered.

The functional responses of Coccinella septempunctata L. to two size classes of an aphid prey are modelled. Predation when both prey classes are present is found to be well described by predictions based on the individual functional responses.

Functional responses of Anthocoris nemorum (L.) to ovae of Pieris brassicae (L.) are examined in a simple arena. Four different arrangements of the prey, of increasing aggregation, are used. The responses to the different arrangements, at three different time intervals, are analysed and compared. Only the most aggregated distribution produces results differing significantly from the others. Recording predation at the three time intervals confirms the casual observation that long periods of predator inactivity occur.

Using a more complex arena, the effects of the distribution and arrangement of the ovae on plants are examined. The functional responses to individual ovae on the edges of the leaves and to clumps of ovae on the centre of the leaves are examined, as well as the predation when both distributions are offered. Predictions based on the functional responses to the individual prey arrangements give a poor description of the observed predation when both arrangements are used. Continuous observations reveal that the anthocorids, by the end of the 20 hour experimental period, search to a greater extent in the areas of highest prey density.

A computer simulation programme is developed to imitate predator searching behaviour. The programme is able to mimic and extend some of the observed behaviour.

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INTRODUCTION

The interactions of polyphagous predators with their prey are complex, and so, it is necessary to abstract simple components of such an interaction and study them individually. The simplest interaction which can be abstracted is that involving one predator species and one prey type. This simple situation can be further broken down into components by considering the effects of the density, distribution, and arrangement of the prey, and the density and life-stage of the predator. The next stage in understanding the complex interactions of polyphagous predators and their prey is to consider the effects of the presence of two prey types. This is the main theme of this work.

In view of the relative simplicity of the single prey type interaction, most previous work, as can be seen from the literature review in Chapter 1, has been on interactions of this form. In spite of this, some aspects of the single prey type interaction merit further consideration, and hence, in Chapter 2 various aspects of the functional response are considered, while in Chapter 4 the effects of prey distribution on the functional response are examined.

Because of the complexity of predator-prey interactions with several prey types, two simple abstractions involving two prey types are examined in this work. In Chapter 3, the more simple arrangement is used, of a predator searching in an homogeneous environment for two size classes of prey. If the predation of the two prey types can be predicted from the individual functional responses, then this approach can be extended to higher levels of complexity. In Chapter 5, a more complex situation is examined. Within a relatively heterogeneous environment two parts contain prey: in one part, which is easily and readily searched, prey are widely spaced, while in an alternative area, less easily or readily searched, prey are highly aggregated. Thus, in these

two chapters, the ability of predators to select larger (and, therefore, energetically more rewarding) prey within an homogeneous arena, and the ability to select the most rewarding part of an heterogeneous arena are examined.

The use of computer simulation models in ecology is rapidly increasing, and one area where they are of relevance is predator-prey interactions. In Chapter 6, a simulation model is developed which is used to model predator searching behaviour and hence examine the effects of using various search strategies, prey distributions and combinations, upon the functional and aggregative responses.

CHAPTER 1

LITERATURE SURVEY

1.1 INTRODUCTION

In this section, the previous work of relevance in the field of predator-prey interactions is examined. As intimated in the Introduction, much of this previous work has dealt with interactions involving only one species, and, accordingly, this situation predominates in the following survey. The literature is, here, divided into three categories:

Functional Responses (Section 1.2) introduces the various types of functional responses and the derivations of the models of the normal, type II response are dealt with in some detail. This leads up to the work of Chapter 2, where further aspects are considered and models of non-type II responses examined and proposed. Further models are also developed in Chapter 3.

Preference and Switching (Section 1.3) covers previous work in the field of polyphagy. Various models/indices of preference are examined, including the model which is used in Chapter 3. The evolution of the functional response models to incorporate two prey types is examined, and the resultant models are used in Chapters 3 and 5. The previous work on switching, together with the theories of bird foraging strategies, summarized here, are also of relevance to these two chapters.

The Effects of Aggregation of the Prey (Section 1.4) refers, in particular, to its effects upon predation. Both behavioural observations and theoretical considerations are covered. These provide the background for Chapter 4 and, to a lesser extent, Chapters 5 and 6.

1.2 FUNCTIONAL RESPONSES

1.2.1 Introduction

Solomon (1949) introduced the terms 'functional response' and 'numerical response' to describe two components of predator-prey (and host-parasitoid) interactions. A functional response describes the change in the number of prey killed per predator (or hosts attacked per parasitoid) in response to the prey (or host) density, while a numerical response describes the change in the predator (or parasitoid) reproductive rate in response to prey (or host) density. Through use, the term functional response has tended to become restricted in meaning (Murdoch, 1973) and, as now used, is usually applied to the results from experimental arrangements, such as those described in Chapters 3, 4 & 5, in which the predator (or parasitoid) searches for a fixed time interval, in a restricted area, for a range of prey (or host) densities.

The principal difference between a predator-prey and a host-parasitoid interaction is that predators remove the prey by eating them whereas after parasitization hosts remain present. This means that the prey become unavailable for further predation but hosts continue to be available for parasitization. If each encounter is taken to be instantaneous, the resultant numbers of prey eaten and hosts parasitized will be described by the same model. Once an allowance is made for the time taken to encounter a prey or host, different models will be necessary. This difference is demonstrated in the discussion of models in Section 1.2.2.

Holling (1959a) recognised three distinct types of functional response (Fig. 1.1), although others have since been found (Section 1.2.3). The 'normal' or type II response has been reported and modelled most frequently. Some of these models are reviewed in Section 1.2.2; the type III response, and two other responses which do not fit into the Holling classification, are briefly introduced in Section 1.2.3 and considered in more detail in Sections 2.3 and 2.4.

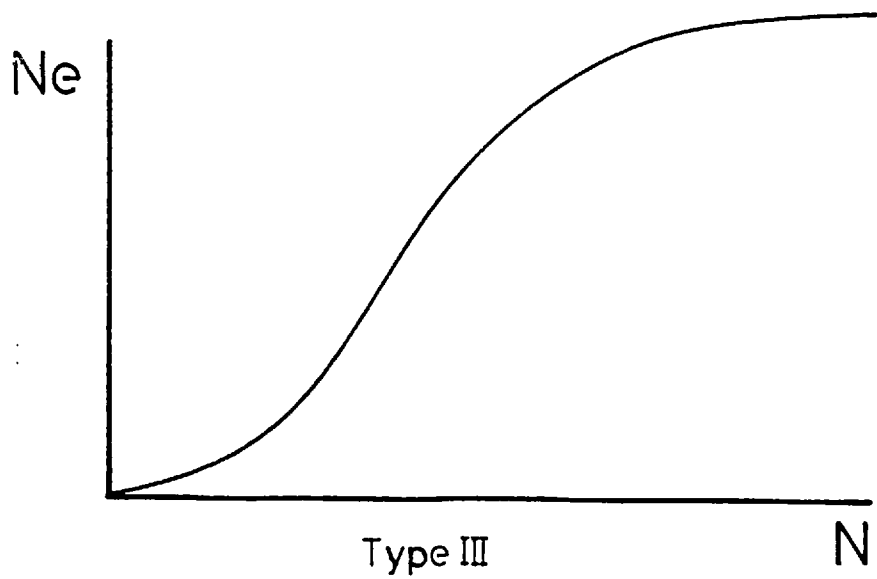
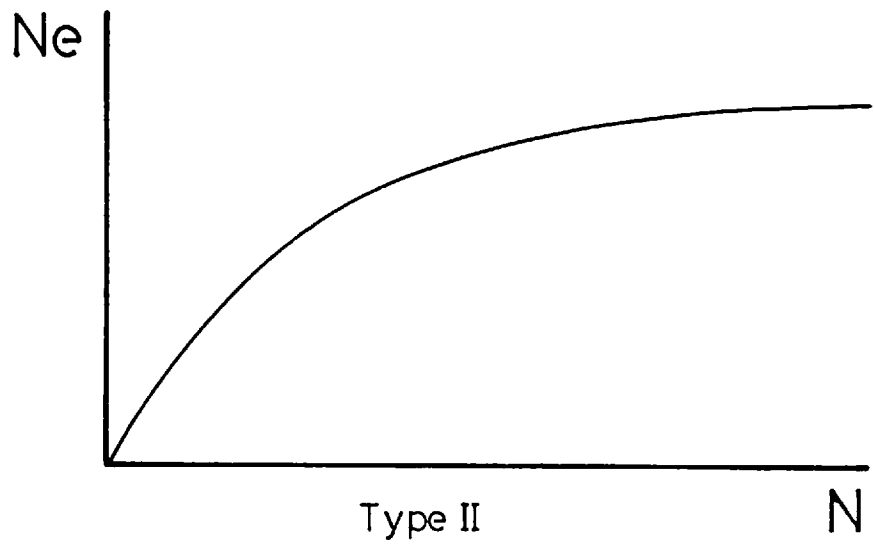
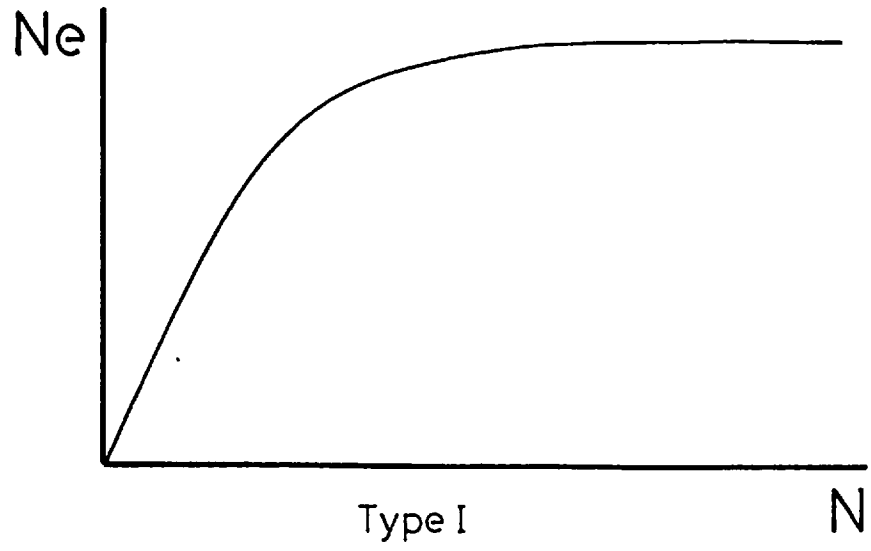


FIGURE 1.1 Classification of functional responses after Holling (1959a).

1.2.2 Type II Functional Responses

There are a number of models of the type II functional response. The models of Thompson (1924), Nicholson & Bailey (1935), Holling (1959b), Rogers (1972) and Griffiths & Holling (1969) will be reviewed in this section. Royama (1971) has reviewed these and other models, including those of Ivlev (1961), Hassell & Varley (1969) and Watt (1959).

The models of Thompson (1924, 1939) and Nicholson & Bailey (1935) are of a similar form. Both formulate the average number of encounters per 'prey-position' or host which will occur in the time available, and distribute these attacks at random amongst the 'prey-positions' or hosts. 'Prey-position' will be used in this work to refer to the position of a prey, which, once that prey has been eaten, can be searched again. The encounters, if distributed at random, will generate a Poisson distribution of the frequency of encounter per 'prey-position' or host (Fig. 1.2). Knowing this, the frequency with which a given 'prey-position' will be searched (or host attacked) n times is given by the standard equation (e.g. Southwood, 1966):

$$\frac{Nenc_n}{N} = \exp\left(\frac{-Nenc}{N}\right) \cdot \left(\frac{(Nenc/N)^n}{n!}\right) \quad \dots 1.2.1$$

where $Nenc_n$ is the number of 'prey-positions' searched n times per predator (or hosts attacked n times per parasitoid), $Nenc$ is the total number of encounters per predator (or attacks per parasitoid), and N is the initial prey (or host) density. Using Eqn. 1.2.1, the frequency with which a prey (or host) escapes detection for the whole time period can be found:

$$\frac{Nenc_0}{N} = \exp\left(\frac{-Nenc}{N}\right) \cdot \left(\frac{(Nenc/N)^0}{0!}\right) = \exp\left(\frac{-Nenc}{N}\right) \quad \dots 1.2.2$$

and hence, the number of prey eaten (or the number of hosts attacked) is defined by the number of 'prey-positions' searched (or hosts attacked) one or more times:

$$Na = Ne = N(1 - \exp(-P Nenc/N)), \quad \dots 1.2.3$$

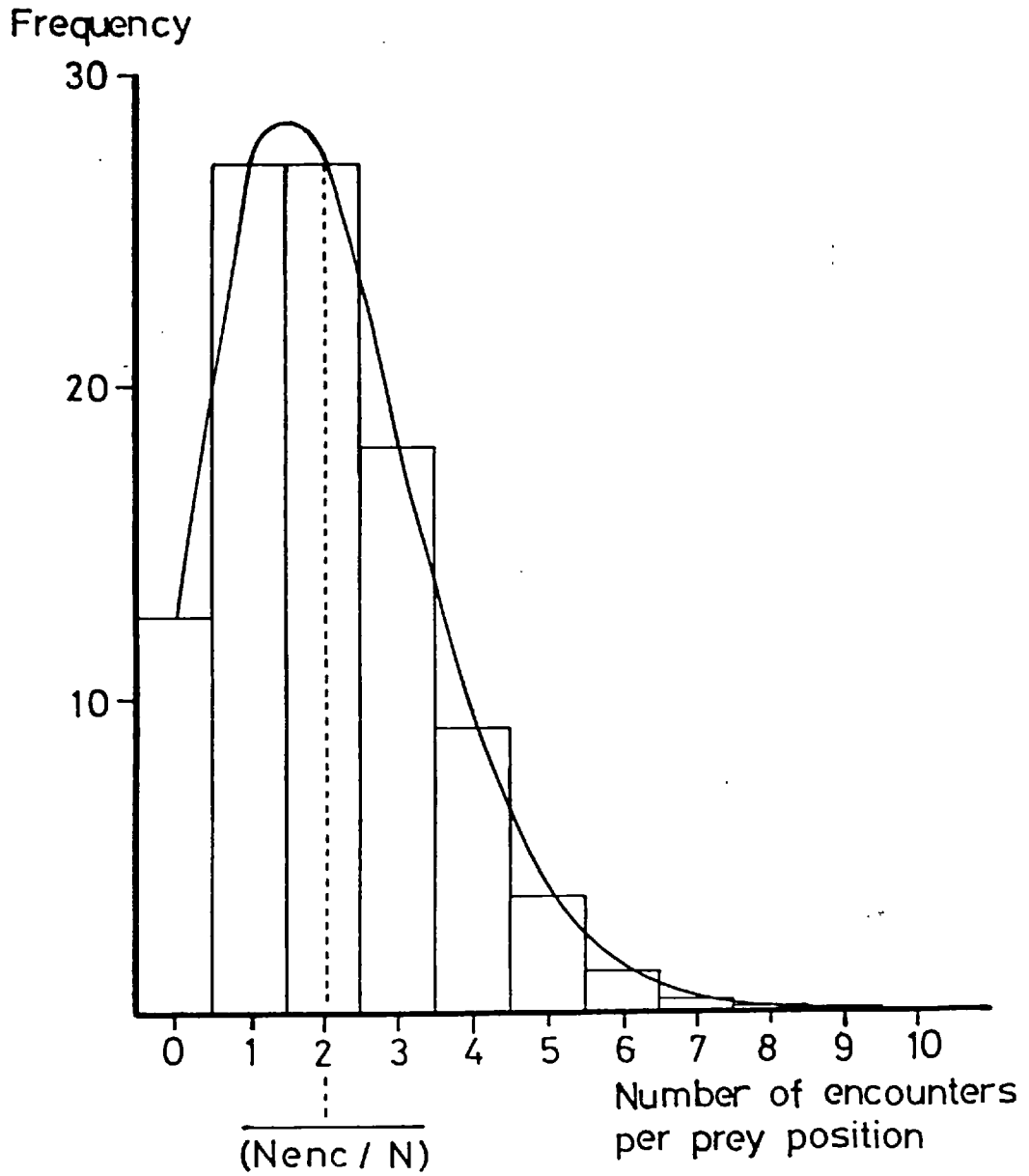


FIGURE 1.2

An example of a Poisson distribution of the frequency of encounter per prey-position or host. In this case, 200 encounters are distributed amongst 100 prey-positions, and 13.4 prey escape detection.

where N_a is the number of hosts attacked, N_e is the number of prey eaten and P is the number of predators (or parasitoids).

The models of Thompson and Nicholson & Bailey differ in the formulation of the term $-P N_e/N$. Thompson, whose model is applicable to host-parasitoid interactions only, suggests that the number of attacks made by a parasitoid is determined by the number of eggs it can lay, and that all parasitoids lay all their eggs. Therefore, if the average number of eggs laid per parasitoid is N_x , substitution in Eqn. 1.2.3 gives:

$$N_a = N(1 - \exp(-P N_x/N)).$$

Nicholson & Bailey, however, define the number of encounters in terms of the 'area of discovery', an approach which can be applied to both predator-prey and host-parasitoid interactions. Nicholson (1933), in describing the searching behaviour of parasitoids, introduced the term 'area of discovery'. This he described as the total area searched, under the given conditions, by an average individual during her lifetime. In modelling functional responses, the animal's lifetime can be taken as the period of the experiment. Since the parasitoid (or predator) is assumed to search at random, it will search some areas more than once, and so, as the 'area of discovery' increases, the proportion of the total area searched (one or more times) will asymptotically approach unity. Nicholson (1933) called this relationship (Fig. 1.3) the 'competition curve'. The number of encounters with prey-positions per predator (or hosts per parasitoid) is now defined as the product of the 'area of discovery', the number of prey-positions (or hosts) and the number of predators (of parasitoids). Substitution in Eqn. 1.2.3 gives:

$$N_a = N_e = N(1 - \exp(-A N P/N)) = N(1 - \exp(-A P)),$$

. . . 1.2.4

where A is the 'area of discovery'. Although Nicholson & Bailey do not formally state Eqn. 1.2.4, it can be readily obtained from their work by substitution.

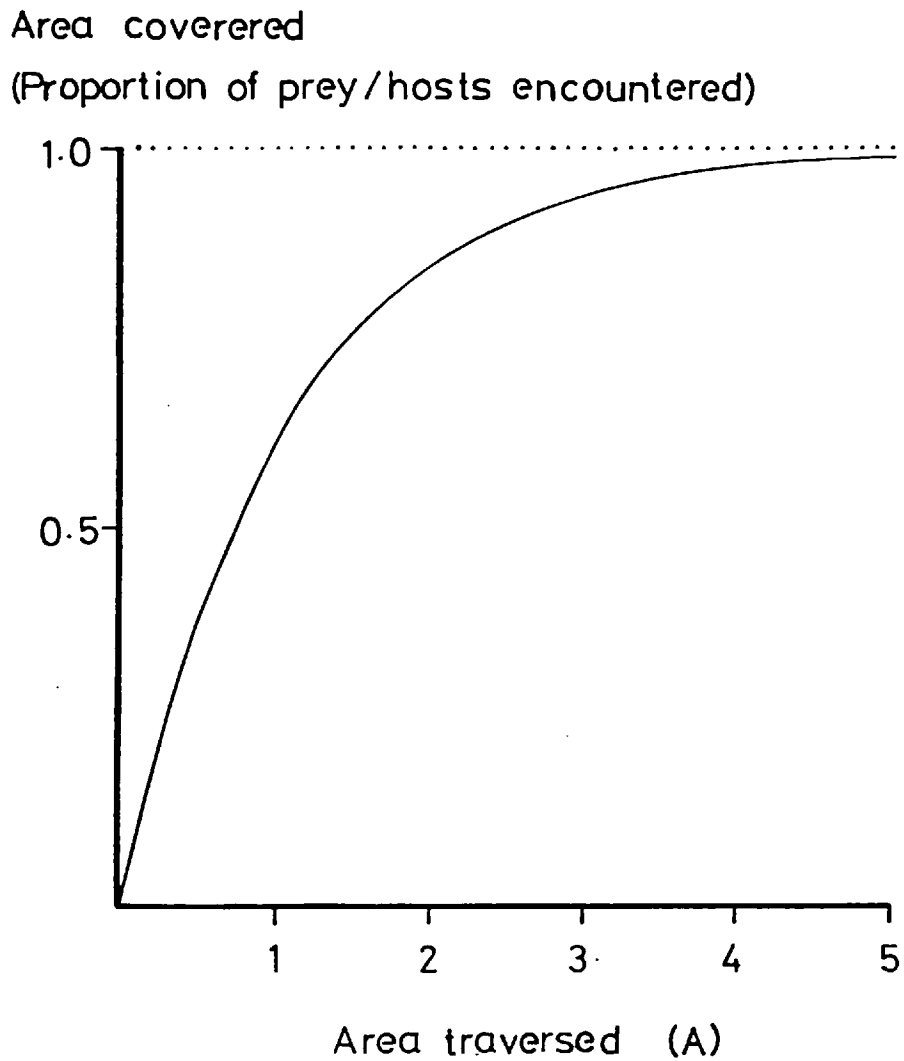


FIGURE 1.3 The competition curve of Nicholson (1933). This shows the relationship between the 'area of discovery' (A) and the proportion of the area searched one or more times.

The number of encounters (N_{enc}) and the number of prey eaten (N_e) (or hosts attacked, N_a) as functions of the prey density, and the logarithm of the proportion of prey (or hosts) surviving as a function of the number of prey eaten, are plotted in Fig. 1.4 for the models of Thompson and Nicholson & Bailey. It can be seen that for the Nicholson & Bailey model, the number of encounters and the number of prey eaten are proportional to the prey density (slope of the former = AP , and of the latter = $1 - \exp(-AP)$), and hence, a constant proportion of the prey survives. In the case of Thompson's model, however, the number of encounters is constant, irrespective of prey density and is defined by the number of eggs laid per parasitoid. This means that the number of hosts attacked levels off at this value, giving a type II functional response. At low prey densities, a large number of eggs is distributed amongst a small number of hosts, leading to a small proportion of hosts surviving (Fig. 1.4F).

Holling (1959b) described a simulation experiment, in which a blindfolded subject, by tapping with a finger, searched for sandpaper discs pinned upon a square table. Whenever a disc was found, it was removed from the table. The functional response thus obtained was a 'normal' type II response, and Holling deduced that the levelling off was due to the time necessary to remove each disc leading to a maximum rate at which the discs could be removed. To describe these results, Holling deduced an equation which has become known as the Disc Equation. To do so, he defined the situation:

$$N_e = a P T_s N, \quad \dots 1.2.5$$

where a is the 'instantaneous rate of discovery' (i.e. the proportion of the area searched in unit time; this is equivalent to A/T) and T_s is the time available for searching. This definition is not accurate, since no allowance is made for exploitation of the prey (or host), a point which will be discussed below. The time available for searching will be reduced by the time taken to 'handle' prey (or hosts):

$$T_s = T - T_h N_e, \quad \dots 1.2.6$$

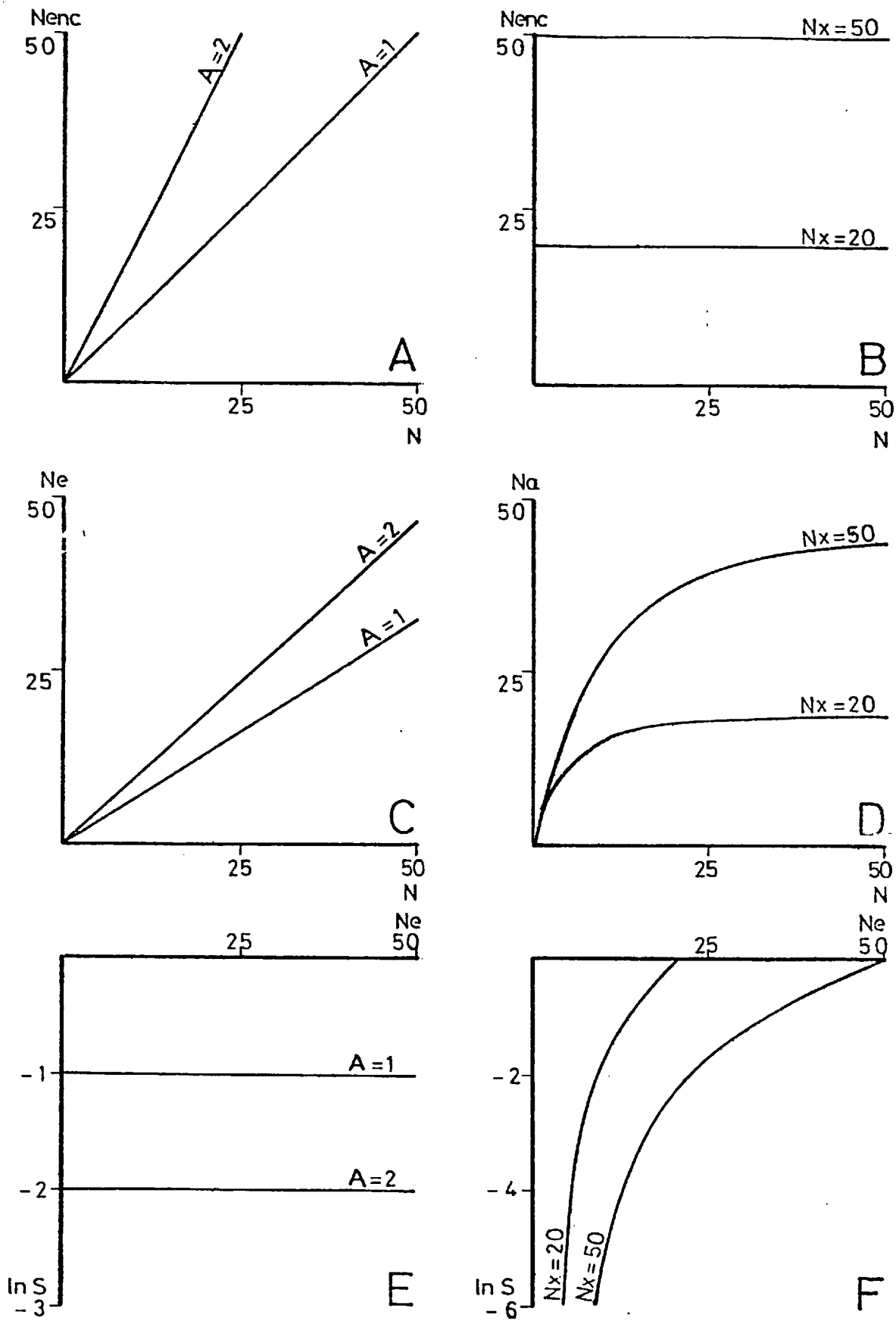


FIGURE 1.4 Figures to demonstrate the models of Nicholson & Bailey (1935) (A, C & E) and Thompson (1924) (B, D & F).

where T_h is the handling time for each prey and T is the total time of the experiment. The handling time, T_h , is taken as the total time made unavailable for searching by the removal of a prey (or parasitization of a host), and can include such elements as identification time, digestive pause, grooming, and time lag until the next egg is ready to be laid. T_s , as defined in Eqn. 1.2.6, can now be substituted in Eqn. 1.2.5 to give:

$$N_e = a P N(T - T_h N_e),$$

which rearranges to give the Disc Equation:

$$N_e = a P T N / (1 + a P T_h N). \quad \dots 1.2.7$$

Holling used the Disc Equation to describe several published functional responses, and, by abstracting the parameters a and T_h , obtained good descriptions of the experimental data.

However, as mentioned above, Eqn. 1.2.5 can not be considered a suitable description of searching behaviour. The prey density does not remain constant during a predator-prey interaction, because prey are removed by predation. Similarly, the density of unparasitized hosts changes as parasitization occurs, and Eqn. 1.2.5 should thus be written as :

$$N_{enc} = a T_s N, \quad \dots 1.2.8$$

where N_{enc} is the number of encounters, with prey-positions or hosts. Since the predator (or parasitoid) searches at random, these encounters can then be distributed amongst the prey-positions or hosts, by the same reasoning as for the models of Thompson and Nicholson & Bailey. Substitution can now take place for $P N_{enc}/N$ in Eqn. 1.2.3. A difference between predator-prey and host-parasitoid interactions now becomes important. $P N_{enc}/N$ can be defined for a predator by substituting Eqn. 1.2.6 into Eqn. 1.2.8 and rearranging to give:

$$P N_{enc}/N = a P(T - T_h N_e),$$

which can be substituted in Eqn. 1.2.3 to give:

$$N_e = N(1 - \exp(- a P(T - T_h N_e))). \quad \dots 1.2.9$$

For a host-parasitoid interaction, however, Eqn. 1.2.6 is not suitable; at each encounter T_h is used. Therefore, T_s should be defined as:

$$T_s = T - T_h N_{enc},$$

which can be substituted into Eqn. 1.2.8, and rearranged to give:

$$N_{enc}/N = a T / (1 + T_h N).$$

This can be substituted into Eqn. 1.2.3:

$$N_a = N(1 - \exp(- a P T / (1 + a T_h N))) \dots \dots \dots 1.2.10$$

Rogers (1972) derives Eqns. 1.2.9 and 1.2.10 which he calls the Random Predator Equation and the Random Parasite Equation.

Royama (1971) derives Eqn. 1.2.10 as above, but obtains Eqn. 1.2.9 in a different manner. Since Eqn. 1.2.5 and hence Eqn. 1.2.7 are correct if the instantaneous number of prey present, N , is correct, these equations can be considered as instantaneous equations for the predation rate. Therefore, the Disc Equation (Eqn. 1.2.7) can be written in the differential form as:

$$dN/dT = -a P N / (1 + a P T_h N), \dots \dots \dots 1.2.11$$

where dN/dT is the rate of change of prey density, which, since prey density is decreasing, causes the minus sign in front of the right hand side of the equation. Equation 1.2.11 can now be integrated with respect to N , over the period T :

$$\begin{aligned} N_e &= \int_{T=0}^{T=T} (- a P T N / (1 + a P T_h N)) dN \\ &= N(1 - \exp(- a P(T - T_h N_e))) \end{aligned}$$

which is the Random Predator Equation (Eqn. 1.2.9).

The Random Predator Equation (Eqn. 1.2.9) and the Random Parasite Equation (Eqn. 1.2.10) provide a good, simple description of the type II functional response, based on random search by predators and parasitoids, and constant values of the parameters for search efficiency and handling time.

The models considered so far have been based on a random (or Poisson) distribution of attacks. Griffiths & Holling (1969) suggest a model for a host-parasitoid interaction based on a negative binomial distribution of attacks. For such a distribution to be suitable, some hosts must be more likely to be found than others; hence they will have disproportionately more attacks than would be expected if the parasitoids searched at random. However, whereas the Poisson distribution is described by only one parameter (the mean), the negative binomial is described by two (the mean and K, an index of aggregation which varies from infinity to zero with increasing aggregation).

The equation corresponding to Eqn. 1.2.1 (for the Poisson distribution) is, for the negative binomial (Bliss, 1953):

$$\frac{Nenc_n}{N} = \frac{(K + n - 1)! (m/(K + m))^n}{n! (K - 1)! (1 + m/K)^K},$$

where m is the mean number of attacks per host (i.e. Nenc/N). Hence, the equation corresponding to Eqn. 1.2.2 (for the Poisson distribution) is:

$$\frac{Nenc_0}{N} = \frac{(K + 0 - 1)! (m/(K + m))^0}{0! (K - 1)! (1 + m/K)^K} = (1 + m/K)^{-K},$$

and substituting Nenc/N for m:

$$Nenc_0 / N = (1 + Nenc/N K)^{-K}.$$

Hence, the number of hosts attacked can be formulated:

$$Na/N = (1 - Nenc_0 / N) = 1 - (1 + Nenc/N K)^{-K},$$

and therefore:

$$N_a = N - N(1 + N_{enc}/(N K))^{-K} \quad . . . 1.2.12$$

To test the negative binomial distribution of attacks, Griffiths & Holling fitted it to thirty sets of data of the frequency distribution of eggs of the ichneumonid, Pleolophus basizonius, parasitizing the sawfly, Neodiprion sertifer. Comparing the fit obtained by this method with that obtained using the Poisson distribution, they found that the negative binomial gave a better fit to more sets of data. This effect was more marked when just the zero and greater than zero frequency classes were considered. However, since two parameters are estimated from the data in fitting the negative binomial distribution, and only one in fitting the Poisson, the better fit obtained using the former distribution is not very surprising. To use Eqn. 1.2.12 as a model for the functional response assumes that K has a constant value. In order to test this, Griffiths and Holling plotted K against the number of eggs laid per host offered, and found that the regression did not differ significantly from zero, showing that K is not affected to any great extent by the number of attacks. However, examination of the values of K in Table IV in Griffiths & Holling (1969) shows that K varies widely. They fitted this model to the distribution of attacks to data from a number of published host-parasitoid interactions and obtained good fits. Rogers (1972), however, pointed out that the host-parasitoid interactions quoted are suspect. Due to the confined experimental conditions, many of the parasitoids, which normally avoid superparasitism, were induced to exhibit this behaviour.

Griffiths & Holling used the Disc Equation (1.2.7) to substitute for N_{enc}/N in Eqn. 1.2.12, giving the functional response equation:

$$N_a = N \left[1 - \left(1 + \frac{a P.T}{(1 + a Th N)K} \right)^{-K} \right] \quad . . . 1.2.13$$

This was criticized by Rogers (1972) on the grounds that, having demonstrated that eggs are distributed in a non-random manner,

Griffiths & Holling assume that the parasitoid searches at random when they generate the number of attacks to substitute into Eqn. 1.2.12. Thus, Eqn. 1.2.13 is unsuitable as a functional response model. The use of the negative binomial to distribute attacks amongst hosts could prove suitable in some cases. It seems likely that parasitoids will restrict their searching, and that some hosts will be more obvious. The major drawback to this approach is the formulation of the term N_{enc}/N of Eqn. 1.2.12, if non-random search is assumed. The work of Thompson (1924) suggests one solution; if the number of encounters is defined by the number of eggs laid by the parasitoid (N_x), substitution in Eqn. 1.2.12 gives:

$$N_a = N - N(1 + N_x/(N K))^{-K}$$

The negative binomial distribution of attacks could also be applied to a predator showing aggregative behaviour (Section 1.4), but the difficulty of formulating the term N_{enc}/N makes this approach difficult to apply.

1.2.3 Other Functional Responses

Although the Holling type II functional response is probably the most widely found, other types of response have been predicted and recorded.

Sigmoid, or Holling type III, functional responses (Fig. 1.1c) were recorded by Holling (1959a) when small mammals fed on sawfly cocoons. The experimental arrangement differed from that normally used in that an excess of a less preferred alternative food (dog biscuits) was always present. Hassell, Lawton & Beddington (1977) give further examples and suggest a possible model. This model is examined and one of related form is used in Chapter 3 (Section 3.3.2).

The dome shaped functional response (Fig. 1.5A) was first found by Welty (1934), who considered it to be due to a confusion effect. He suggested that, when several prey are present simultaneously in the field of vision of a fish, feeding is inhibited. Mori & Chant (1966) also found a dome shaped response for a predatory mite, but concluded that this was due to interference with the predator by the prey at high densities. Holling (1965) on the basis of some assumptions about learning, predicted dome shaped functional responses to distasteful prey. Reeve (pers. comm.) and Williams (pers. comm.) both found dome-shaped responses in aquatic systems. The latter example (see Section 2.4.3.1) was thought to be due to confusion effects.

Complex or 'stepped' functional responses (Fig. 1.5B) have been found by Haynes & Sosojevic (1966), Sandness & McMurty (1970) and Savan (pers. comm.). Hassell, Lawton & Beddington (1976) pointed out that the example of Haynes & Sosojevic is adequately described by the Random Predator Equation.

Rogers (pers. comm.) suggests a model for varying the parameters of the Random Predator Equation. This model, and the functional responses introduced above, are examined in Chapter 2 (see Sections 2.3 & 2.4).

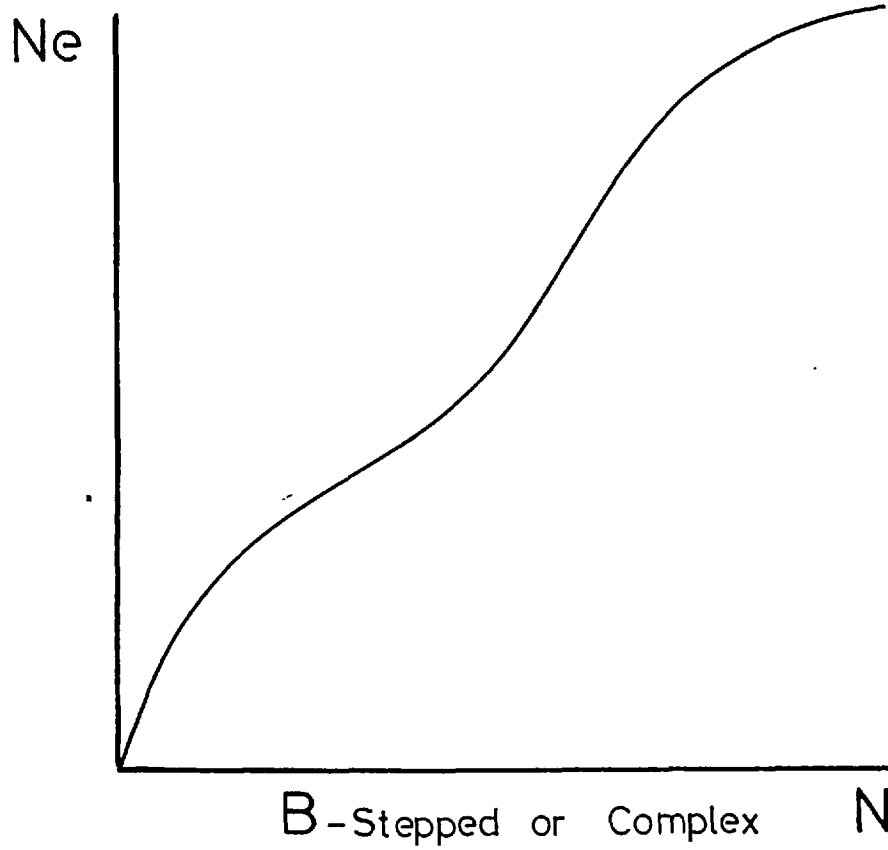
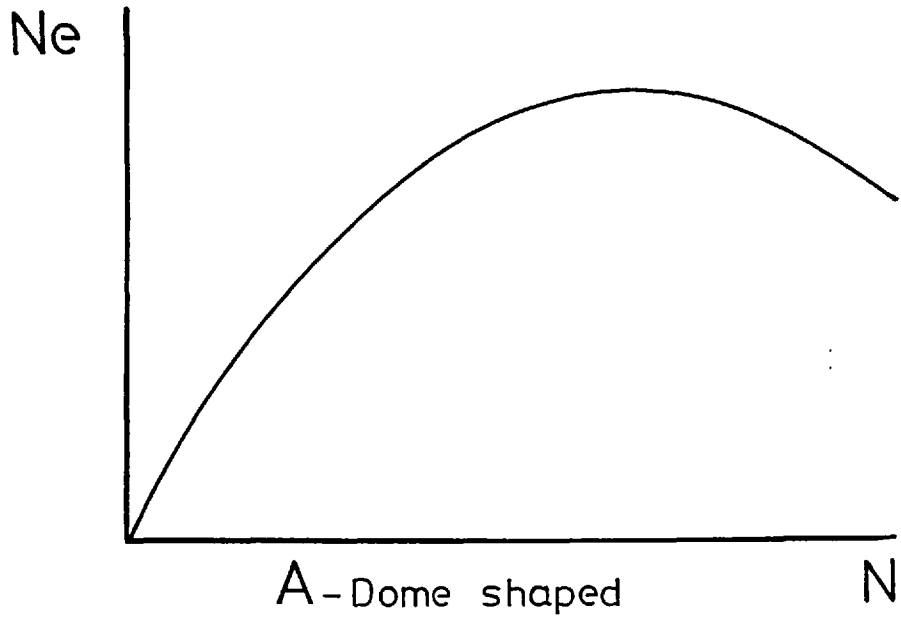


FIGURE 1.5 Two types of functional response which do not fit into the classification of Holling (1959a).

1.3 PREFERENCE AND SWITCHING

1.3.1 Introduction

Animals may show a hierarchy of preference towards different food types. This can occur for various reasons; for example a food type may be easier to find and capture, or it may provide a richer food source, and as a result animals will concentrate on finding and feeding upon that food type. However, if a preferred food type becomes scarce, there will arise a point at which it is no longer feasible to concentrate on that type, and the animal will switch to the most suitable alternative food. Conversely, if a formerly scarce, preferred prey becomes common, animals will change over to that food type. This phenomenon is called switching and has been commonly found in vertebrates. The term switching was introduced by Elton (1927) as a contributory factor in the regulation of animal numbers; since as a food type becomes too scarce for its consumers to feed upon it, it will have the opportunity to recover in numbers, whilst as it becomes common more animals will switch to it, and so reduce its numbers.

More recently, ecologists have looked for preference and switching in invertebrate predators (Murdoch, 1969; Murdoch & Marks, 1973; Lawton, Beddington & Bonser, 1974) and, in some cases, have found evidence of such behaviour.

The cases examined can be divided into two types: those in which an homogenous mixture of prey is available and those in which different prey types occupy different parts of the habitat. The former arrangement is used in Murdoch (1969), Murdoch & Marks (1973), Lawton, Beddington & Bonser (1974) and in Chapter 3 of this work, whilst the latter arrangement is used in Ivlev (1961), Murdoch, Avery & Smyth (1975) and Chapter 5 of this work. Tinbergen (1960) proposed an hypothesis which would make the occurrence of preference and switching equally likely in either case, whereas the work of Royama (1970a)

suggests that this behaviour will be more readily found in the latter case (see Section 1.3.5).

In this section on preference and switching, some methods for measuring preference will be examined in Section 1.3.2; the possibility of predicting preference from functional response data will be covered in Section 1.3.3, the published models and examples of switching will be reviewed in 1.3.4, and the theories of Tinbergen and Royama and the effects of spatially separated prey types will be examined in 1.3.5.

1.3.2 Indices of Preference

In order to evaluate the effects of preference, some method of quantifying it is necessary. A number of different methods and indices have been used in the past. These will be described and discussed to show their drawbacks, and to indicate that many of them are basically similar, although often introduced in new forms or as new methods.

In interpreting these methods, the following symbols will be used:

- Ne - number of prey type I eaten
- Ne' - number of prey type II eaten
- N - number of prey type I present in the environment
- N' - number of prey type II present in the environment
- Se - total number of prey eaten; for the two prey situation = $Ne + Ne'$
- S - total number of prey present in the environment; for the two prey situation = $N + N'$
- C - index of preference; subscripted symbols refer to the various indices.

Further symbols are introduced and defined in the text as necessary.

Scott (1920) measured preference by the term (N_e/N) , the ratio of food items in the diet to food items in the environment. The former was measured as numbers per unit time (dimension T^{-1}), whilst the latter was measured as numbers per unit area (dimension L^{-2}), resulting in an index, which should have been dimensionless, having dimensions of $L^2 T^{-1}$. No measure of the total food eaten or available is incorporated in this index, and so, it can not give any real estimate of preference. This measure does not seem to have been used since.

Savage (1931) defined the index:

$$C_S = (N_e/S_e) / (N/S).$$

Positive preference causes the value of this index to increase from unity to infinity, which can be difficult to interpret. Shorygin (1939), Greze (1939), and Ivlev (1961) all independently re-established this index. It has since been used by Menge (1974).

Larsen (1936) used the reciprocal of C_S :

$$C_L = (N/S) / (N_e/S_e).$$

This has the disadvantage that as preference increases, the value of the index decreases from one to zero. The small range, however, is easier to use than the index of Savage (C_S).

Ivlev (1961) developed a more sophisticated index of the form:

$$C_I = \frac{(N_e/S_e) - (N/S)}{(N_e/S_e) + (N/S)}$$

This index will vary from zero to minus one for increasing negative preference; and from zero to plus one for increasing positive preference. As such, it is much easier to use and to understand. Due to the different scale, the index is more sensitive to slight preference. However, as Landenberger (1968)

has pointed out, the maximum (or minimum) value attainable for C_I varies with the prey ratio in the environment. For example, if five of each of prey types I and II are present, the greatest preference which could be shown for prey type I (i.e. all of prey type I eaten and none of prey type II) would result in a value for C_I of 0.33 ($C_I = (1 - 0.5) / (1 + 0.5)$), whereas, if two of prey type I and eight of prey type II are present, the greatest preference which could be shown for prey type I would result in a value for C_I of 0.67 ($C_I = (1 - 0.2) / (1 + 0.2)$). Thus, preferences calculated using this index for different prey ratios are not directly comparable. The proportion of the maximum attainable value for each ratio could be compared, but this is rather cumbersome.

Murdoch (1969) defined an index to measure preference:

$$C = (N_e/N_e') / (N/N'). \quad . . . 1.3.1$$

This has a similar disadvantage to the index introduced by Savage in that the scales are again awkward to handle; one to zero for negative preference and one to infinity for positive preference. This index is less sensitive to slight preference than that of Ivlev, because of the scale used.

Jacobs (1974) considered two previously proposed indices and suggested two new ones. Firstly, he referred to "the so-called Forage Ratio". He gave no references for the term; there do not seem to be any. He defined it as, in the symbols used here:

$$\text{Forage Ratio} = (N_e/S_e) / (N/S) = C_S,$$

which is the index suggested by Savage (1931). Secondly, he derived the formula:

$$\text{Index} = \frac{(N_e/S_e) (1 - N/S)}{(N/S) (1 - N_e/S_e)} = C,$$

which, by substituting for S_e and S and by rearranging, can be shown to be identical to the index of Murdoch (C), and so, suffers from the same drawbacks. However, as Jacobs points out, this can be alleviated by taking the logarithm of the index. Negative preference would then vary from zero to minus infinity, and positive preference from zero to plus infinity. The second index, based on that of Ivlev, he defined as:

$$C_J = \frac{(N_e/N_{e'}) - (N/N')}{(N_e/N_{e'}) + (N/N')} .$$

This index, like that of Ivlev (C_I), varies from zero to minus one for negative preference, and from zero to plus one for positive preference; unlike that of Ivlev, its maximum values are not defined by the ratio of the prey types available.

Population geneticists, studying the maintenance of polymorphisms, have also approached this problem. Cain & Sheppard (1950, 1952, 1954, etc.) worked on the selection of colours and patterns in Cepaea nemoralis by predatory birds (e.g. thrushes). In presenting their data, they did not formalize an index as such, but they did compare the ratio of the prey types in the diet with the ratio in the environment. This is equivalent to the index introduced by Murdoch (1969). Kettlewell (1957 etc.) presented his results on predator selection of the Peppered Moth, Biston betularia in a similar manner.

Elton & Greenwood (1970) suggested a mathematically derived description of preference and switching. In the absence of switching, this model is of the form:

$$(N_e/N_{e'}) = (N/N') \cdot (v/v') , \quad . . . 1.3.2$$

where v and v' are the visibilities of the two species to the predator. As used, the ratio v/v' is equivalent to the preference index of Murdoch (C). The adaptation of this model to describe switching is described in Section 1.3.4.

Another relationship was proposed by Manly, Miller & Cook (1972):

$$\text{Prob} = \text{Ne}/\text{Se} = N/(N + \alpha' N'), \quad . . . 1.3.3$$

where Prob is the probability of the next prey being of type I (which is equivalent to Ne/Se), and α' is an index of preference to prey type II. Solving for α' gives:

$$\alpha' = (N/N') / (\text{Ne}/\text{Ne}') = 1/C. \quad . . . 1.3.4$$

Hence, if the preference towards type I is the reciprocal of the preference towards type II, this index is, once again, equivalent to that proposed by Murdoch (C). They also pointed out that, if prey are offered in equal numbers, Eqn. 1.3.3 will take the form:

$$\text{Prob} = 1/(1 + \alpha') = C_M,$$

where C_M provides another measure of preference. For this index, positive preference will give values varying from 0.5 to 1.0, and negative preference will give values from 0.5 to zero. This means that it can be readily understood.

Tinbergen (1960), studying predation by small insectivorous birds in the field, approached this problem from a slightly different angle. He defined a model which, for two prey types, takes the form:

$$(\text{Ne}/\text{Se}) = r N / (r N + r' N'), \quad . . . 1.3.5$$

where r and r' are the 'risk indices' of the two prey types. The risk index is defined as the instantaneous rate of capture per prey individual ($\text{Ne}/N T$). Rearranging Eqn. 1.3.5 gives:

$$(\text{Ne}/\text{Ne}') = (N/N') \cdot (r/r'), \quad . . . 1.3.6$$

showing that r/r' is equivalent to the index of Murdoch (C).

This model will be returned to in Section 1.3.3. The searching image hypothesis of Tinbergen and the work of Royama will be discussed in Section 1.3.5.

Rapport & Turner (1970) proposed a model of preference based on the use of 'standard prey densities'. This term they defined as the minimum density of prey at which the predator can obtain its food requirements. To measure food requirements, the most feasible approach is to take the upper asymptote of a functional response. This, however, makes estimation of the standard density subject to large errors. In Fig. 1.6A, it can be seen that a small error in estimating food requirements at the asymptote, will lead to a large error in the standard density. This drawback seems unavoidable. The 'no preference' model assumes that, when two prey types are present at half their standard densities, the predator obtains half its food requirements from each:

$$\mu = (\mu' + \mu'') / 2, \quad . . . 1.3.7$$

where μ is the total consumption, and μ' and μ'' are the consumptions of prey types I and II at their standard densities. When preference occurs, Eqn. 1.3.7 can be written as:

$$\mu = (p' \mu' + p'' \mu'') / 2,$$

where the parameters p' and p'' are stated to "have an obvious interpretation", presumably the ratio of the observed consumption to the expected consumption. They continue by defining the preference for prey type I to prey type II, P_{12} , as the difference between p' and p'' . Since, due to the use of standard densities, p' and p'' will vary from zero to two, and sum to two, preference will vary from zero to minus two for negative preference and from zero to plus two for positive preference. If the predator has different functional responses to the two prey types, strong preference may result automatically. For example, if the two responses are as shown in Figs. 1.6B & C, strong preference will result for the second prey type. Although this model can be expanded to include more than two species of prey, the difficulties caused by its structure and interpretation

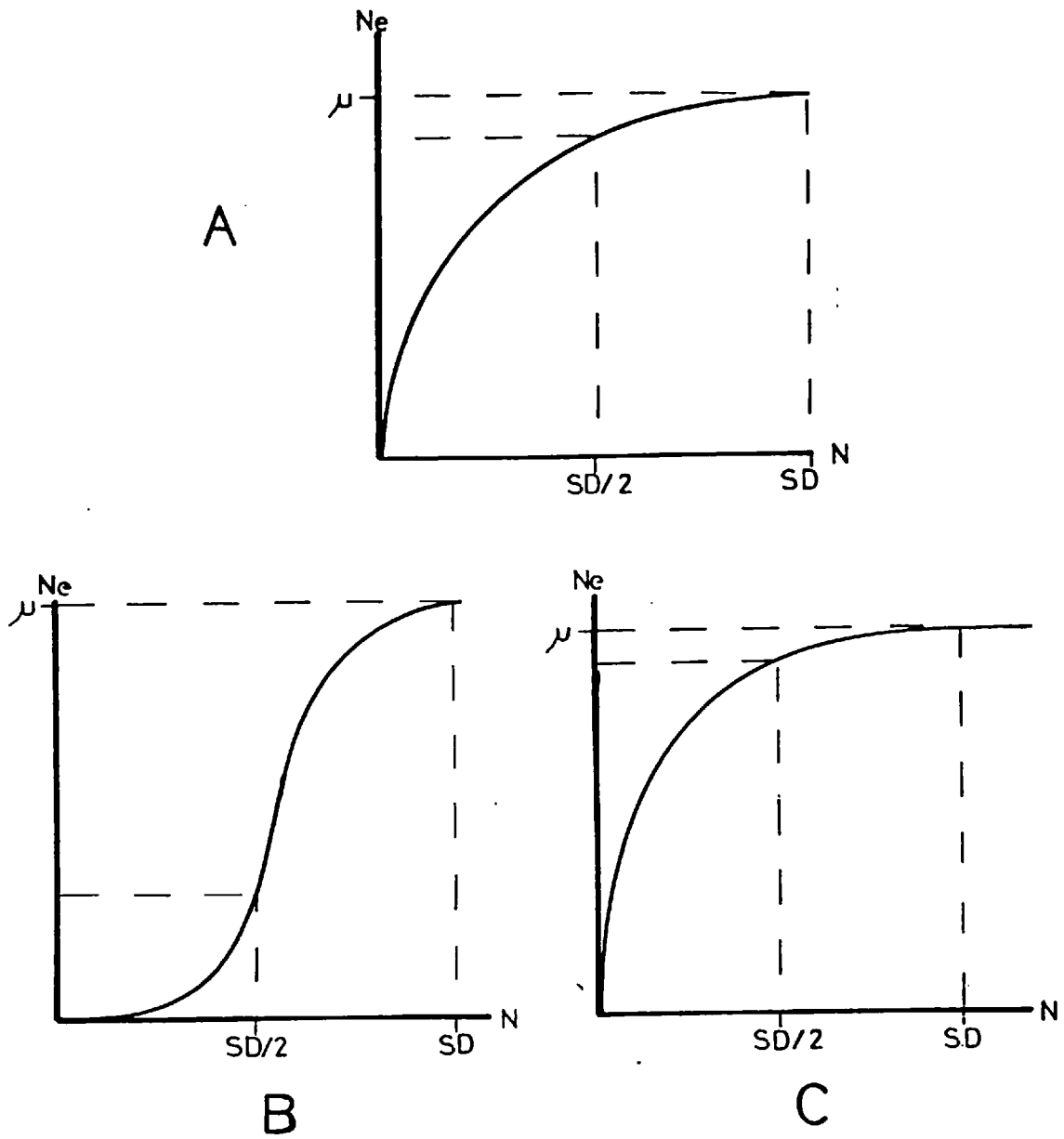


FIGURE 1.6 Hypothetical functional responses used in the interpretation of Rapport & Turner's (1970) model of preference (see text).

render it an unsuitable alternative to the models previously described. This approach has been used by Rapport, Berger & Reid (1972) studying food preference of Stentor coeruleus; but it does not seem to have been used elsewhere.

Of the methods used to describe preference, it can be seen that some are unsuitable (Scott, 1920) or difficult to apply (Rapport & Turner, 1970), Some have awkward ranges (Murdoch, 1969; Manly, 1973) and others are difficult to interpret due to their formulation (Ivlev, 1961; Jacobs, 1974).

The most widely used and readily understood method is to compare the ratio of the prey types found in the diet with the ratio of the prey types available in the environment. This is the method used by Cain & Sheppard (1950 etc.) and Kettlewell (1957). It was formally defined as an index by Murdoch (1969), and has also been introduced and defined in various forms by Tinbergen (1960), Elton & Greenwood (1970), Manly et al. (1972) and Jacobs (1974).

The index proposed by Jacobs (1974), C_J , has the advantage of varying from minus one to plus one as does that of Ivlev (1961), C_I . Jacobs' index does not suffer from the drawbacks of Ivlev's index (Landenberger, 1968), and so may prove to be a useful index.

1.3.3 Predicting Preference from Functional Responses

Murdoch (1969), in proposing his model of preference (Eqn. 1.3.1), suggested that an appropriate predation model could be used as a null hypothesis. In this section, the derivation of such a null hypothesis is shown.

Preference can be defined in terms of the search constants used in the Disc Equation of Holling (1959b):

$$N_e = a N T / (1 + a T h N),$$

where, as previously defined, N_e is the number of prey eaten, a is the instantaneous rate of discovery, N is the number of prey present, T is the total time available and T_h is the handling time for the prey (see Section 1.2.2). This, as pointed out by Murdoch (1973) and Lawton, Beddington & Bonser (1974), can be adapted for two prey types:

$$N_e = a N T / (1 + a T_h N + a' T_h' N'),$$

$$N_e' = a' N' T / (1 + a T_h N + a' T_h' N'),$$

where the primed symbols refer to a second prey type. Dividing the equation for N_e by that for N_e' gives:

$$N_e/N_e' = (a/a') N/N'.$$

This is analogous to Murdoch's model. Therefore, if exploitation is negligible, or prey are replaced as they are eaten, preference (C) can be defined as the ratio of the search constants for the two prey types (a/a'). This situation is similar to the preference models of Tinbergen (1960) (Eqn. 1.3.6) and of Elton & Greenwood (1970) (Eqn. 1.3.2). It can be seen that the risk index of Tinbergen (r) and the visibility of Elton & Greenwood (v) correspond to the instantaneous rate of discovery of Holling (a). Indeed, the definition of the risk index of Tinbergen ($r = N_e/N T$) is the same as that of the instantaneous rate of discovery.

As previously noted, however, exploitation of prey is often significant, making the Random Predator Equation (Rogers, 1972) (Section 1.2.2) more appropriate than the Disc Equation. This Random Predator Equation:

$$N_e = N(1 - \exp(- a(T - T_h N_e))),$$

can be adapted simply to the two prey form (Lawton, Beddington & Bonser, 1974):

$$N_e = N(1 - \exp(- a(T - T_h N_e - T_h' N_e')))) \quad \dots 1.3.8$$

$$N_e' = N'(1 - \exp(- a'(T - T_h N_e - T_h' N_e'))).$$

Dividing the equation for Ne by that for Ne' now gives:

$$\frac{N_e}{N_{e'}} = \frac{N}{N'} \cdot \frac{1 - \exp(-a T_s)}{1 - \exp(-a' T_s)}, \quad \dots 1.3.9$$

where $T_s = (T - T_h N_e - T_h' N_{e'})$. The definition of C is now more complex and dependent on T_s , the time available for searching, which itself depends on the numbers of prey types eaten. Indeed, C is now variable, suggesting that Murdoch's model is too simple a description when exploitation occurs over the time considered. Although the preference term in Eqn. 1.3.9, $((1 - \exp(-a T_s))/(1 - \exp(-a' T_s)))$, can not be estimated directly, the Random Predator Equations can be used to predict actual consumption, and hence, the ratio $N_e/N_{e'}$, when both prey types are present.

Using this approach, preference can be calculated to show how the term in Eqn. 1.3.9 differs from a/a' derived from the Holling Disc Equation. Thus, four combinations of high and low handling times have been used to calculate preference in Fig. 1.7. It can be seen that when the handling times for either both prey or the highly preferred prey are low, the preference approaches a/a' . When the handling times for both, or for the preferred prey, are high, the resultant preference is considerably less than a/a' , this effect being more marked when both handling times are high. Therefore, as handling time increases, and hence searching time decreases, the effective preference will decrease. This, therefore, is an important qualitative difference between the non-exploitation model (Holling Disc Equation) and the exploitation model (Random Predator Equation) of the functional response.

This approach is used in this work. The functional responses to individual prey types will be used to predict the null hypothesis of predation when both prey types are present (see Chapters 3 and 5). An alternative approach, used by Lawton, Beddington and Bonser (1974) is to carry out but a single experiment using prey mixtures and then fit Eqns. 1.3.8 to these data of predation on the two prey types.

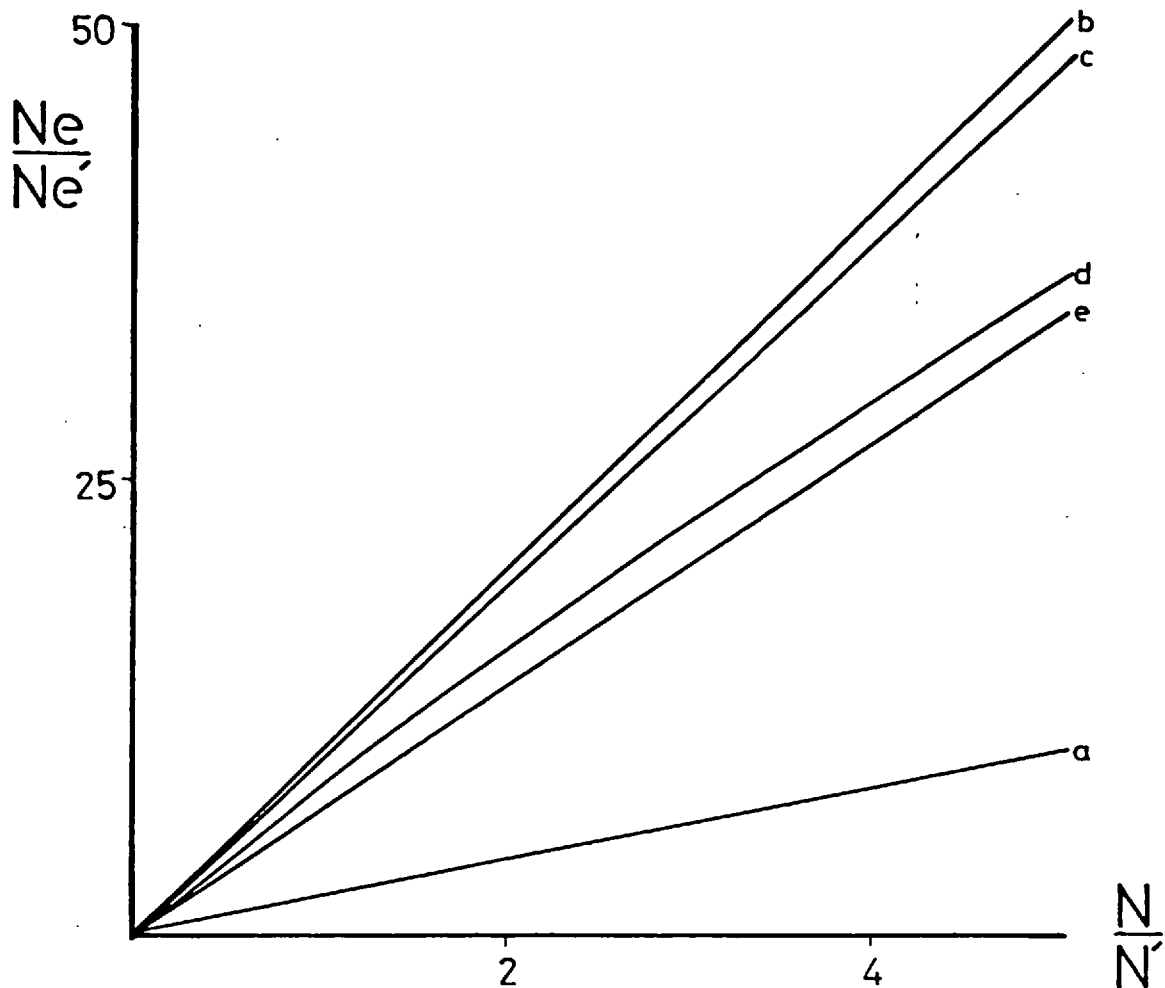


FIGURE 1.7 Hypothetical preference situations calculated using the two prey-type Random Predator Equation (Eqns. 1.3.8), showing the effects of the handling times. Parameters used: $a = 1.0$, $a' = 0.1$, $T = 1.0$, and initial prey densities such that $N + N' = 120$. A - no preference ($a = a'$, $C = 1.0$); B - no handling times ($C = a/a' = 10$); C - both handling times low ($Th = Th' = 0.001$) and low handling time for preferred prey, high handling time for less preferred prey ($Th = 0.001$, $Th' = 0.1$); D - high handling time for preferred prey, low handling time for less preferred prey ($Th = 0.1$, $Th' = 0.001$); E - high handling times for both prey ($Th = Th' = 0.1$).

1.3.4 Switching

Preference is measured in terms of a deviation of the ratio of the numbers of two prey types in the diet from the ratio of the numbers or densities of the two prey types in the environment. The no-preference null hypothesis normally used states that these are equal. It can be seen from the last section (1.3.3) that the null hypothesis can also be based on predictions from the individual functional responses.

Switching is assessed by the variation of preference from the null hypothesis situation. Murdoch (1969) stated that, for a switching behaviour to occur, there will be negative preference when the term N/N' is less than unity and positive preference when it is greater than unity. In other words, if predators show positive preference towards whichever is the commoner prey, switching occurs. As described in the last section, a more sophisticated alternative hypothesis, based upon the prediction of predation from the individual functional responses can be derived and used. Preference is considered to be acting if the ratio of the actual numbers eaten differs from the ratio of the expected numbers eaten. Hence, switching will occur if there is negative preference when the ratio of the expected number of prey eaten is less than unity, and there is positive preference when the ratio is greater than unity.

Elton & Greenwood (1970) described a model of switching based on the same null hypothesis as that used by Murdoch (1969) (Section 1.3.2; Eqn. 1.3.2). This null hypothesis:

$$N_e/N_{e'} = (v/v') N/N'$$

is modified to the form:

$$N_e/N_{e'} = (vN/v'N')^b.$$

The effect of varying b when the ratio v/v' (which is equivalent to C) is unity, can be seen in Fig. 1.8. The switch-over point is defined by the preference (v/v') . Values of b greater than one result in a switch to the commoner prey type, whilst values

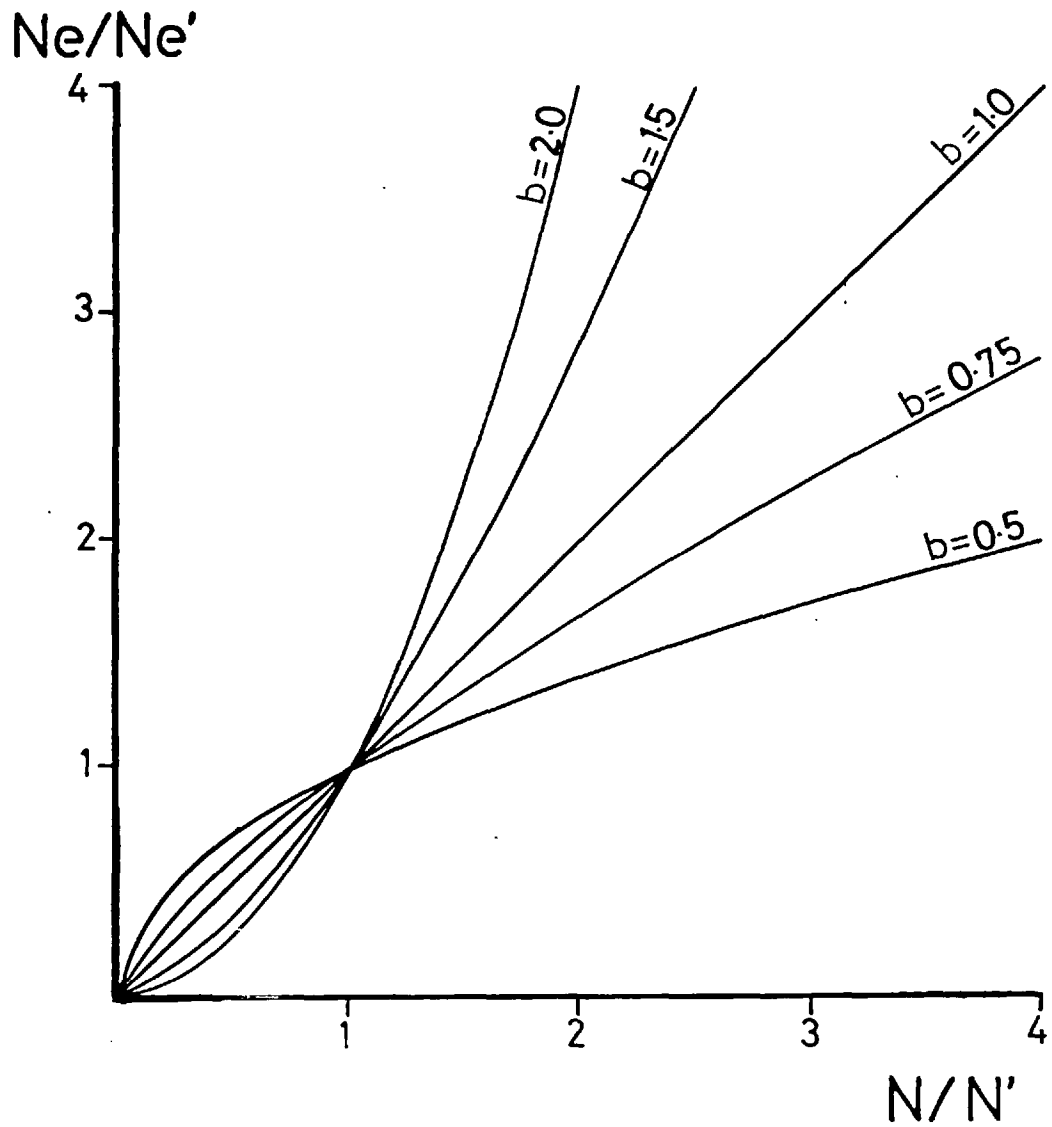


FIGURE 1.8 A generalized diagram of Elton & Greenwood's (1970) model of switching. The preference term, v/v' , is taken as unity, and the effects of several values of the switching term, b , are shown. The switch-over point is defined by the preference term.

of less than one lead to a switch to the rarer prey type. The alternative null hypothesis based on the functional responses (Section 1.3.3) can be used in this model.

Manly (1973) also developed a switching model based on a null hypothesis equivalent to that of Murdoch (Section 1.3.2; Eqns. 1.3.3 and 1.3.4). The total preference, α , is defined as:

$$\alpha = d + s(N/S),$$

where d and s are constants, and N and S , as used in Section 1.3.2, are the number of prey type I and the total number of prey respectively in the environment. For switching to occur, d must be less than unity and s must be greater than zero. The effects of varying s , with d equal to zero, are shown in Fig. 1.9. It can be seen that the switch-over point is defined by both constants, (cf. the model of Elton & Greenwood (1970), Fig. 1.8, where the switch-over point is defined by the preference constant alone). This, more general model is likely to be of greater use than that of Elton & Greenwood.

A coccinellid-aphid interaction was examined for preference and switching by Marks (Marks, 1970; Murdoch & Marks, 1973). The coccinellids were reared on one of three aphid species, and in experiments were offered a choice of two of the species in various ratios. He found that the ratio of the prey in the diet was the same as the ratio of prey present (i.e. the results fit Murdoch's null hypothesis), and that this result was largely unaffected by the species on which the coccinellid was reared. In view of this, it seems likely that the coccinellid has a similar search efficiency for all the aphid species.

Ivlev (1961, Chapter 4, Fig. 17) demonstrated switching by carp. When offered a choice of four prey types, carp initially showed a strong preference for chironomid larvae; after three days the larvae had become rare, and the fish then showed a strong negative preference for the larvae, and an increased positive preference for the previously second most preferred prey, amphipods.

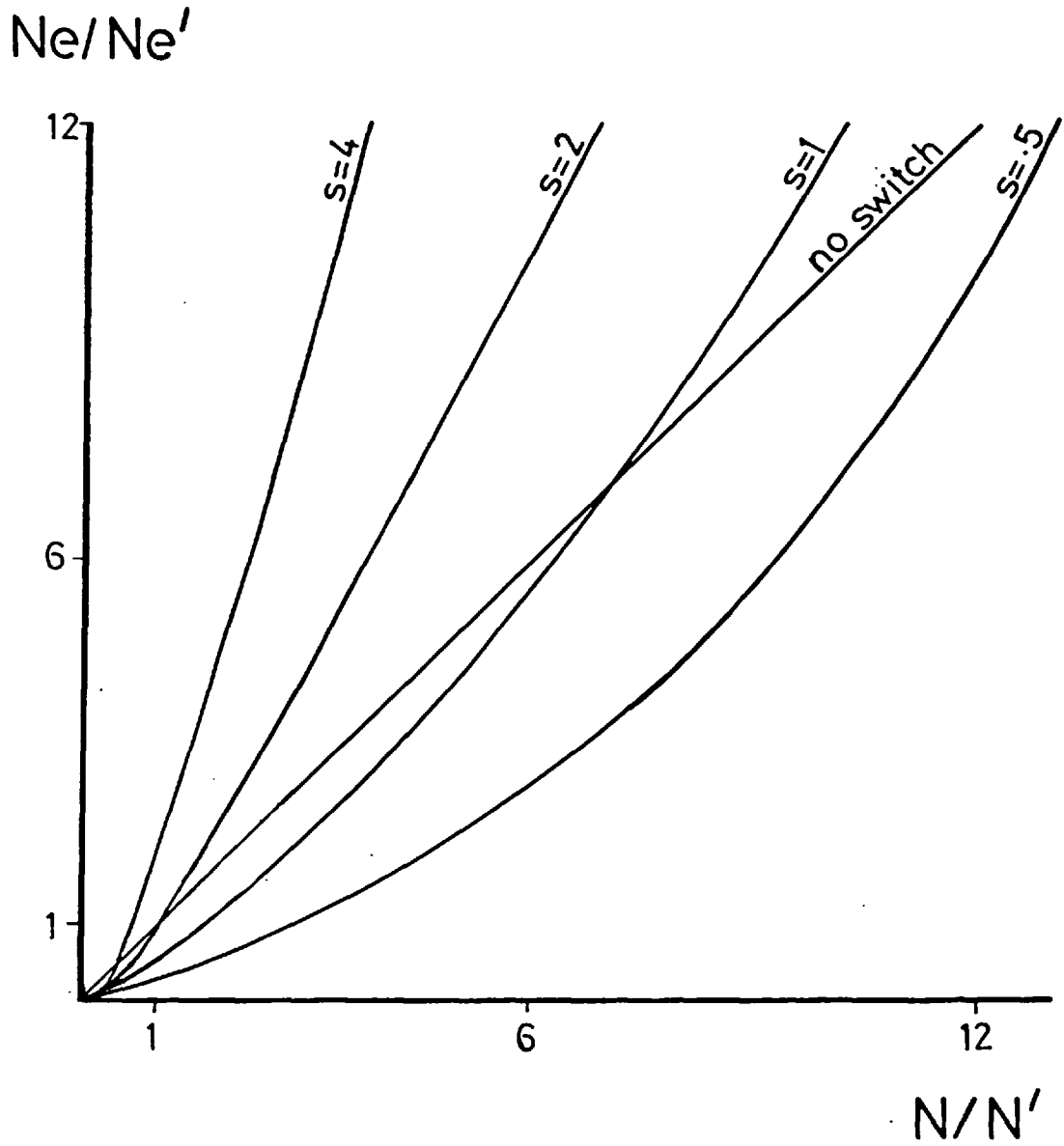


FIGURE 1.9

A generalized diagram of Manly's (1973) model of switching. The residual preference term, d , is taken as zero, and the effects of several values of the switching term, s , are shown. The switch-over point is defined by both terms.

Murdoch (1969) examined the predation of marine whelks (Thais emarginata and Acanthina spirata) when offered mussels (Mytilus edulis and M. californianus) and barnacles (Balanus glandula). In several laboratory experiments, Thais and Acanthina showed a strong and consistent preference for M. edulis over M. californianus. This was not due to a difference in encounter rates, since observation showed that the prey were encountered in the ratio at which they were present. Both whelks showed weak overall preference when results were pooled, and strong individual preference when offered M. edulis and Balanus. When Thais were offered a selection of ratios of M. edulis and Balanus, there was no evidence of switching. However, when Murdoch 'trained' the Thais on a diet of one prey type only, switching occurred when both were offered. This was considered to be analogous to the predator becoming trained within a patch of one prey type.

Murdoch, Avery & Smyth (1975) looked for evidence of switching by predatory fish. Guppies, Poecilia reticulatus, were given two prey: Drosophila on the water surface and Tubifex worms on the bottom of the aquarium. The guppies showed high individual variation in preference when the prey were offered in equal numbers. Over twelve days the ratio of the food offered was varied from 1:4 to 4:1 for one half of the fish and from 4:1 to 1:4 for the other half. The diets and time spent in different parts of the aquarium, (top, bottom, or middle), were recorded. In response to the changes in the available prey, the guppies were found to switch to the more common type. A separate group of fish, with a preference for the bottom of the aquarium (and hence, for the tubificid worms), were slow to switch, and, as a group were less efficient predators.

1.3.5 Foraging Strategies of Birds

Tinbergen (1960) and Royama (1970a) have proposed two contrasting strategies to account for the predation of insectivorous birds. These strategies and their implications for the general theory of preference and switching will be examined below.

Tinbergen (1960) made extensive observations on the diet of great tits, Parus major, and the available food in pine woods. He found that the tits do not immediately notice a new food source. For example, Panolis larvae of suitable age occur in the diet of some individuals several days before it is taken by others. These others then switch to the new prey and often take it in large numbers. Food is often collected in runs of the same prey type, and individuals specialize in different prey types. Tinbergen states that these phenomena can be due to local differences in the prey available, different hunting techniques or conditioning to different parts of the habitat. Some cases, however, suggest that none of these explanations are adequate. To account for all cases, Tinbergen suggests that the birds may be using a 'specific searching image'; if, by chance, a bird comes across several prey of one type, it will become 'aware' of the specific characteristics of that prey type, and these will be assimilated in a learning process as a specific searching image. Having acquired such an image, the birds concentrate on that prey type.

By observation and the examination of the crop contents of drugged birds, Murton (1971) obtained data on the diet of wood-pigeons. Within an experimental area, the 'prey' (leguminous seeds of various species) were distributed in known arrangements and numbers. These seeds contained a drug, and when the birds succumbed, their crop contents were examined. The pooled data showed that the flock fed at random; the seed types were eaten in the ratio at which they were present. However, examination of individual diets showed that many birds specialized in feeding on one particular prey type. For example, when offered tic beans and maple beans at approximately equal densities, 33% of the birds selected tic beans, 39% selected maple beans and 28% took either by chance. Murton was also able to demonstrate that the specialists tended to be more efficient; invariably the most successful birds in a run were specialists. Various risk indices were obtained and used to test Tinbergen's model of preference (Section 1.3.2); the deviations found were considered to be caused by social facilitation of feeding within the flock.

Gibb (1962) presented the now generally unaccepted hypothesis of 'searching by expectation'. Tits, (Parus spp.), are predators of the larvae of an eucosmid moth, Ernarmonia conicolona. The larvae feed in pine cones, and the tits locate them by tapping the cones, leaving obvious signs of successful predation. Gibb sampled cones from a 15 x 15 metre grid in a pinewood. (One might expect this to result in 225 metre square plots; Gibb lists 302). He counted the number of larvae per cone, and the number eaten from each cone. He then plotted his results as the percentage predation against the intensity of larvae per ten cones. Intensities of from nine to sixteen occur infrequently, and, in replotting his data (Fig. 1.10A) the results at these intensities are pooled into two groups. Gibb suggested that the tits hunt by expectation; having established some estimate of the normal density of the prey, they search a cone until they have found this number and then cease searching. In Fig. 1.10B, Gibb's data is plotted as the number of larvae eaten per cone against the intensity of larvae per cone. It can be seen that, at nearly all densities of larvae, a constant proportion is eaten. This suggests that tits spend a set time searching on any one cone. The predation at the highest larval density implies that this behaviour can be modified at very high densities of larvae. Thus, the somewhat elaborate hypothesis put forward by Gibb seems to be at variance with his results when plotted in this form.

A somewhat different approach to that of Tinbergen is put forward by Royama (1970a). This, like Gibb's work, is based on the fact that the distribution of prey is naturally discontinuous and different parts of the environment, on both a macro- and a micro-scale, suit different types of prey. For example, within a wood, a given lepidopterous species of larva may be found on only one species of tree, and within individual trees it will occur only in restricted areas, such as within crevices of the bark or between spun leaves at the tips of branches. Royama (1970a) worked on Great Tits, and recorded the food brought by the parent birds to the nestlings, and compared it with the food available in the environment. Based on his observations, he proposed a searching strategy dependent on maximization of profitability by the parent birds. Each prey type

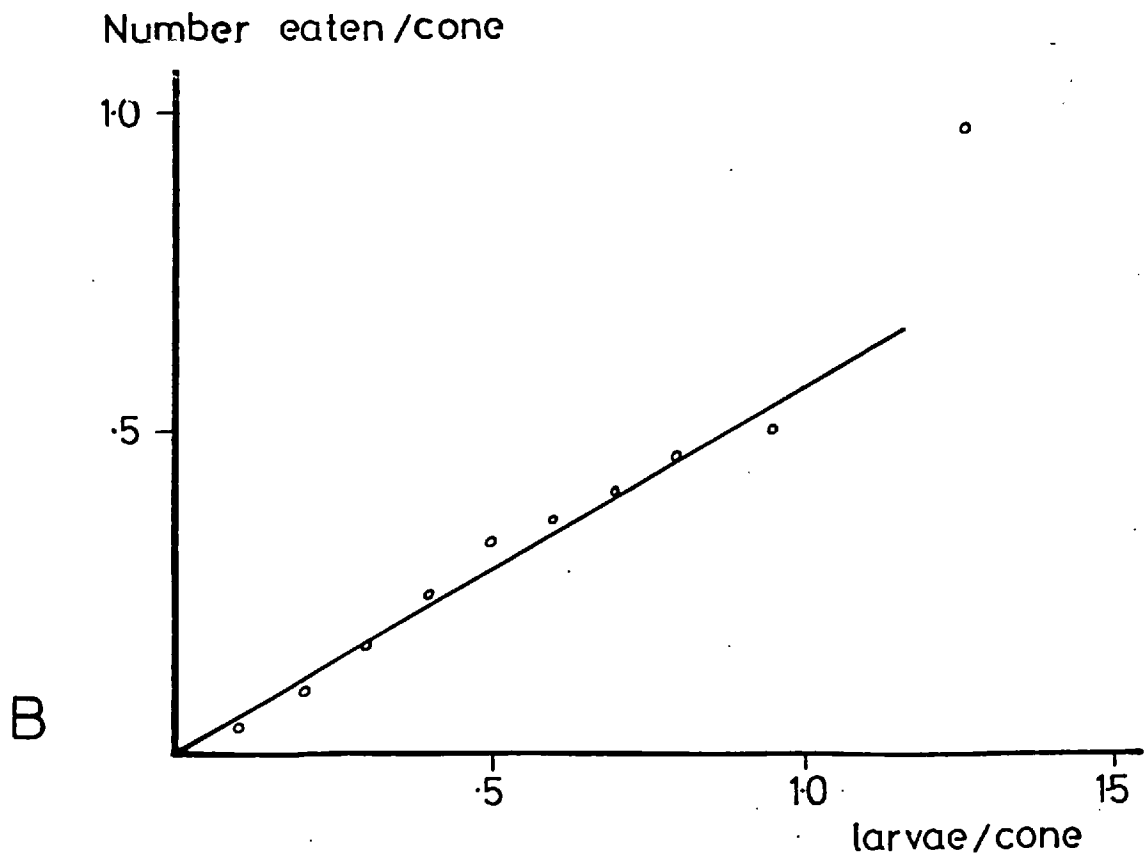
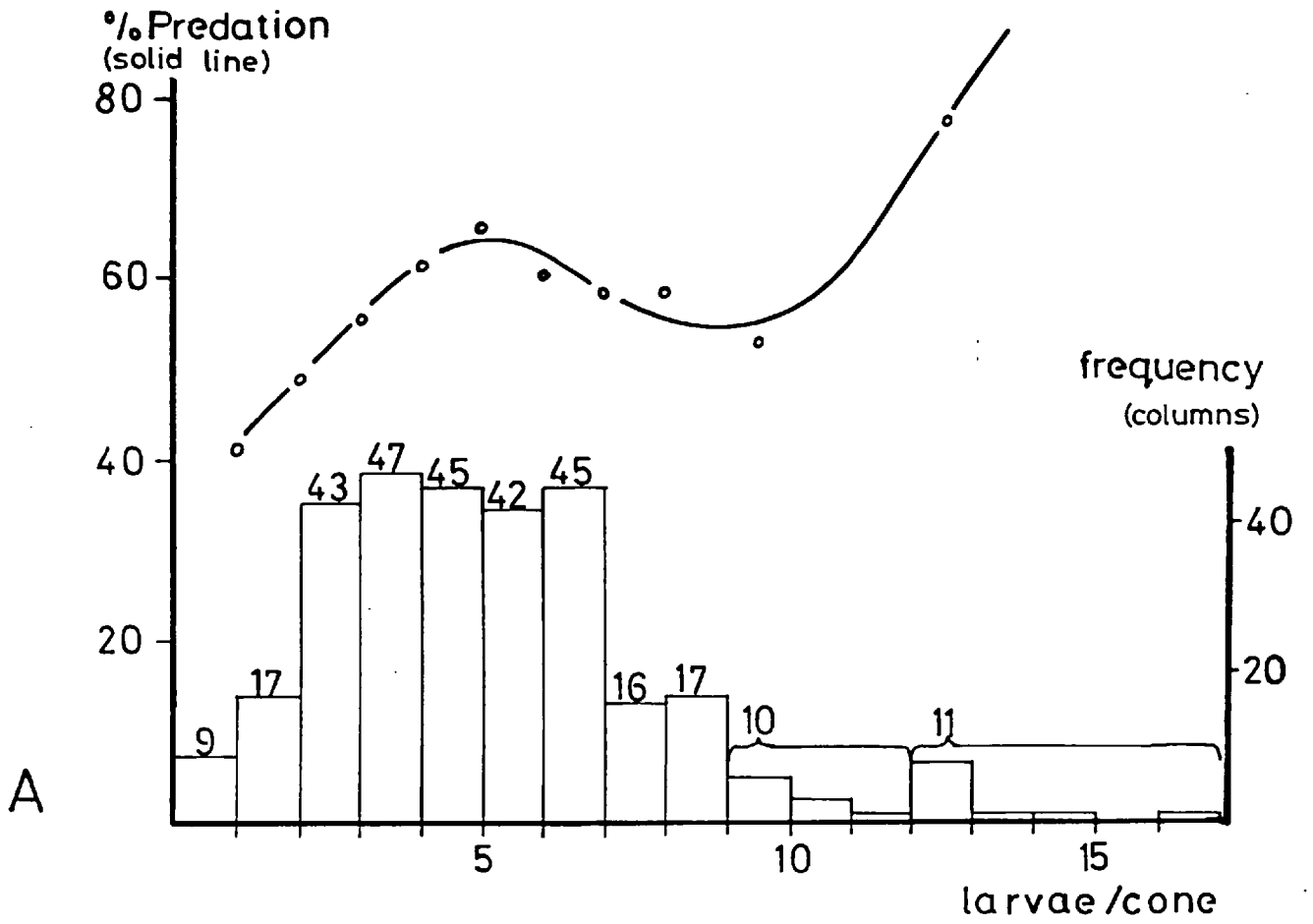


FIGURE 1.10 Predation of tits on Ernarmonia conicolona; data from Gibb (1962), (see text).

has a profitability measured in terms of calorific return per unit of effort expended in obtaining the prey and bringing it to the nest. There is a minimum profitability below which it is more profitable for the parent bird to eat the prey rather than take it back to the nest. The environment can be divided into areas or niches of profitability. The birds concentrate on the most profitable niches, occasionally checking the other niches to see whether new food sources have become available. If such a new food source makes some other niche more profitable, the birds will respond by spending more time searching in that niche, and hence, give the appearance of switching. Therefore, Royama considered the search image hypothesis put forward by Tinbergen to be redundant, its apparent effects being caused by habitat selection in response to changes in niche profitability.

Smith & Sweatman (1974) made observations on feeding tits, which support Royama's hypothesis. In laboratory experiments, they showed that search intensity and predation are maximized in the areas of highest prey density. Furthermore, if the area of greatest density and area of least density were changed over, the birds tended, initially, to concentrate on what had been the area of second greatest prey density. In a further experiment, involving a choice of areas of constant prey density, the tits concentrated their searching activity in the area with the largest (i.e. most profitable) prey. Field observations showed that hunting birds specialize in a particular habitat (niche), until the time taken to find the prey is similar to the overall average for the environment. These results support the views of Royama rather than those of Tinbergen.

1.4 THE EFFECTS OF AGGREGATION OF THE PREY

1.4.1 Introduction

So far in this chapter, the effects upon the prey death rate of prey density and the preference of the predator have been considered. In this section, the effects of the distribution of the prey upon the searching behaviour of the predator, and hence upon the prey death rate, will be considered.

Many species of animals are normally found in patches. This is true of both prey species used in this work: aphids (Chapter 3) and Pieris brassicae eggs (Chapters 4 & 5). Although the effects of aggregation will not be considered with respect to the aphid prey, this aspect will be of importance in the work done with eggs as prey.

The work done on the effects of prey aggregation with respect to predator-prey and host-parasitoid interactions can be divided into two aspects. In Section 1.4.2, the searching behaviour of predators in response to prey and their distribution will be examined, and in Section 1.4.3, some models of the effects of prey distribution will be reviewed.

1.4.2 Searching Behaviour in Response to Prey Distribution

The searching behaviour of predators often results in their collecting in areas of high prey density. Such behaviour is predicted by Royama (1970a) for foraging tits, and this work is described and compared with the work of Tinbergen (1960) in Section 1.3.5. Ecologists studying insect predation have tended to concentrate on small scale behavioural responses to prey, which cause predators to collect in areas of high prey density; other workers studying foraging birds have tended to look on a broader, more generalized, scale. Results from these two approaches will be considered in turn.

One widespread mechanism which causes predators to spend more time searching in areas of high prey density than would be expected on the basis of random search, involves a change in searching behaviour subsequent to feeding. The search path of many predators becomes more tortuous after feeding. This is achieved by shortening the distance between turns, and increasing the angle of turn. Frequently, the speed of movement decreases simultaneously. This behaviour results in an intensification of search in the area where the prey was found. Examples of such behaviour have been found in sticklebacks (Thomas, 1975), coccinellids (Banks, 1957; Marks, 1970), and anthocorids (Evans, 1973). The behaviour of anthocorids will be considered in Chapters 4 & 5.

Murdie & Hassell (1973) studied the behaviour of houseflies feeding on various arrangements of sugar droplets in square perspex arenas. The search track of the flies was traced on the lid of the arena, and time intervals of three seconds marked. They found that, after feeding, the searching behaviour changed; the angles of turning were increased and the distance between turns decreased. This behaviour became rapidly less pronounced and normal search was resumed within half a minute. Computer simulations produced not dissimilar tracks. The resultant functional responses showed that the flies were more efficient at finding the clumped droplets; but, as the authors pointed out, the normal functional response models are not applicable due to the non-random search of the flies. Hassell & May (1974) extended this work using mathematical models, as will be described in the next section.

Krebs et al. (1974) examined the searching behaviour of chickadees in the artificial habitat of an aviary. They concluded that the birds do not hunt by expectation (Gibb, 1962) (Section 1.3.5). Within one patch of the environment, the 'giving up' time was found to be constant; i.e. if the time which passed, in which the bird searched within a unit of habitat without finding any food, reached a threshold level, the bird gave up and tried another patch (cf. Murdoch & Oaten (1975), Section 1.4.3). The 'giving up' time was found to be inversely proportional to the overall feeding rate for the environment.

Thus, if the environment is rich in prey, the birds will quickly give up any patch where they are finding food infrequently.

Tinbergen et al. (1967) studied the effects of spacing within a clump. They put out camouflaged eggs in an area of sand dunes, arranged in a small group of set inter-egg distance. The attention of predatory crows was drawn to the eggs by putting an uncamouflaged, conspicuous egg in the centre of the grid. As a result, they found that closely spaced eggs were more heavily preyed upon than those more widely spaced. On measuring 'giving up' times, they found that crows searching for widely-spaced eggs searched for the longest time. One might conclude that camouflaged animals will tend to be widely spaced, yet a small dense clump may escape detection. The distribution of prey and searching behaviour of predators will interact as natural selection acts on the prey to maximize survival, and on the predator to maximize foraging success.

1.4.3 Models of the Effects of Prey Distribution

In this section, the following models will be reviewed: Ivlev (1961), Royama (1970b), Hassell & Rogers (1972) and Hassell & May (1974).

Ivlev (1961) produced a generalized description of the effect of aggregation of prey. It is based on an index of clumping which is effectively the variance of the local prey densities. The unit of local density is not defined, but is important since the aggregation will appear greatest at the mean clump size of the prey. (Plant ecologists, by comparing the variance from different quadrat sizes, estimate the clump size of plants). The relationship between the number of prey eaten and their aggregation is, Ivlev suggested, curvilinear. Experiments with fish feeding on various prey aggregations vindicated such a viewpoint. He described this relationship with an equation of the form:

$$N_e = (K - N_r) (1 - \exp(-k A)) + N_r,$$

where K is the maximum possible consumption in the time available, N_r is the consumption when prey are arranged regularly, A is the index of aggregation and k is a constant defining the curve. By combining this equation with his functional response equation, Ivlev derived a general equation to define how the number of prey eaten varies in response to prey density and aggregation. Such a mathematical description could well be useful in some cases, but the biology and behaviour involved should also be considered.

Royama's hypothesis of maximization of profitability by niche selection (Royama, 1970a) has been considered in Section 1.3.5. This hypothesis has been stated mathematically (Royama, 1970b), and will be described here. The model is in two parts: firstly, the relationship between the number of prey eaten and the local prey density, and secondly, the relationship between the number of prey eaten and the time spent searching by the predator. To describe the first, curvilinear relationship, Ivlev's equation for a functional response (Ivlev, 1961) was used, and to describe the second, Royama used a 'generalized Nicholson & Bailey model' i.e. the Random Predator Equation. By combining these two relationships, he obtained an isocline of the ideal distribution of predator time. Thus, for a given prey density, the optimum time to spend there and hence the prey consumption can be found. For any hypothetical distribution of predator time with prey density, the corresponding numbers of prey attacked at each density can be found, and hence the proportion eaten. This model was found to fit the percentage predation of parasitization data obtained by Varley (1941) (a slightly curvilinear relationship), Gibb (1958) (a strongly curvilinear and a domed relationship) and Holling (1959a) (a strongly domed relationship).

Another approach, not dissimilar to that of Royama, was used by Hassell & Rogers (1972). Nemeritis, when given a choice of prey chambers containing various densities of hosts, spent most time in areas of greatest host density. The percentage time spent in each chamber increased as a function of the prey density, giving a graph of exponential shape. The density of Nemeritis altered this response; if four or more were used, the percentage time spent in each chamber was proportional to the density.

Extending this approach, Hassell & May (1974) considered the aggregative response as the time spent per unit area in response to the prey density in that area. If a predator (or parasitoid) enters an area of known prey (or host) density, the time spent there and hence, the number of prey attacked (or hosts parasitized) can be defined. The authors constructed a model based on the searching behaviour of house flies, as described by Murdie & Hassell (1973) (Section 1.4.2). The flies show two modes of searching behaviour: random walk with short step lengths (mode I) and, forward directed or on-going random walk with long step lengths (mode II). Mode I is used for 30 seconds after feeding. It is followed by mode II if no further sugar droplets are found. By assuming the prey density remains constant, the authors were able to derive a model of the time spent per unit area as a function of prey density in that area. By introducing stochastic variation, a smoothed response of sigmoid shape was obtained. They continued by suggested other shapes for this response, and conducting stability analyses.

Murdoch & Oaten (1975) suggested a slightly different description of aggregative searching within a patch. This involves a time limit, analogous to that described by Krebs et al. (1974), at which, if the predator has not found a prey, it leaves the patch. If the predator finds a prey, it then has a further time limit to find the next prey. The aggregative response (time spent per patch as a function of patch density), as in the model of Hassell & May, is sigmoid in shape. Murdoch & Oaten show that this would have a stabilizing effect over part of the range of the overall functional response.

The aggregative response, as used by Hassell & May and Murdoch & Oaten, provides a useful, simple description of the aggregative behaviour of predators and parasitoids.

CHAPTER 2

THEORETICAL ASPECTS OF THE FUNCTIONAL RESPONSE

2.1 INTRODUCTION

During the course of this work a number of theoretical aspects of the functional response, and modifications of the Random Predator Equation (Rogers, 1972) were examined, and these will be described in this chapter. Rogers (1972) suggested that, to abstract the parameters of the Random Predator Equation, a regression analysis of the logarithm of the proportion of prey surviving ($\ln S$) against the number eaten (N_e) could be used. This technique is examined in Section 2.2, and alternative techniques proposed. Although the regression technique is not considered suitable, the figure of the logarithm of the proportion of prey surviving plotted against the number of prey eaten has been found to be useful in the interpretation of functional responses; some examples are given in Section 2.3. In modelling functional responses other than the normal, type II, one approach is to vary the parameters of the Random Predator Equation as functions of the prey density or the number of prey eaten; in Section 2.4, some such models are examined together with some observations on varying parameters during the experimental period.

2.2 ABSTRACTING THE PARAMETERS OF THE RANDOM PREDATOR EQUATION

Royama (1971) and Rogers (1972) both suggested a simple model for the type II functional response, for which Rogers proposed the name "The Random Predator Equation". It is of the form:

$$N_e = N(1 - \exp(- aP(T - T_h N_e))), \quad \dots 2.1$$

where N_e is the number of prey eaten, N is the initial prey density, a is the search efficiency, P is the number of predators (taken as one in the following discussion), T is the total time available, and T_h is the time taken to handle one prey. The derivation of this model is given in Section 1.2.2.

Since the parameters (a and T_h) offer difficulties for direct measurement, they are normally abstracted from predation data. Thus, Rogers (1972) suggested the technique of linear regression analysis to abstract the parameters from data of the number of prey eaten (N_e) for various values of initial prey density (N). To do this, the Random Predator Equation (Eqn. 2.1) is transformed to the linear form:

$$\ln((N - N_e)/N) = \ln S = - a T + a T_h N_e, \quad \dots 2.2$$

where S is the proportion of the prey surviving. The natural logarithm of S will, in this work, be referred to as $\ln S$. By treating Eqn. 2.2 as a regression of the form $y = c + mx$, and performing a regression analysis of $\ln S$ on N_e , estimates of the intercept ($- a T$) and the slope ($a T_h$) can be obtained. This technique has since been used by a number of workers (e.g. Evans, 1973, Hokyo & Kawauchi, 1975).

However, in applying a regression analysis, certain assumptions are made about the data:

1. the two variables are independent of each other,
2. the x values (N_e) are arbitrarily defined and not subject to variation,
3. the variance of y ($\ln S$) is the same for all values of x (N_e).

In this situation, it should be noted that $\ln S$ and N_e are not independent (N_e occurs in both terms), and that the values of x (N_e) are not arbitrarily defined but are the means of a number of replicates, and hence subject to variation. When the variance of $\ln S$ is considered, another problem becomes apparent. As this technique has been used in the past, the logarithm of the mean value of S has been used; in fact, it can be seen that the mean of the logarithmic values of S should be used. One reason why the mean of $\ln S$ has not been used in the past is that, at low prey densities, it is not unusual for all the prey to be eaten in some replicates and this leads to values of zero for S and hence, minus infinity for $\ln S$ i.e. the mean of $\ln S$ can not be evaluated if total predation occurs in any of the replicates. Furthermore, it can be seen that that small changes in the value of N_e will, at low prey densities, lead to large changes in the corresponding values of $\ln S$, which leads to the variance of $\ln S$ at low prey densities (and hence values of N_e) being much greater than the variance at high prey densities. In view of these problems, the regression analysis of $\ln S$ x N_e is not a suitable technique for the abstraction of parameters. The resultant figure of $\ln S$ plotted against N_e is, however, often more informative than the functional response figure, as will be described in Section 2.3.

If there is no data involving total predation, an improved method of parameter extraction would be to find the best-fit linear relationship of $\ln S$ x N_e , allowing for both variables being subject to error. Such a method is described by Davies (Davies, 1971; programme 22). However, in as much as $\ln S$ is still subject to greater variation at low prey densities, this method is also unsuitable. Most functional response experiments result in data involving total predation, and in order to overcome this drawback, a least squares technique was developed, and the computer programme BESTFIT (see Appendix Section A1.3 for a description and listing) was written. The values of the para-

meters which give the best fit to the observed data are taken as the best estimates. The major drawback with this approach, (apart from the large amount of computing time which may be necessary), is that the higher values of N_e have a larger effect upon the results than the smaller ones.

In Chapter 4, these three techniques are used to abstract the parameters of the Random Predator Equation for twelve functional responses, and the resultant estimates are tabulated in Table 4.5. It can be seen that the technique of the least squares best fit to the functional response consistently yields parameters which give a better fit to the data. The results of Chapter 4 also provide a means of comparing the effects of using the mean of $\ln S$ and the \ln of mean S . Both values, where they can be calculated, are given in Tables 4.1-4.4, and it can be seen that the deviation is most marked at the low values of N_e (and hence N). The \ln of mean S consistently underestimates the proportion of the prey eaten; the values of mean $\ln S$ tend to 'tail off' towards minus infinity at low values of N_e . This phenomenon is sometimes found when \ln mean S values are considered, and this is examined in Chapter 3 (Section 3.3.5).

2.3 INTERPRETATION OF $\ln S \times N_e$ FIGURES

It was mentioned in Section 2.2 that $\ln S \times N_e$ figures can be more informative than functional response figures. In this brief section, some examples will be given.

The Random Predator Equation is simply interpreted in a $\ln S \times N_e$ figure, in particular the effect of the search efficiency being more evident than in a functional response figure. In Fig. 2.3 the effects of varying the parameters a (search efficiency) and T_h (handling time) are shown using both functional response and $\ln S \times N_e$ figures. The effects of the different search efficiencies are more evident in the latter figure, the intercept on the $\ln S$ axis showing the values of a when the total time available (T) is unity, as in this case. The intercept on the N_e axis can be shown, from Eqn. 2.2, to be equal to T/T_h i.e. the maximum consumption rate. The straight line relationship makes both of these intercepts easier to interpret.

Deviations from the normal, type II functional response may be more obvious in the $\ln S \times N_e$ figures. A type III or sigmoid functional response is often very close to the type II in shape. In Fig. 2.4A, an obviously sigmoid functional response drawn freehand is interpreted as a $\ln S \times N_e$ figure; in place of the straight line relationship of the Random Predator Equation, a clear cut U or V shape is now apparent. This obvious shape was noted in the functional response of C. septempunctata to type I aphid prey in Section 3.4.2, enabling suitable models to be fitted. The freehand dome shaped functional response shown in Fig. 2.4C results in a curve of similar shape in the $\ln S \times N_e$ figure (Fig. 2.4D). In order to establish such a curve from experimental data, it may be necessary to link data points in a prey density sequence (see Fig. 2.10B of the analysis of data of Yao (pers. comm.)). One factor which becomes more clear from the $\ln S \times N_e$ figure of the dome-shaped functional response is that $\ln S$ can not be defined by any simple function of N_e , a model of at least the complexity of the quadratic form being necessary.

Therefore, in view of the extra information and insight which may be obtained from a $\ln S \times N_e$ figure, it is worthwhile examining $\ln S \times N_e$ figures during the course of the analysis of functional response data.

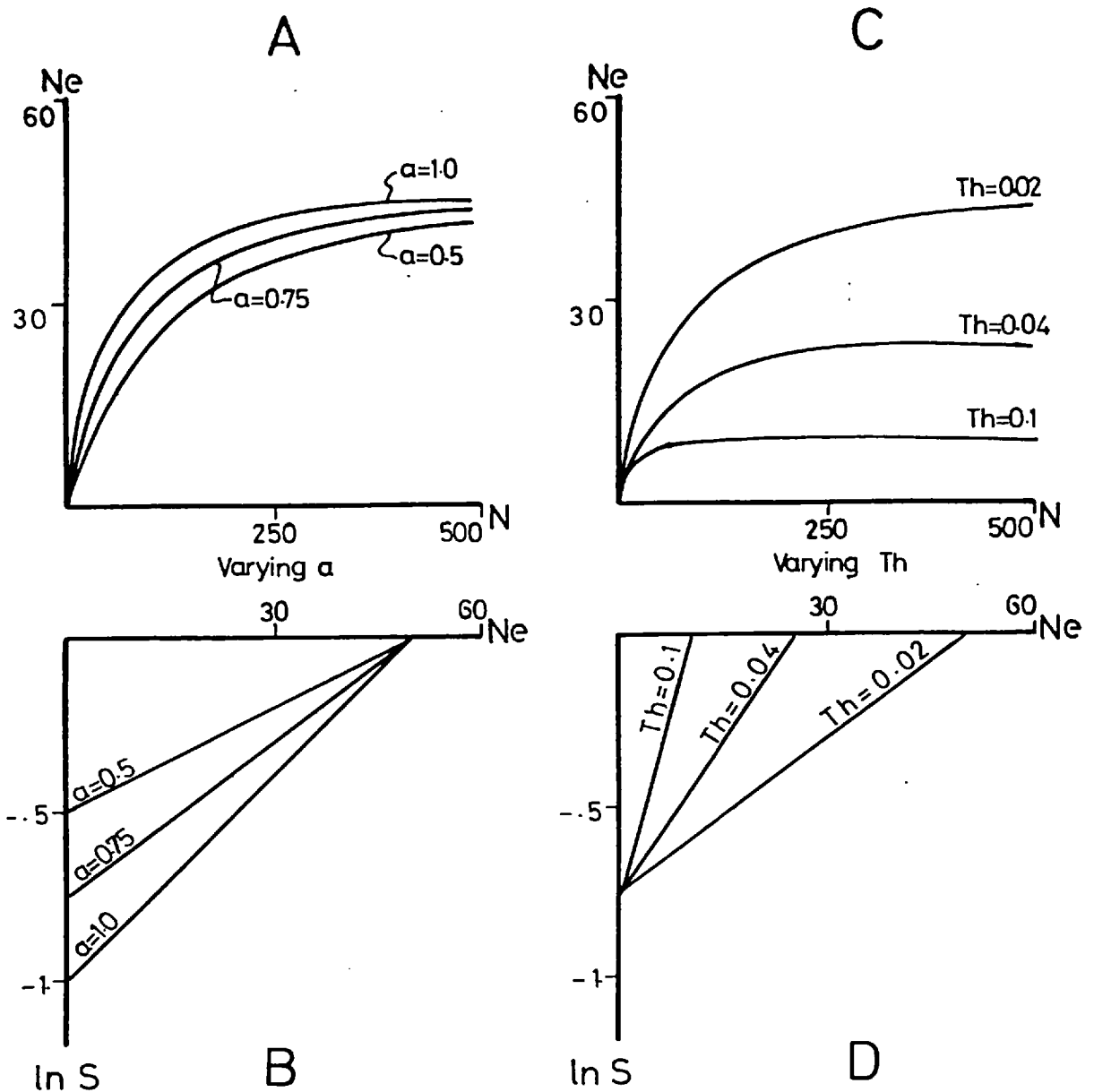


FIGURE 2.1 Hypothetical functional responses, and $\ln S \times Ne$ figures, calculated using the Random Predator Equation, to show the effects of varying the search efficiency (α) and the handling time (Th).

(A) - functional responses and (B) - $\ln S \times Ne$ figures for various values of the search efficiency, with the total time ($T = 1.$) and the handling time ($Th = 0.02$) held constant.

(C) - functional responses and (D) - $\ln S \times Ne$ figures for various values of the handling time, with the total time ($T = 1.0$) and the search efficiency ($\alpha = 0.75$) held constant.

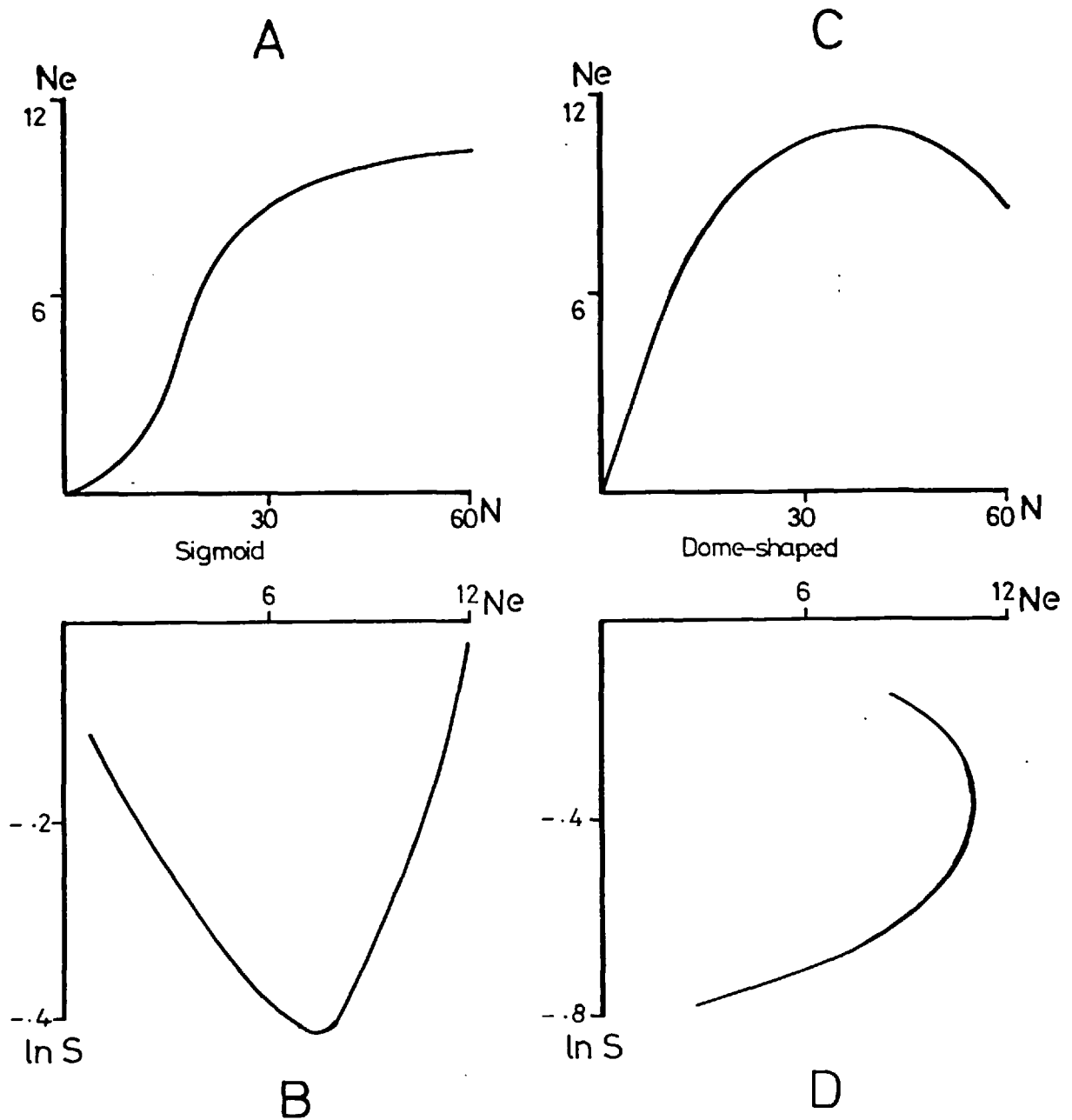


FIGURE 2.2 Hypothetical sigmoid and dome-shaped functional responses to show the relationships with the corresponding $\ln S \times Ne$ figures.

(A) - functional response and (B) - $\ln S \times Ne$ figures for a sigmoid or type III functional response.

(C) - functional response and (D) - $\ln S \times Ne$ figures for a dome shaped functional response.

2.4 VARYING PARAMETER MODELS

2.4.1 Introduction

In order to describe functional responses other than the normal, type II response, the Random Predator Equation can be modified by defining the parameters (a - search efficiency, T_h - handling time) as functions of the prey density or the number of prey eaten

There are two approaches to defining the parameters, analogous to the instantaneous and overall forms of the functional response equations described in Section 1.2.2. Thus, in the first approach, the search efficiency and handling time can be instantaneous functions of the prey density or the number of prey eaten, in which case the functions must be integrated over the period of the experiment before they can be substituted in the Random Predator Equation. Alternatively, the instantaneous relationships can be substituted into an instantaneous equation such as the Holling Disc Equation (Section 1.2.2; Eqn. 1.2.7), and the whole equation integrated over the experimental period. In the second approach, the parameters can be defined in an overall form i.e. used as a mean search efficiency or handling time, and substituted directly into the Random Predator Equation. The former approach may be easier to apply from the practical viewpoint, but the latter is easier to incorporate into and handle as a modified Random Predator Equation.

Rogers (pers. comm.) has suggested a simple linear model using the latter approach, and the possibilities of this model are examined in Section 2.4.2. In Section 2.4.3, data from dome shaped functional responses suggest alternative models. Two sigmoid functional responses models, one suggested by Hassell (pers. comm.) and the other by the results of Chapter 3 of this work, will be described and compared in Chapter 3 on the work using coccinellids and aphid prey.

2.4.2 Rogers' varying parameter model

Rogers (pers. comm.) has found data showing that the parameters of the Random Predator Equation (a - search efficiency, T_h - handling time) can be defined as linear functions of the number of prey eaten. Accordingly, he has suggested a model of the form:

$$N_e = N(1 - \exp(-\bar{a}(T - \bar{T}_h N_e))) \quad . . . 2.3$$

where \bar{a} , the mean search efficiency, and \bar{T}_h , the mean handling time, are defined by the linear relationships:

$$\begin{aligned} \bar{a} &= m N_e + Q \\ \bar{T}_h &= n N_e + H, \end{aligned}$$

where m , n , Q and H are constants. Substitution in Eqn. 2.3 gives:

$$N_e = N(1 - \exp(-(Q + m N_e)(T - (H + n N_e)N_e))), \quad . . 2.4$$

which can be rearranged to give:

$$\ln S = -Q T + (Q H - T m)N_e + (H m - Q n)N_e^2 - m n N_e^3.$$

This equation can be treated as a multiple regression equation of the form:

$$y = a + b x + c x^2 + d x^3.$$

The results of a multiple regression analysis can, using Newton's approximation, yield estimates of the parameters (m , n , Q , H) defining the mean search efficiency and handling time.

The range of functional response shapes which this model describes, can be seen by varying the parameters m (Fig. 2.3) and n (Fig. 2.4) - the effects of varying H and Q being similar to varying a and T_h in the Random Predator Equation (Fig. 2.1). Varying m , the change in the mean search efficiency for each prey eaten, produces a range of apparently normal type II responses.

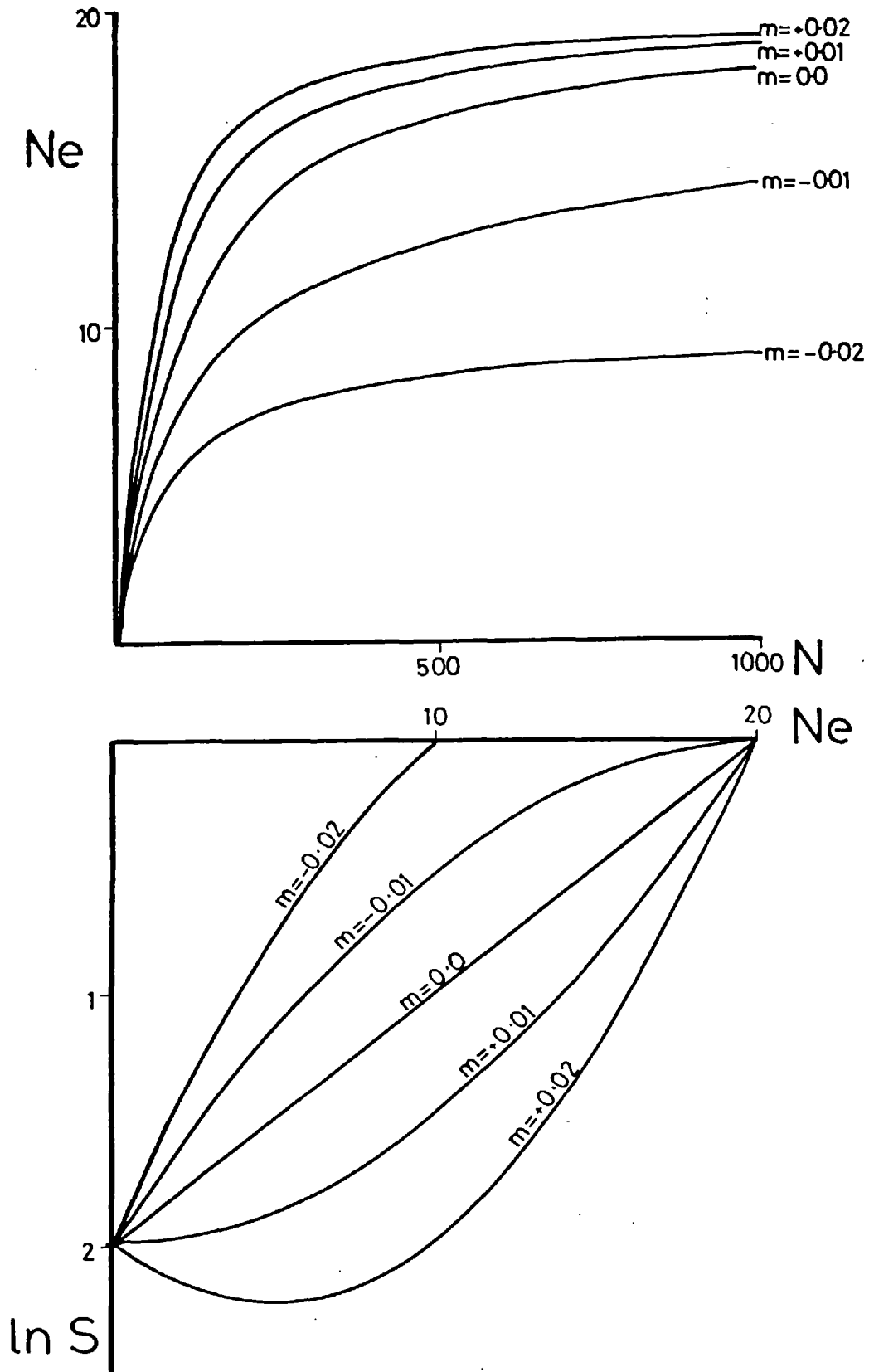


FIGURE 2.3 Hypothetical functional responses and $\ln S \times N_e$ relationships, calculated using the Rogers' varying parameter model (Eqn. 2.6), to show the effects of varying the parameter m (change in mean search efficiency per prey eaten) with the other parameters held constant ($T = 1.0$, $\bar{T}_h = 0.05$, $Q = 0.2$).

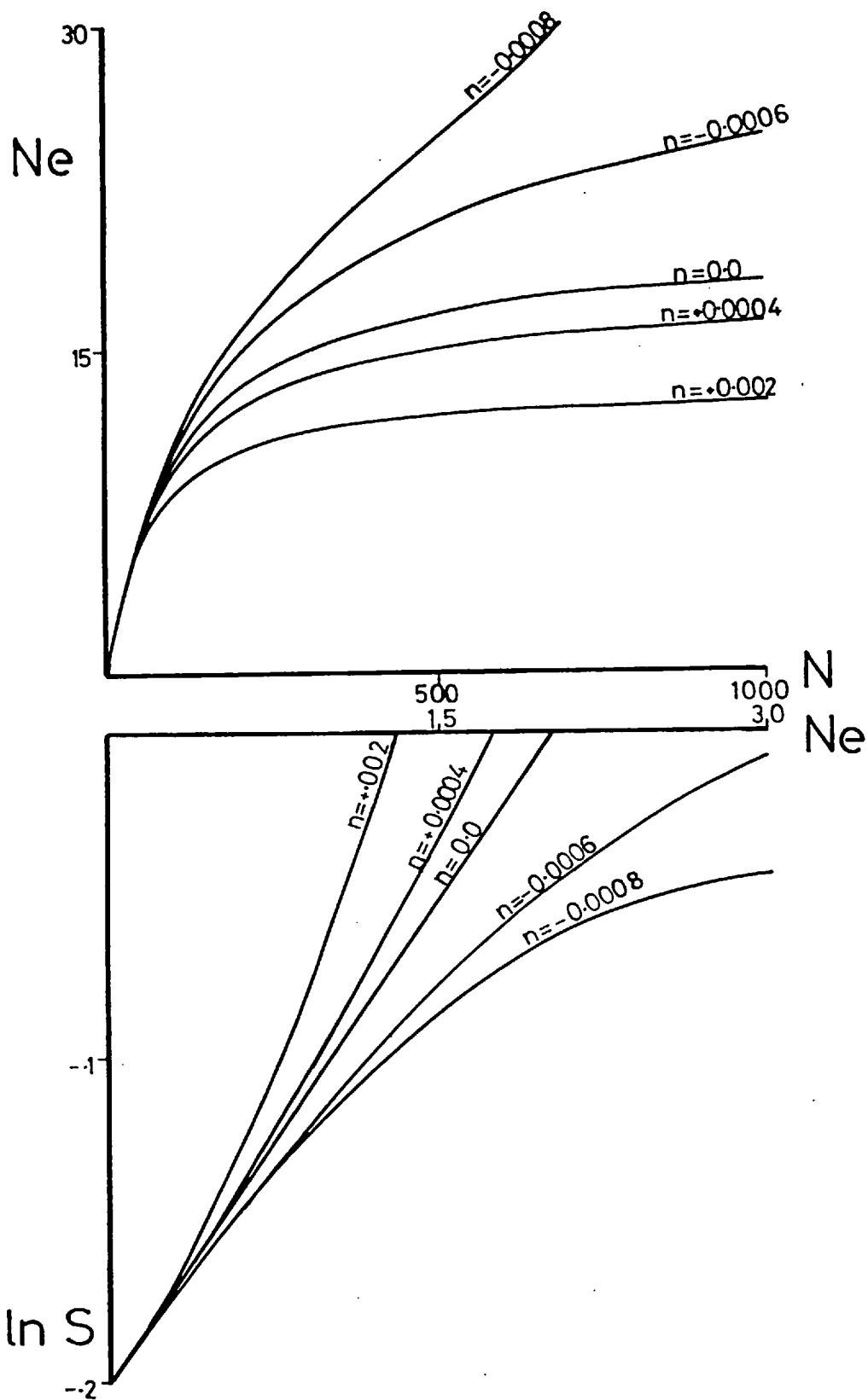


FIGURE 2.4 Hypothetical functional responses and $\ln S \times N_e$ relationships, calculated using the Rogers' varying parameter model (Eqn. 2.6), to show the effects of varying the parameter n (change in mean handling time per prey eaten) with the other parameters constant ($T = 1.0$, $\bar{a} = 0.2$, $H = 0.05$).

Comparing Fig. 2.3 with Fig. 2.1 of the Random Predator Equation, it can be seen that decreasing m has a similar effect to decreasing the handling time of the Random Predator Equation, while increasing m produces patterns similar to the effect of increasing the search efficiency of the Random Predator Equation. Increasing m , however, also adds a sigmoid element to the functional response, which is only apparent in the $\ln S \times N_e$ figure. Comparing the figure of the effects of varying n , the change in the mean handling time for each prey eaten, (Fig. 2.4.) with Fig. 2.1 of the Random Predator Equation, other similarities can be seen. Thus, increasing n has an effect similar to increasing the handling time of the Random Predator Equation, while decreasing n , at least initially, is similar to decreasing the handling time of the Random Predator Equation. However, when the negative value of n becomes too large, the relationship diverges from the Random Predator Equation, a steadily increasing proportion of the prey being eaten. This is due to the individual prey handling time becoming effectively negative in order to produce the necessary decrease in the mean handling time; as a result, the more prey that are eaten, the more time is available to find further prey, and the model becomes unrealistic.

To determine whether this model will adequately describe sigmoid and dome-shaped functional responses (see Section 1.2.3), the parameters necessary to obtain the responses shown in Fig. 2.2, with either the search efficiency of the handling time constant, were calculated and are shown in Figs. 2.5 (sigmoid) and 2.6 (dome-shaped) both as functions of the prey density and as functions of the number of prey eaten. It can be seen that only a as a function of N_e for the sigmoid response approaches a linear relationship; this is in agreement with the fact noted from Fig. 2.3 that when $m = 0.001$, the $\ln S \times N_e$ figure shows a shape suitable to describe a sigmoid response.

Therefore, on the whole, this model results in type II responses adequately described by the Random Predator Equation. However, increasing mean search efficiency as a linear function of the number of prey eaten can lead to a sigmoid functional response.

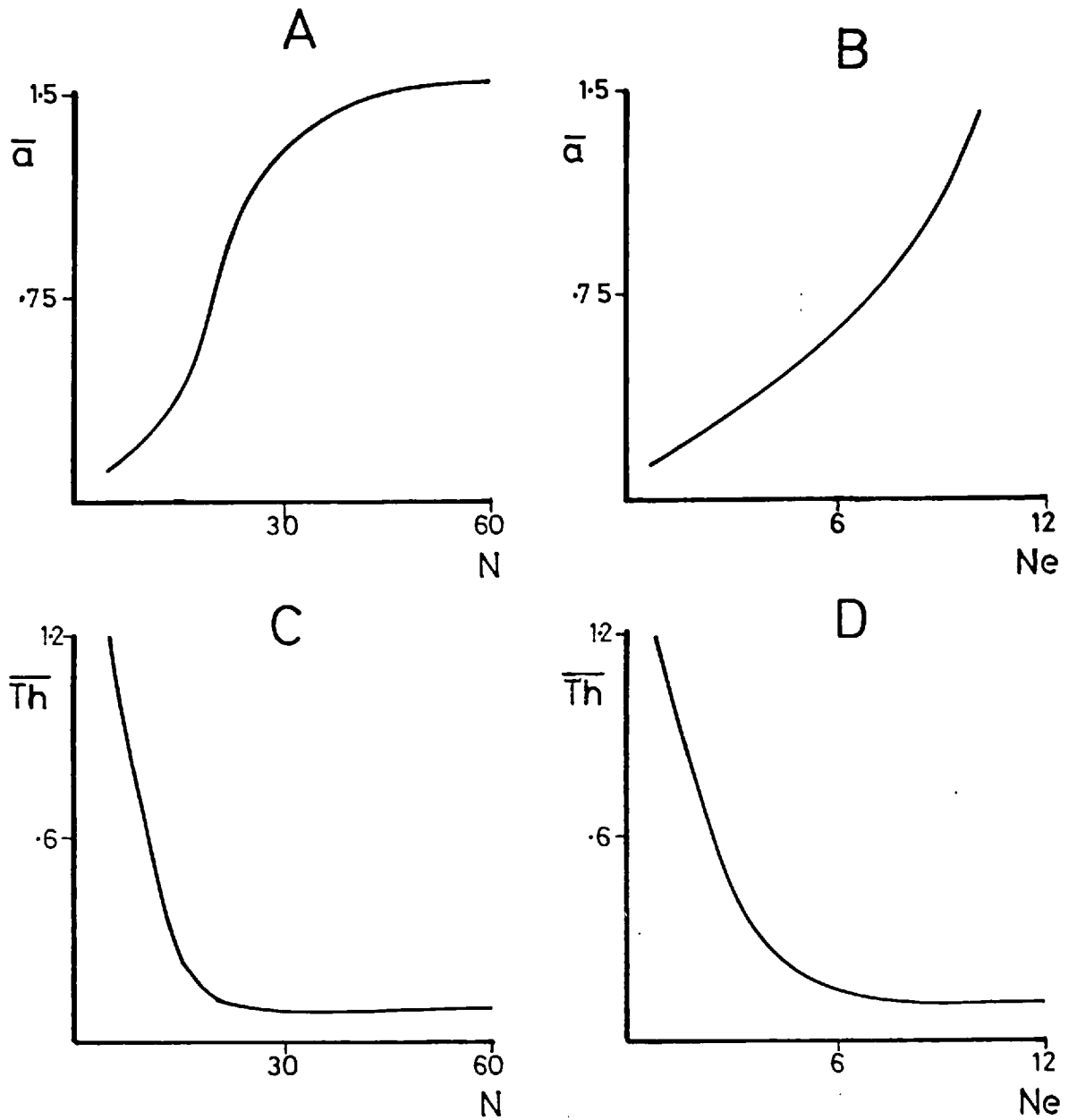


FIGURE 2.5 Mean parameter (\bar{a} , mean search efficiency; \bar{T}_h , mean handling time) values calculated from the hypothetical sigmoid functional response of Fig. 2.2A. \bar{T}_h is kept constant at 0.0833, and \bar{a} is shown as a function of N, the prey density (A), and as a function of N_e , the number of prey eaten (B). \bar{a} is kept constant at 0.8, and \bar{T}_h is shown as a function of N, the prey density (C) and as a function of N_e , the number of prey eaten (D).

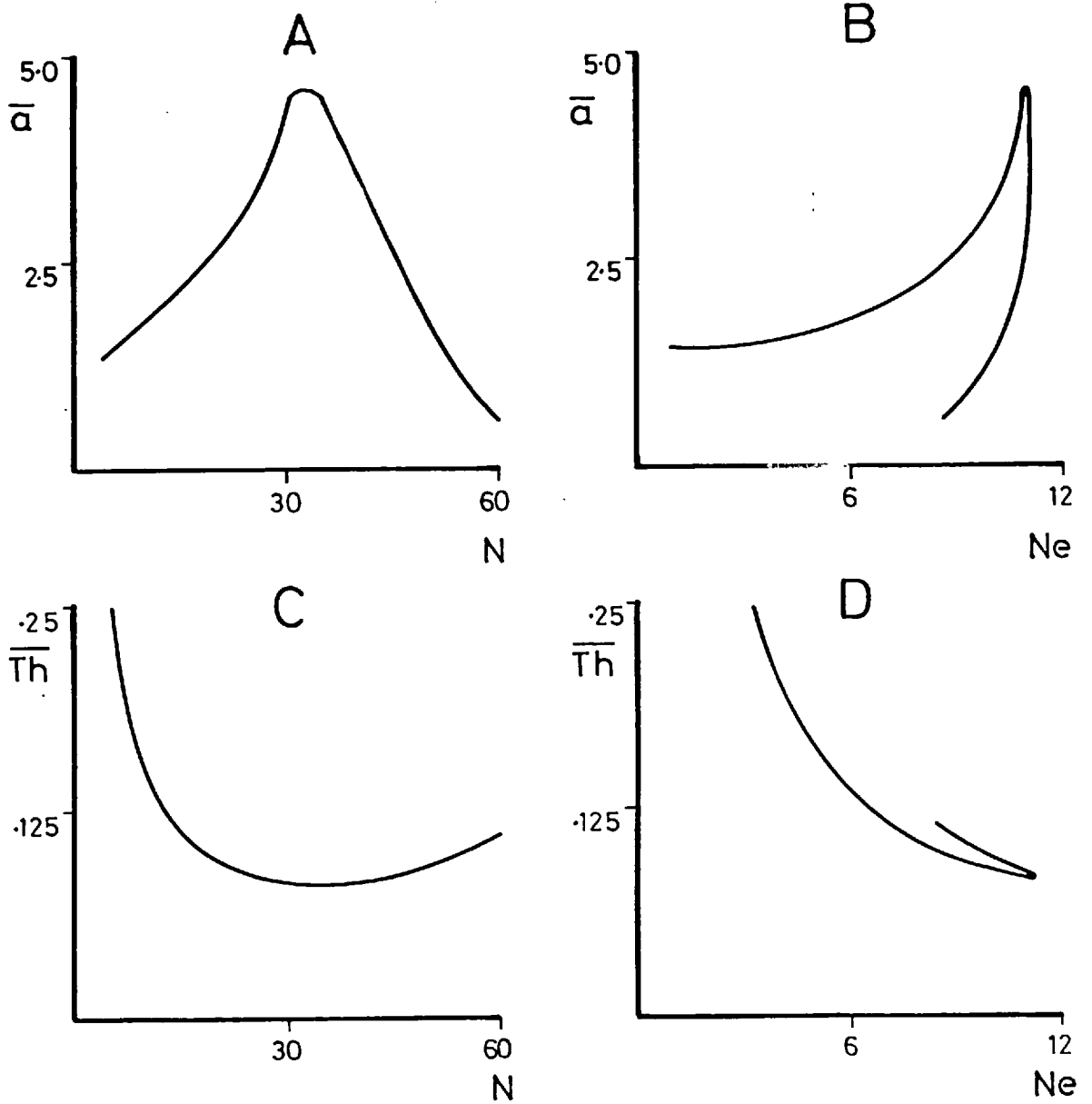


FIGURE 2.6 Mean parameter (\bar{a} , mean search efficiency; \bar{Th} , mean handling time) values calculated from the hypothetical dome-shaped functional response of Fig. 2.2C. \bar{Th} is kept constant at 0.0833, and \bar{a} is shown as a function of N , the prey density (A), and as a function of N_e , the number of prey eaten (B). \bar{a} is kept constant at 0.8, and \bar{Th} is shown as a function of N , the prey density (C) and as a function of N_e , the number of prey eaten (D).

2.4.3 Models of the dome-shaped functional response

2.4.3.1 Model based upon the data of Williams (pers. comm.)

Williams (pers. comm.) obtained data on the predation of Notonecta glauca L. upon Gammarus pulex (L.), in a bucket over a period of five hours. The resultant functional response (Fig. 2.7A) was dome-shaped. To obtain further information, Williams made some continuous observations, and the time taken for successive feeds was recorded.

This data of the individual handling times can be defined using an instantaneous function of the number of prey eaten. A logarithmic relationship of the form:

$$T_h = n \ln N_e + c,$$

where n and c are constants, was found to be suitable. This relationship can be integrated with respect to N_e and substituted into the Random Predator Equation to give:

$$N_e = N(1 - \exp(-a(T - [n(N_e \ln N_e - N_e) + c N_e]N_e))).$$

This equation is rather cumbersome, and the logarithmic relationship did not provide a good description of the data, and so the handling time was defined as an overall function of the number of prey eaten. Thus, transforming the individual handling time to mean handling times, a log/log relationship of the form:

$$\overline{\ln T_h} = n \ln N_e + c \quad . . . 2.5$$

was found to be necessary to obtain a good fit to the data ($n = -0.3288$, $c = 3.836$; $F = 455$, $df = 1,6$, $P < 0.001$). This relationship is shown in Fig. 2.7C. Transforming Eqn. 2.5 gives:

$$\overline{T_h} = \exp(n \ln N_e + c)$$

which can be substituted into the Random Predator Equation to give:

$$N_e = N(1 - \exp(-\bar{a}(T - [\exp(n \ln N_e + c)]N_e))) \quad . . 2.6$$

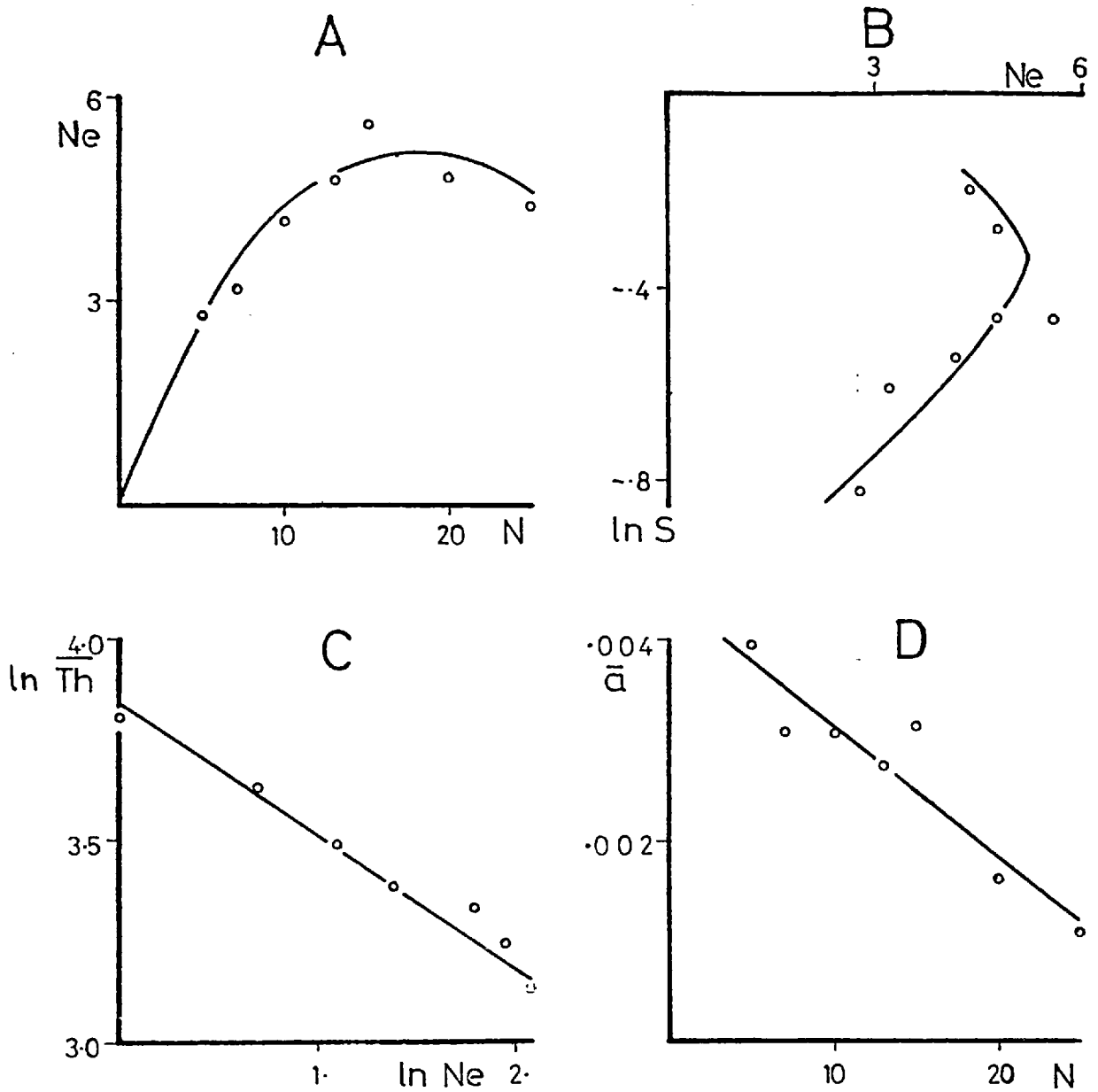


FIGURE 2.7 Figure of the model developed for the dome-shaped functional response based upon the data of Williams (pers. comm.). (A) - functional response and (B) - $\ln S \times Ne$ figures fitted with the model (Eqn. 2.8) with parameters calculated from (C) and (D). (C) - $\ln \bar{Th}$ plotted against $\ln Ne$ to show the relationship of Eqn. 2.5 ($\bar{Th} = \exp(n \ln Ne + c)$; $n = -0.3288$, $c = 3.836$; $F = 455$, $df = 1,6$, $P < 0.001$). (D) - \bar{a} (calculated by substituting Eqn. 2.5 into the Random Predator Equation and, for each set of predation data, solving for \bar{a}) plotted against N (the prey density) to show the relationship of Eqn. 2.7 ($\bar{a} = mN + d$; $m = -0.0001284$, $d = 0.004407$; $F = 41$, $df = 1,5$, $P < 0.01$).

By substituting for N and N_e in Eqn. 2.6, a series of values for \bar{a} (the mean search efficiency) was obtained. These were described by the relationship:

$$\bar{a} = m N + d, \quad . . . 2.7$$

as shown in Fig. 2.7D ($m = -0.0001284$, $d = 0.004407$; $F = 41$, $df = 1,5$, $P < 0.01$). Substituting Eqn. 2.7 into Eqn. 2.6 now gives:

$$N_e = N(1 - \exp(-[m N + d](T - [\exp(n \ln N_e + c)] N_e))) \quad . . . 2.8$$

Using this Equation (Function XNEWTW, Appendix Section A1.2.3), the functional response fitted to the data (Fig. 2.7A; $F = 41$, $df = 1,5$, $P < 0.01$) and the $\ln S \times N_e$ relationship (Fig. 2.7B, $F = 120$, $df = 1,5$, $P < 0.001$) were obtained.

It can be seen that, at low prey densities, the effects of the decreasing search efficiency and handling time cancel each other out, leading to a normal type II functional response. At high prey densities, however, the rate of change of the handling time is greatly reduced, and the continuing decrease in the search efficiency leads to a drop off in the numbers of prey found.

Comparing this model with the values of the search efficiency and handling time suggested by Fig. 2.6, differences can be seen. Thus, the initial increase in search efficiency in Fig 2.6 is not necessary to produce a dome-shaped functional response, but is a result of the initial freehand figure of the functional response (Fig. 2.2). In the case of the handling time, Fig. 2.6D shows a relationship which could be described by Eqn. 2.5. The two parts of the dome in Fig. 2.6A (increasing N_e and decreasing N_e) could, if symmetrical, be described by the one equation. The occurrence of a minimum handling time at the maximum prey consumption would not, by itself, produce a dome-shaped response, but it would accentuate one.

Thus, decreasing the mean search efficiency as a linear function of prey density will produce a dome-shaped functional response. Extrapolating such a model to higher prey densities

would lead to negative values for the search efficiency; a more suitable function is found in the next section.

2.4.3.2 Model based upon the data of Yao (pers. comm.)

Another model of a dome-shaped functional response was developed in collaboration with D.J. Rogers and D. Yao using data of Yao (pers. comm.). In Yao's work, 24 hour continuous observations were made of the predation of the mite Phytoseilus persimilis Athias-Henriot on another mite, Tetranychus urticae Koch. This yielded estimates of the handling time and search efficiency over a range of prey densities.

The handling time was found to be described by the linear relationship:

$$\bar{T}_h = n N_e + c, \quad . . . 2.9$$

where n and c are constants (Fig. 2.8C; n = - 0.000451, c = 0.0224; F = 176, df = 1,4, P < 0.001). The search efficiency, however, was best described by the relationship:

$$\begin{aligned} \ln \bar{a} &= m \ln N + d \\ \text{or } \bar{a} &= \exp(m \ln N + d), \quad . . . 2.10 \end{aligned}$$

where m and d are constants (Fig. 2.8C, line 1; m = - 1.940, d = 6.324; F = 31, df = 1,4, P < 0.01). Hence substitution of Eqns. 2.9 and 2.10 into the Random Predator Equation gives:

$$N_e = N(1 - \exp(- [\exp(m \ln N + d)](T - [n N_e + c]N_e))) \quad . . . 2.11$$

This equation, together with the parameters (n, c, m, d) derived from the continuous observations, was used to calculate the functional response (Fig. 2.8A, line 1) and the ln S x N_e relationship (Fig. 2.8B, line 1). It can be seen that these calculated lines give a very poor fit to the data.

Since, in making continuous observations, the search efficiency is more likely to be estimated incorrectly than the handling time, substitution of N and N_e in Eqn. 2.11 was used to

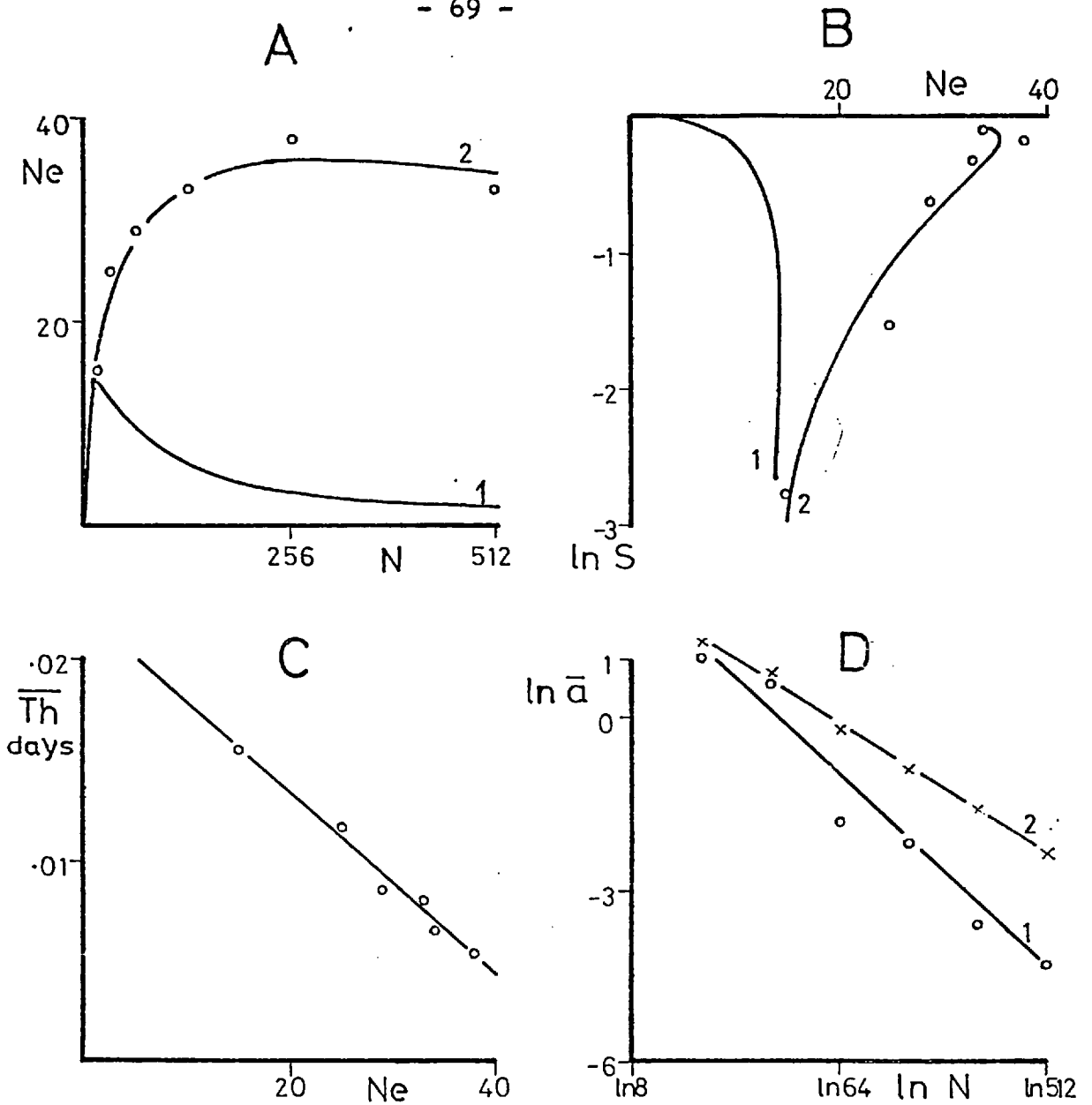


FIGURE 2.8 Figures of the model developed for the dome-shaped functional response based on the data of Yao (pers. comm.). (A) - functional response and (B) - $\ln S \times Ne$ figure fitted with the model (Eqn. 2.11): line 1 - all parameters obtained by continuous observation; line 2 - parameters describing \bar{a} abstracted from functional response data. (C) - \overline{Th} plotted against Ne (the number of prey eaten) to show the relationship of Eqn 2.9 ($\overline{Th} = n Ne + c$, $n = -0.000451$, $c = 0.0224$; $F = 176$, $df = 1,4$, $P < 0.001$). (D) - $\ln \bar{a}$ plotted against $\ln N$ to show the relationship of Eqn. 2.10: line 1 - data obtained by continuous observation ($\bar{a} = \exp(m \ln N + d)$, $m = -1.940$, $d = 6.324$; $F = 31$, $df = 1,4$, $P < 0.01$); line 2 - data obtained by substituting Eqn. 2.9 into the Random Predator Equation and solving for \bar{a} ($\bar{a} = \exp(m \ln N + d)$, $m = -1.082$, $d = 4.361$; $F = 258$, $df = 1,4$, $P < 0.001$).

obtain estimates of the search efficiency. The resultant estimates were found to be well described by Eqn. 2.10 (Fig. 2.8D, line 2; $m = -1.082$, $d = 4.361$; $F = 258$, $df = 1,4$, $P < 0.001$). Using the new values for the parameters m and d , the functional response and $\ln S \times N_e$ relationship were recalculated (Fig. 2.8A line 2 and 2.8B line 2) and resulted in a good fit to the data (functional response - $F = 120$, $df = 1,4$, $P < 0.001$; $\ln S \times N_e$ - $F = 252$, $df = 1,4$, $P < 0.001$).

The use of Eqn. 2.10 to describe \bar{a} is applicable over any range of prey densities, and so is more useful than Eqn. 2.7 proposed in the last section. The model of the handling time (Eqn. 2.5) of the last section is, however, applicable over a wider range of prey consumption, and so may be more useful than the relationship used in this section. Accordingly, a more widely useable equation to describe a dome-shaped functional response would be:

$$N_e = N(1 - \exp(- [\exp(m \ln N + d)] \times (T - [\exp(n \ln N_e + c)] N_e))).$$

2.5 SUMMARY AND CONCLUSIONS

- 1 In abstracting the parameters of the Random Predator Equation from functional response data, the $\ln S \times Ne$ regression technique suggested by Rogers (1972) is not suitable, and an alternative least squares best fit technique is proposed. The figure of $\ln S \times Ne$ can, however, often be informative in the interpretation of functional response data (Sections 2.3-2.4).
- 2 Type II functional responses can often be obtained by varying the parameters of the Random Predator Equation (Section 2.4.2; Figs. 2.3 & 2.4). These responses can still be adequately described by the Random Predator Equation, the parameters giving an overall measure of searching efficiency and handling time (Hassell, Lawton & Beddington, 1976).
- 3 Sigmoid functional responses can be obtained by defining the mean search efficiency (\bar{a}) as an increasing function of the prey density or the number of prey eaten. This relationship can be linear (Section 2.4.2, Fig. 2.3) or curvilinear (Fig. 2.5). Hassell, Lawton & Beddington (1977) and Hassell (pers. comm.) have suggested sigmoid functional response models based on an increasing value of a in response to the prey density which levels off at some maximum value (i.e. similarly to the type II functional response). Since predation at high prey densities is largely defined by the handling time, rather than the search efficiency, this difference is unimportant. Functional response equations based on this description of \bar{a} are introduced in Section 3.4.2. An alternative approach which results in sigmoid functional responses is to define the mean handling time (\bar{T}_h) as a curvilinear function of the prey density or number of the prey density or number of prey eaten, such as are shown in Fig. 2.6C & D.
- 4 The dome shaped functional response is obtained by defining \bar{a} as a decreasing function of the prey density. This can be linear (Section 2.4.3.1, Fig. 2.7D) or curvilinear (Section 2.4.3.2, Fig. 2.8D). The dome shaped functional response is emphasized by defining \bar{T}_h as an increasing function of the prey density (Section 2.4.2, Fig. 2.6C).

CHAPTER 3

PREFERENCE EXPERIMENTS WITH COCCINELLA SEPTEMPUNCTATA L. AND BREVICORYNE BRASSICAE (L.)

3.1 INTRODUCTION

In this section, a predator-prey interaction is examined, in which two types of prey are available. The functional responses to the individual prey types are used in an attempt to predict predation when both are present. The predators used are adults of the coccinellid beetle, Coccinella septempunctata L. (the seven spot ladybird). The prey are the cabbage aphid, Brevicoryne brassicae (L.), either as first instar aphids (type I) or as apterate adults and large aphids of similar size in the penultimate instar (type II).

Various descriptions of preference have been discussed in the literature survey (Section 1.3.2). In measuring preference, Murdoch's (1969) model is a simple starting point. He suggested that, in the absence of switching, a constant parameter C can be used to describe preference. He defined C as the proportional difference between the ratio of the prey types in the environment and the ratio in the diet:

$$N_e / N_e' = C N / N' \quad . . . 3.1$$

where N and N' are the numbers of the two prey types present and N_e and N_e' are the numbers which are eaten. This relationship is shown in Fig. 3.1 where the null hypothesis is represented by a slope of unity. Murdoch (1969) also suggested that an appropriate predation model may be used as a null hypothesis in preference

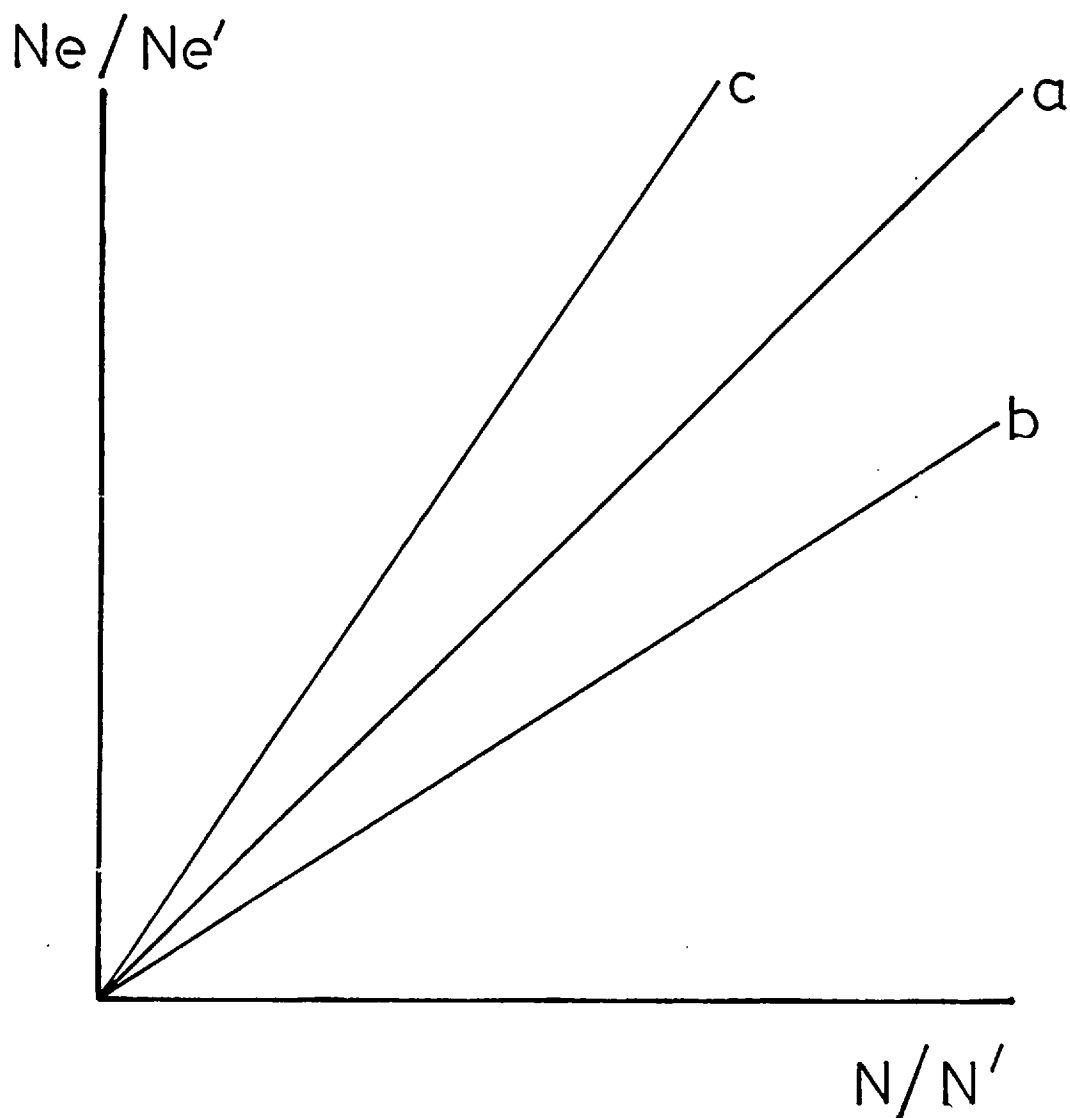


FIGURE 3.1 Generalized graph illustrating Murdoch's (1969) model of preference: $Ne/Ne' = C N/N'$, where N is the number of prey type I present, Ne is the number of prey type I eaten, and N' & Ne' refer to the same figures for prey type II. The lines a,b,c show three possible situations: a - no preference ($C = 1$); b - preference for prey type II ($C < 1$); c - preference for prey type I ($C > 1$).

studies. The derivation of such a model is given in Section 1.3.3.

In this section, the functional responses are used to predict predation when both prey types are present; hence, the ratios used in the Murdoch plot (Fig. 3.1) are found. These predictions are compared with the actual numbers and ratios observed.

3.2 EXPERIMENTAL METHOD

3.2.1 The Arenas

The arenas used in this study are based on those used by Marks (Marks, 1971; Murdoch & Marks, 1973) in similar experiments using coccinellid larvae. The arenas were plastic petri dishes of diameter 9 cm, with a moistened filter paper on the bottom. The sides of the petri dish top were coated with fluon to prevent the experimental animals leaving the bottom of the arena. The aphids were distributed on the filter paper at 10.00 h, a conscious effort being made to distribute them at random. The aphids were then left to disperse and settle down until 11.00 h when the coccinellids were introduced. One coccinellid was put in the middle of each arena. Each run lasted two hours and was conducted at 20°C under constant illumination from fluorescent tubes. At the end of each experiment, the number of prey eaten, and prey types if appropriate, were scored.

3.2.2 The Prey: *Brevicoryne brassicae* of two size classes

Cultures of *B. brassicae* were maintained on potted brussels sprout plants in a greenhouse, and in a constant environment experimental room (20°C and 60% R.H.). The two types of prey mentioned in the introduction were:

Type I: first instar aphids. A sample of ten was weighed giving a mean weight of 0.0324 g (S.E. of mean = 0.007),

Type II: adult apterous aphids or nymphs of similar size in the penultimate instar. Weighing a sample of ten gave a mean weight of 0.624 g (S.E. of mean = 0.095).

3.2.3 The Predators: *Coccinella septempunctata* adults

Adults of *C. septempunctata* were collected daily during the course of the experiments at approximately 15.00 h. They were obtained from the patch of broad beans at Hill Bottom (Silwood Park). It is assumed that when collected all the coccinellids were satiated, due to feeding upon the large numbers of

Aphis fabae Scop. present on the bean plants. The coccinellids were then kept without food in individual 3" X 1" glass tubes at 20°C until the experiments started at 11.00 h the next morning. Any coccinellids which did not look healthy or which had appendages missing were discarded. No differentiation of the sexes was made for this work, since there was no difference in the mean numbers of aphids eaten by males or females in experiments when ten type I prey were exposed to predation under experimental conditions (Table 3.1). These results are sufficiently homogeneous to warrant pooling of the experimental results using male and female coccinellids. Details of the sexual differences are given by Pope (1953).

3.3 RESULTS AND ANALYSIS

The predation results are tabulated in Tables 3.2 (both prey present), 3.3 (type I present only) and 3.4 (type II present only).

SEX	NUMBERS EATEN	S.E. OF	
		MEAN	MEAN
Male	5 4 9 5 7 10 7 3 7 5	6.58	0.66
Female	5 5 8 3 8 6 9 10	6.75	0.84

TABLE 3.1 Predation of C. septempunctata when offered ten type II prey under experimental conditions. The means are not significantly different ($t = 1.45$, $df = 18$, $P > 0.1$).

PREY DENSITY TYPE I / TYPE II	NUMBER OF PREY EATEN TYPE I / TYPE II	NUMBER EATEN		RATIO OF N/N'	RATIO OF Ne / Ne'	
		MEAN	S.E.		MEAN	S.E.
		TYPE I / II	TYPE I / II			
16 / 2	6/2 8/2 11/2 6/2 11/1 16/2 15/2	10.43 / 1.86	1.53 / 0.14	8.00	6.00	1.13
12 / 4	3/3 10/4 10/4 7/2 8/4 10/4	8.00 / 3.50	1.13 / 0.34	3.00	2.33	0.33
8 / 6	8/4 7/6 2/4 0/3 0/3 1/5	3.00 / 4.17	1.46 / 0.48	1.33	0.64	0.32
4 / 8	0/4 1/4 1/7 2/5 4/6 2/4	1.67 / 5.00	0.56 / 0.52	0.50	0.33	0.10

TABLE 3.2 Predation of C. septempunctata on B. brassicae when both prey types are present.

DENSITY	NUMBER EATEN	\bar{N}_e	S.E.	$\ln \bar{S}$	$\overline{\ln S}$	S.E.
1	0 0 1 1 1 1 1 1 1 1 1	0.82	0.12	- 1.71	*	
2	0 0 1 1 1 1 1 2 2 2 2	1.18	0.23	- 0.89	*	
4	0 0 0 1 1 2 2 2 3 4 4 4 4	2.08	0.45	- 0.73	*	
8	0 2 2 4 4 5 6 6 7 8 8 8	5.00	0.77	- 0.98	*	
16	9 10 12 13 14 14 14 16	12.75	0.82	- 1.59	*	
32	14 18 20 25 27 31	22.50	2.57	- 1.21	- 1.54	0.43
64	15 20 27 30 32 32 33	27.00	2.62	- 0.55	- 0.56	0.07
100	10 17 24 28 29 34 35	25.29	3.43	- 0.29	- 0.30	0.04

TABLE 3.3 Predation of C. septempunctata on B. brassicae with type I present only. Data given of the number eaten (N_e), the mean number eaten (\bar{N}_e), the logarithm of the mean proportion of prey surviving ($\ln \bar{S}$), and the mean of the logarithmic values of the proportion of prey surviving ($\overline{\ln S}$). The symbol * is used to denote a value of $\overline{\ln S}$ which can not be evaluated due to total predation in one or more replicates.

DENSITY	NUMBER EATEN (Ne)	\bar{N}_e	S.E.	$\ln \bar{S}$	$\overline{\ln S}$	S.E.
1	0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	0.94	0.06	- 2.81	*	
2	0 1 1 2 2 2 2 2 2 2 2 2	1.67	0.19	- 1.80	*	
4	0 1 1 1 2 2 3 3 4 4 4 4	2.42	0.42	- 0.93	*	
8	0 2 2 3 3 3 3 3 4 4 6 6 6 6 7 8	4.13	0.54	- 0.73	*	
16	1 3 3 3 3 4 4 4 5 6 8 8 9 14 16	6.07	1.07	- 0.48	*	
25	5 6 8 8 8 8 10 10 11 11 12 12 14 17	10.00	0.85	- 0.51	- 0.54	0.06
50	8 9 10 12 15 15	11.50	1.23	- 0.26	- 0.26	0.03

TABLE 3.4 Predation of C. septempunctata on B. brassicae with type II present only. Data given of the number of prey eaten (Ne), the mean number of prey eaten (\bar{N}_e), the logarithm of the mean proportion of prey surviving ($\ln \bar{S}$), and the mean of the logarithmic values of the proportion of prey surviving ($\overline{\ln S}$). The symbol * is used to denote a value of $\overline{\ln S}$ which can not be evaluated due to total predation in one or more replicates.

3.3.1 Application of Murdoch's Model of Preference

Murdoch (1969) suggests that preference can be readily examined by plotting the ratio of the numbers of the two prey types occurring in the diet against the ratio of the numbers of the prey types in the environment. The resultant slope C is a measure of preference (see Eqn. 3.1 and Section 1.3.2). This is shown in Fig. 3.2 using the data from Table 3.2. The null hypothesis of no preference implies that the ratios for the diet and the environment are equal (i.e. $N_e/N_{e'} = N/N'$) and C the measure of preference is unity. In Fig. 3.2 the data has been described by a line through the means and origin, giving a value for C of 0.725 which is significantly different from unity ($t = 2.54$, $df = 25$, $.02 > P > .01$). This shows that the coccinellids demonstrate preference towards prey type II.

In order to try to explain this preference, the functional responses to the individual prey types will be used to predict consumption of prey in the mixed prey situation.

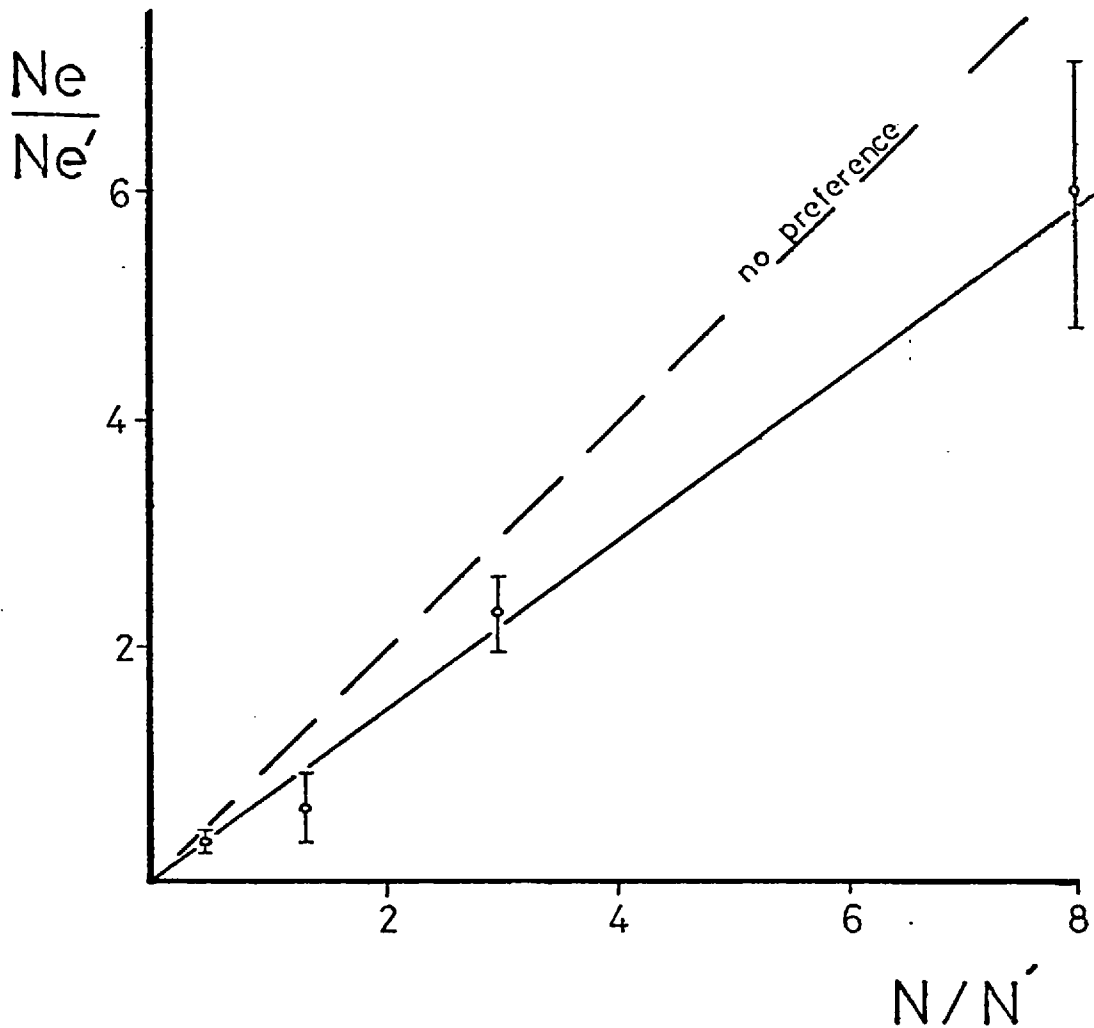


FIGURE 3.2 Predation by C. septempunctata when both prey types of B. brassicae are present - graph of the ratio of the two prey types eaten (N_e/n_e') plotted against the ratio of their initial densities (N/N'). The fitted line (through the means and the origin) has a slope of 0.73 which is significantly different from unity ($t = - 2.54, df = 25, 0.02 > P > 0.01$).

N_e/N_e' plotted as the mean \pm S.E. of the mean.

3.3.2 Functional Responses to Type I Prey

Examination of the plotted functional response (Figs. 3.5, 3.7; from data in Table 3.3), shows that the response is somewhat sigmoid in shape, and that a slightly reduced number of prey is eaten at the highest prey density. This tendency for the response to be dome shaped is probably due to experimental error and will be considered as such in this analysis. Dome shaped and sigmoid functional responses have already been considered in Chapter 2. When the $\ln S \times N_e$ plot (logarithm of the proportion of prey surviving plotted against the number of prey eaten; see Sections 2.3 & 2.4) is examined (Fig. 3.3) the deviations from a Holling type II response are obvious. Interpreting this graph as described in Section 2.3, the relationship can be divided into four parts as shown in Fig. 3.3. Part 1 is due to the phenomenon of 'over-predation' at low prey densities which will be dealt with in Section 3.3.5. Parts 2 and 3 are the two phases of the sigmoid response - part 2 being density dependent and part 3 inversely density dependent. Part 4 is due to the dome shape which is not considered significant. Due to the small number of data points at the high prey densities, a prey-density-sequence plot was necessary to show this dome-shaped response (see Section 2.3).

Rogers (1972) suggested that in order to fit the Random Predator Equation to data, the regression of $\ln S \times N_e$ can be used to find values for the parameters a (search efficiency) and T_h (handling time) (Section 2.2). Figure 3.3 shows the calculated regression line; the resultant functional response gives a poor fit to the data ($F = 19.7$, $df = 1,7$, $P > .05$).

An alternative model of this response is shown in Figs. 3.4 and 3.5. The model involves the elimination of the two points for $N = 1$ and 2, where, as previously noted, 'over-predation' at low prey densities occurs. The remaining points are then considered to form a V shape (Section 2.3) and a regression is fitted to each arm of the V. The points for $N = 4, 8, 16$ are fitted to one regression, while the points for $N = 16, 32, 64, 100$ are fitted to the other. Due to the negative slope and intercept of the first regression, a negative handling time results. This, as discussed below, can be considered in terms of increased appetite or

rate of search, which is measured in terms of increased time available for each prey eaten. The resultant equations are:

$$\begin{aligned} N_e &= N(1 - \exp(-0.0046(T + 17.58 N_e))) \\ N_e &= N(1 - \exp(-0.0226(T - 3.635 N_e))) \end{aligned} \quad \dots 3.2$$

These equations can be solved simultaneously to give an intersection point of $N = 16.46$, $N_e = 13.22$. When the functional response is calculated from Eqns. 3.2, it provides a good fit to the data (Fig. 3.5, $F = 61.6$, $df = 3,4$, $P < 0.001$).

Another model of the sigmoid functional response is suggested by Hassell, Lawton & Beddington (1977). They suggest that, to obtain a sigmoid functional response, the search efficiency varies in response to prey density in much the same way as prey consumption varies with prey density in a type II functional response. Accordingly, they suggest an equation to describe search efficiency of the form:

$$a = b N / (1 + c N) \quad \dots 3.3$$

where b and c are constants. This can be taken as an instantaneous equation for a and substituted into the Holling Disc Equation (Eqn. 1.2.8):

$$N_e = b N^2 / (1 + c N + b Th N^2).$$

To allow for exploitation, this can be integrated over the period T :

$$N_e = N(N - N_e)(c \ln S - b Th N_e - b T) \quad \dots 3.4$$

Alternatively, Eqn. 3.3 can be taken as an overall equation and substituted directly into the Random Predator Equation (Hassell, pers. comm.) to give

$$N_e = N \left[1 - \exp \left(\frac{-b N (T - Th N_e)}{1 + c N} \right) \right] \quad \dots 3.5$$

This simpler approach will be used to model the functional response to type I prey, and subsequently be referred to as the HLB model.

The authors suggest that the parameters of Eqn. 3.4 can be extracted from predation data by multiple regression analysis, but obtained poor descriptions of functional response data by this method. For the HLB model (Eqn. 3.5) this method will be used to find the parameters. Bearing in mind that the logarithm of the mean value of S ($\ln \bar{S}$) is used instead of the mean of the logarithmic values of S ($\overline{\ln S}$), this seems to be a reasonable approach. Furthermore, since the range of variation in the value of $\ln \bar{S}$ is not very great, the fit should not be excessively biased by any particular part of the response (cf. regression technique for the Random Predator Equation in Section 2.2). The resultant parameter values were: $b = 0.0019$, $c = 0.025$, $T_h = 4.09$ min. Once again, the first two points of the response were not included due to the deviation previously noted. The figure of $\ln S \times N_e$ based on these parameters is shown as Fig. 3.6; the functional response (Fig. 3.7) provides a good description of the data ($F = 234$, $df = 2,4$, $P < 0.001$). The shapes obtained are basically similar to those obtained using the two-regression model. The $\ln S \times N_e$ figure shows, however, that the two models diverge at extreme values of N_e . The HLB model shows a lower proportion of prey eaten at extreme values. Other differences will become apparent when predictions of the mixed prey situation are examined.

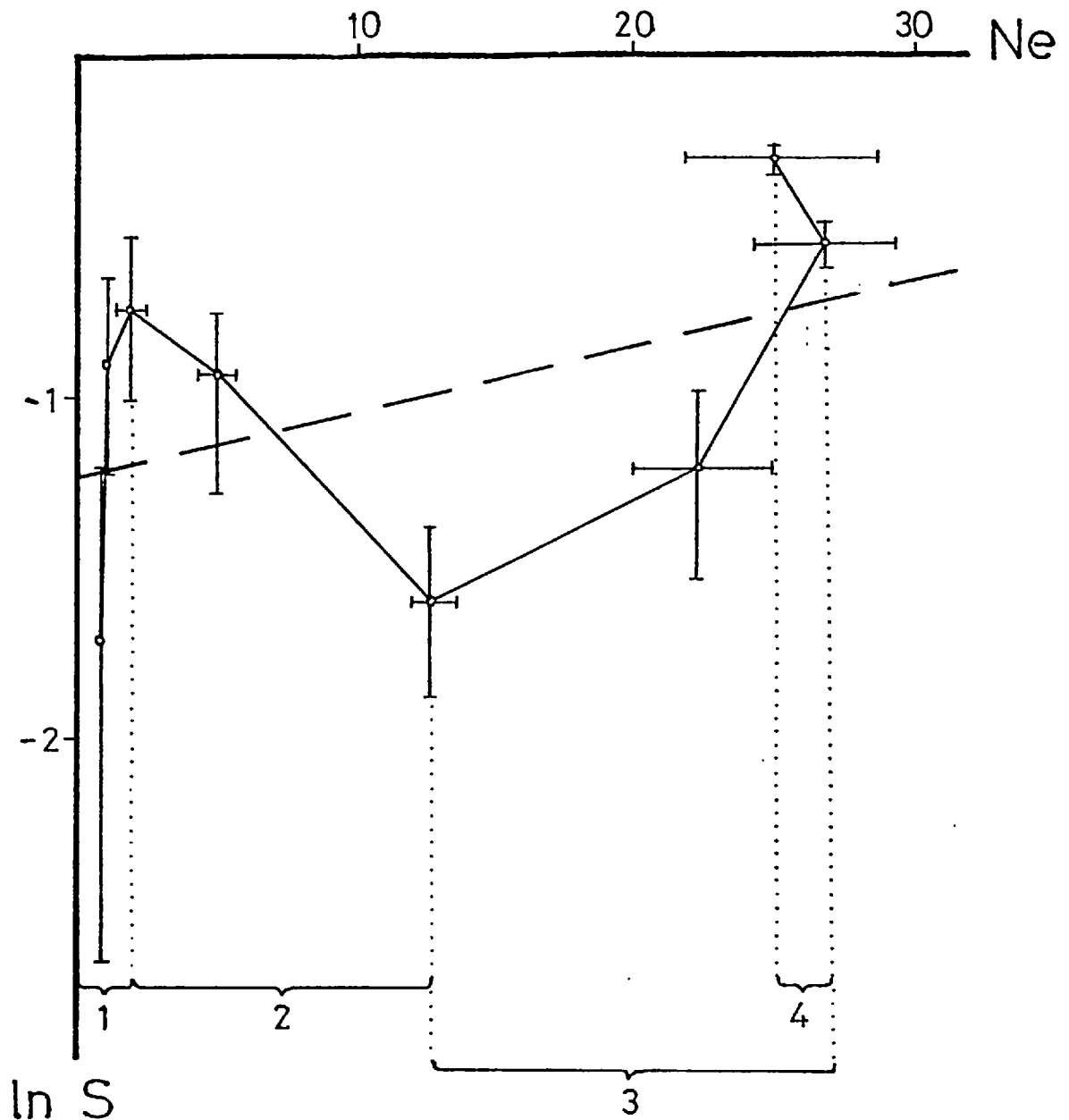


FIGURE 3.3 Predation of *C. septempunctata* on type I *B. brassicae* - figure of the logarithm of the proportion of prey surviving ($\ln S$) plotted against the number eaten (Ne) with the points linked in a prey density sequence and showing the linear regression. The relationship is divided into four parts, as is explained in the text (Section 3.3.2). The regression line (slope = 0.019, intercept = 1.122), clearly, is not a good fit.

Ne plotted as the mean \pm S.E. of the mean, $\ln S$ plotted as the logarithm of mean S ($\ln \bar{S}$) with limits calculated from the S.E. of the mean of Ne .

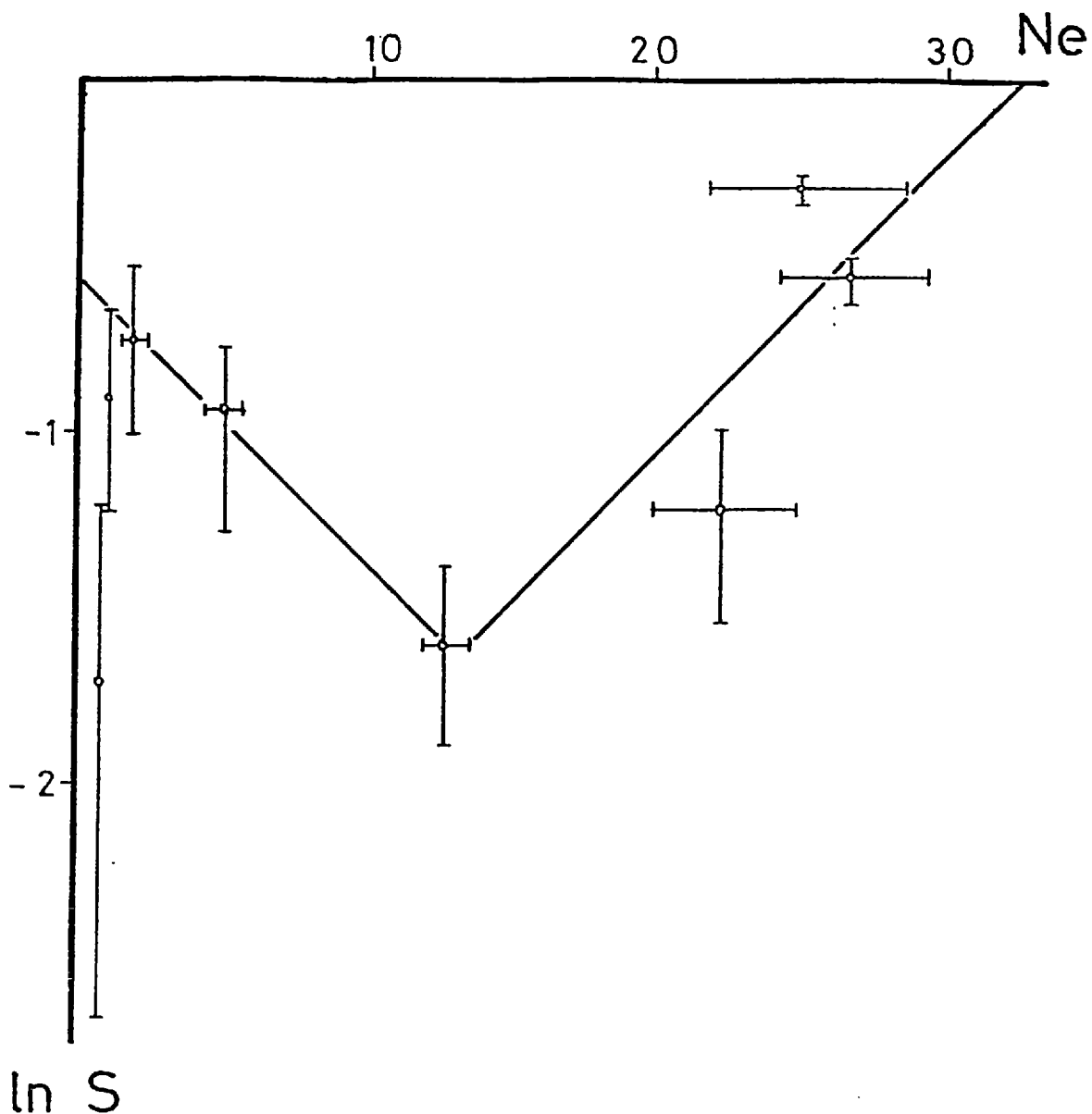


FIGURE 3.4 Predation of *C. septempunctata* on type I *B. brassicae* - figure of the logarithm of the proportion of prey surviving ($\ln S$) plotted against the number eaten (N_e) fitted with the two regression model. First regression (using the points for $N = 4, 8, 16$): slope = -0.081 , intercept = -0.553 ; $a = 0.0046/\text{min.}$, $T_h = -17.58$ min. Second regression (using the points for $N = 16, 32, 64, 100$): slope = 0.082 , intercept = -2.707 ; $a = 0.0226/\text{min.}$, $T_h = 3.635$ min.

N_e plotted as the mean \pm S.E. of the mean, $\ln S$ plotted as the logarithm of mean S ($\ln \bar{S}$) with limits calculated from the S.E. of the mean of N_e .

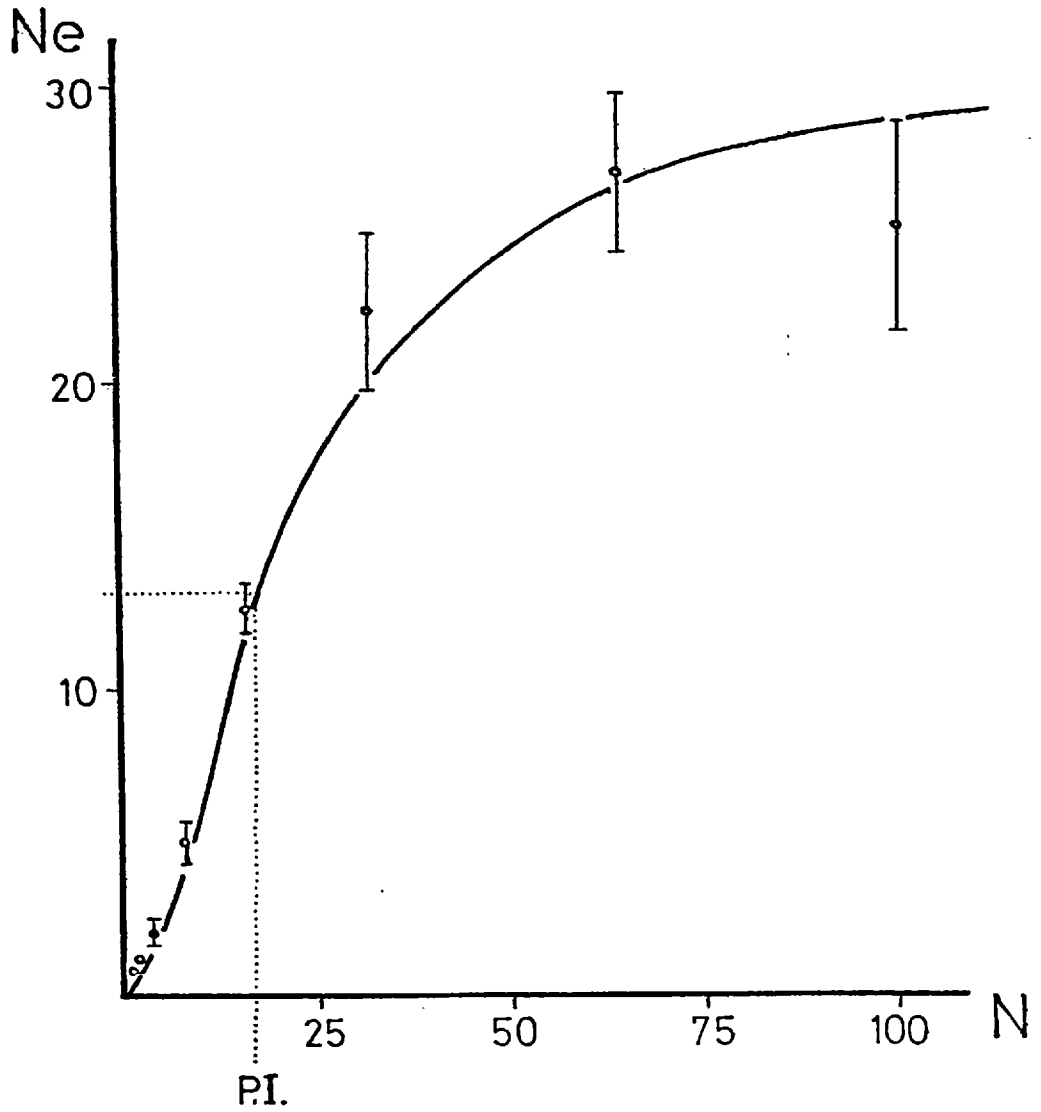


FIGURE 3.5 Functional response of C. septempunctata to type I B. brassicae - the number eaten (N_e) plotted against the initial prey density (N) - with the two regression model fitted. Below the point of inflexion (PI):

$$N_e = N(1 - \exp(- 0.0046(T + 17.58 N_e))),$$

and above the point of inflexion:

$$N_e = N(1 - \exp(- 0.226(T - 3.635 N_e))).$$

The number eaten is plotted as the mean \pm S.E. of the mean.

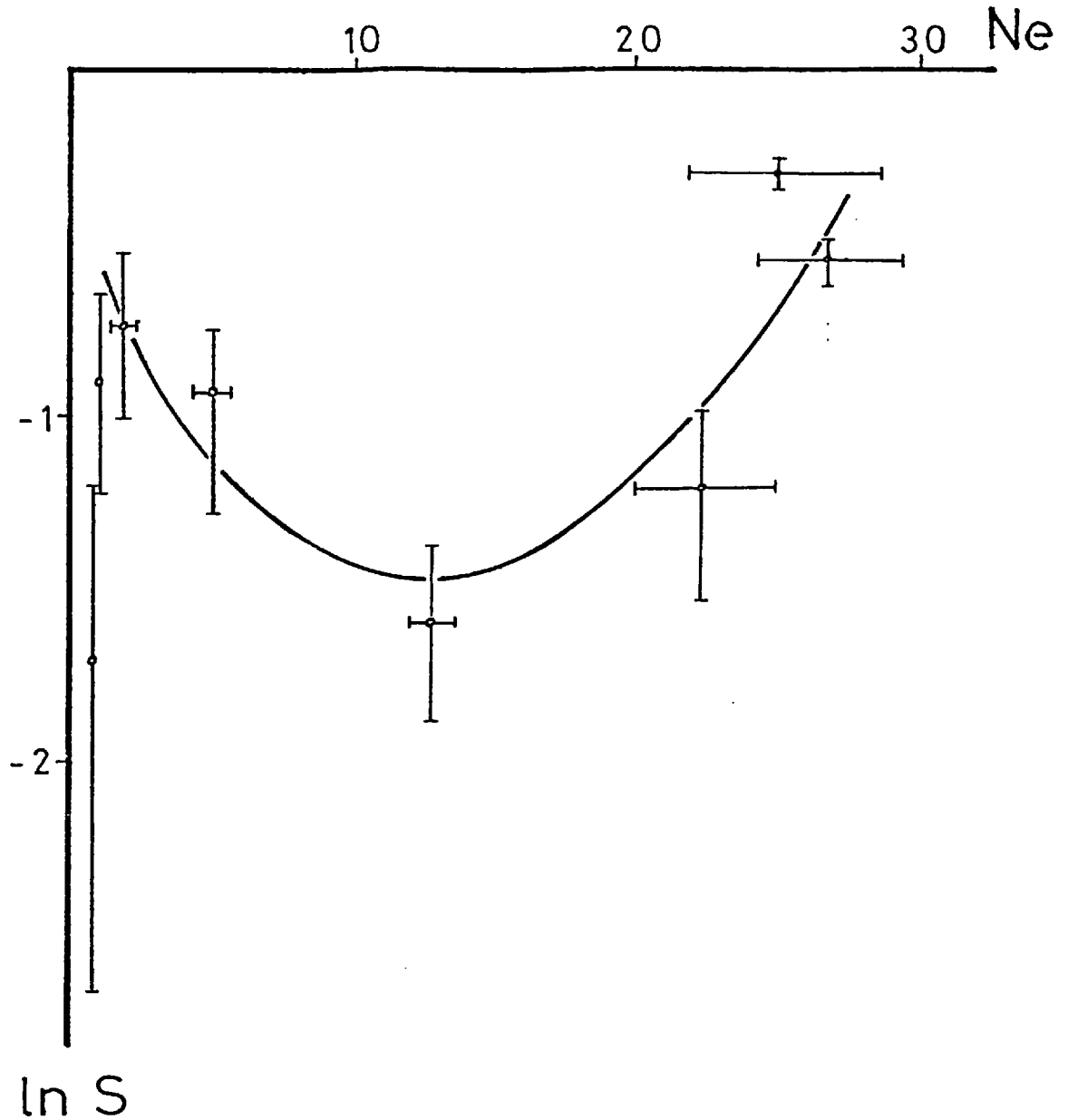


FIGURE 3.6 Predation of C. septempunctata on type I B. brassicae - figure of the logarithm of the proportion of prey surviving ($\ln S$) plotted against the number eaten (N_e) - fitted with the HLB model (Eqn. 3.5). The parameters used to calculate the line are $b = 0.00187$, $c = 0.0252$, $Th = 4.088$ min; these were obtained by a multiple regression analysis on the $\ln S \times N_e$ relationship (Section 3.3.2).

N_e plotted as the mean \pm S.E. of the mean, $\ln S$ plotted as the logarithm of mean S ($\ln \bar{S}$) with limits calculated from the S.E. of the mean of N_e .

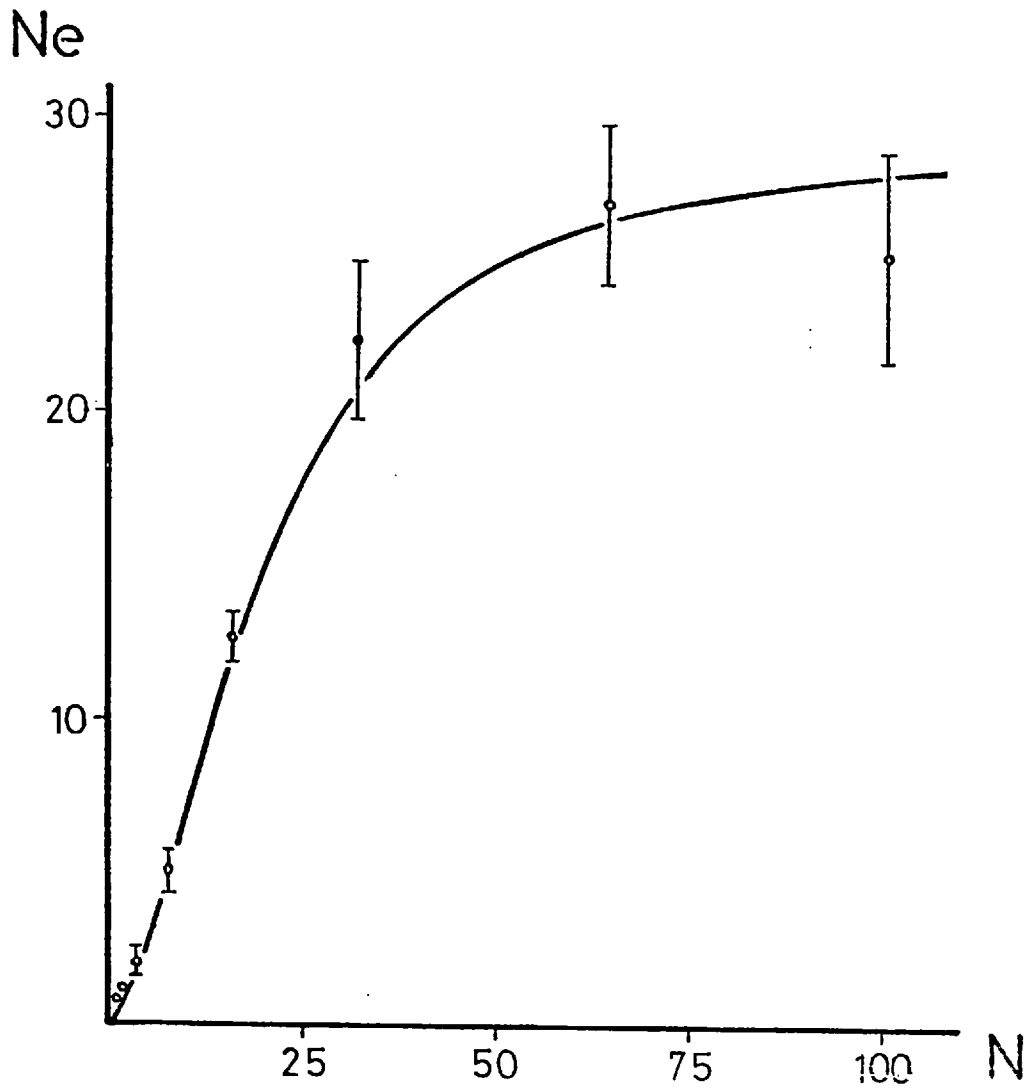


FIGURE 3.7 Functional response of C. septempunctata to type I B. brassicae - the number eaten (N_e) plotted against the initial prey density (N) - fitted with the HLB model (Section 3.3.2). Parameters as for Fig. 3.6.

The number eaten (N_e) plotted as the mean \pm S.E. of the mean.

3.3.3 Functional Response to Prey Type II

The functional response to prey type II is rather simpler than that to prey type I. Examination of the $\ln S \times N_e$ figure (Fig. 3.8) shows that the first two points again demonstrate 'over-predation' at low prey densities, which is dealt with in Section 3.3.5. It can be seen from the figure that the regression line based on all the points gives a poor fit to the data. The regression obtained by eliminating the first two data points, and the line obtained using the parameters resulting from the least squares technique (see Section 2.2 and Appendix Section A1.3) are effectively identical in this case, and provide a good description of the functional response (Fig. 3.9; $F = 169$, $df = 1,89$, $P < 0.001$).

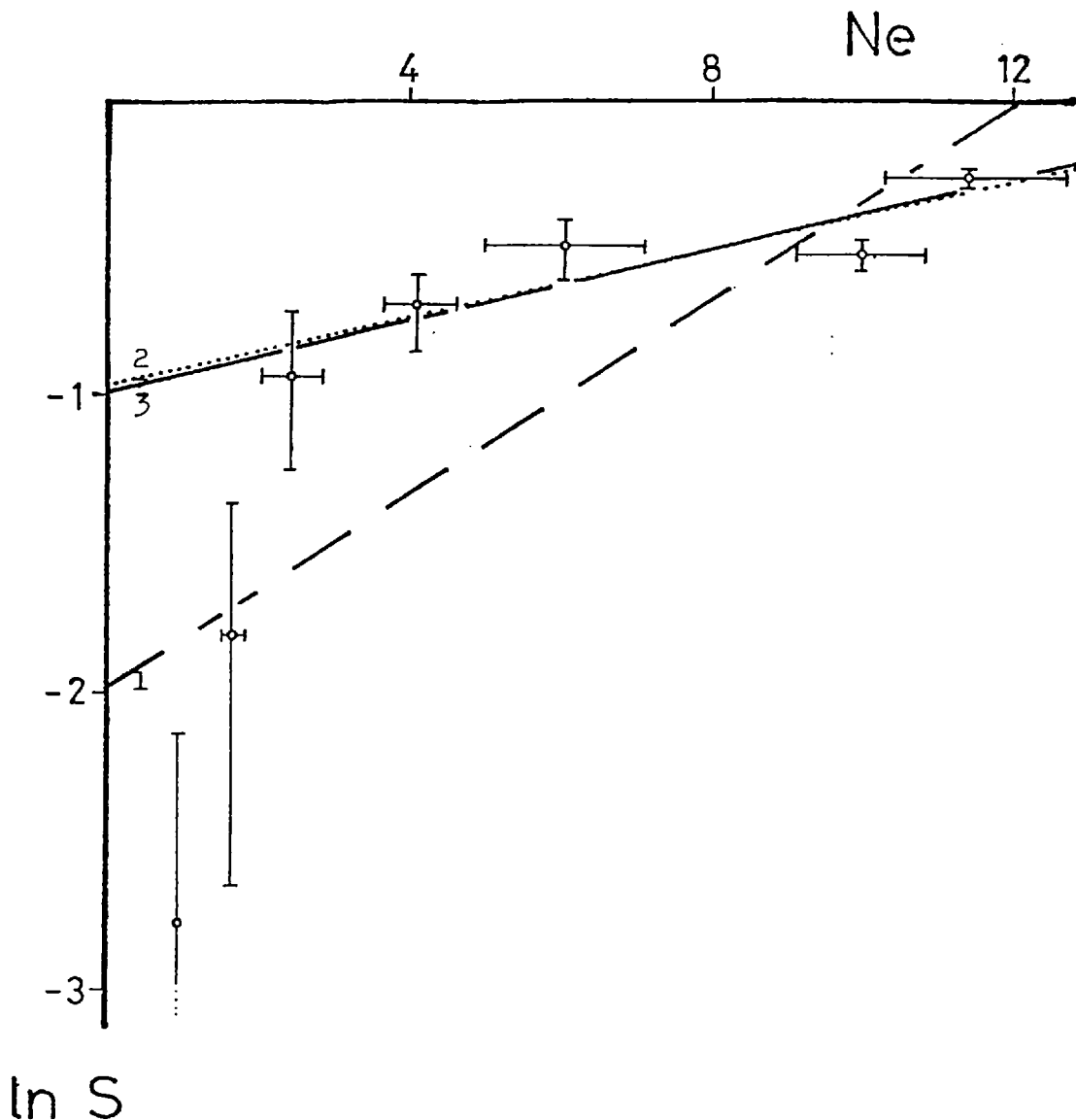


FIGURE 3.8 Predation of C. septempunctata on type II B. brassicae - figure of the logarithm of the proportion of prey surviving ($\ln S$) plotted against the number eaten (N_e) - with three fitted lines. Line 1: fitted regression using all points ($a = 0.017/\text{min.}$, $T_h = 10.0 \text{ min.}$), line 2: fitted regression ignoring points for $N = 1, 2$ ($a = 0.00808/\text{min.}$, $T_h = 7.21 \text{ min.}$), line 3: parameters obtained by the least squares best fit to the functional response ($a = 0.00817/\text{min.}$, $T_h = 7.185 \text{ min.}$).

N_e plotted as the mean \pm S.E. of the mean, $\ln S$ plotted as the logarithm of mean S ($\ln S$) with limits calculated from the S.E. of the mean of N_e .

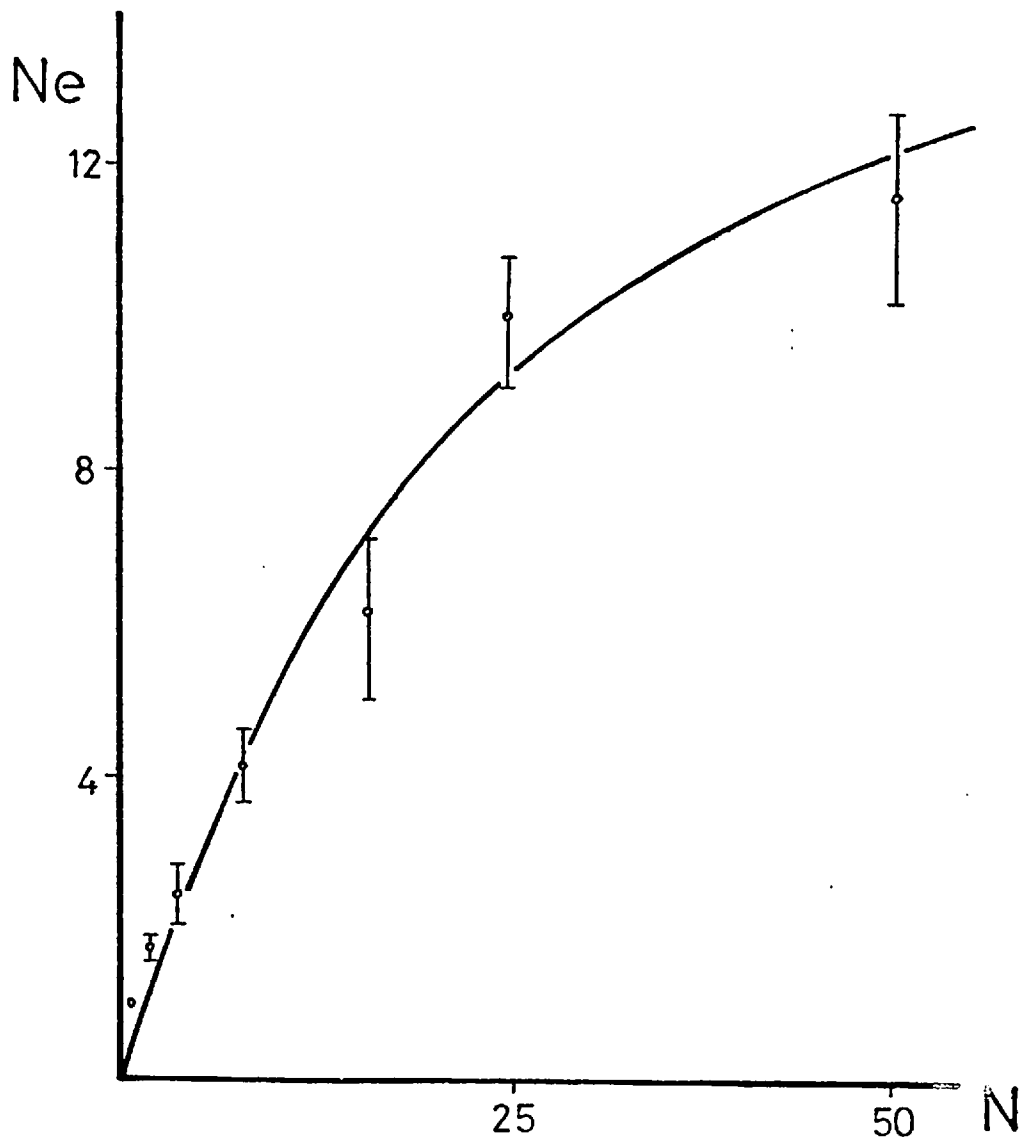


FIGURE 3.9 Functional response of C. septempunctata to type II B. brassicae - the number eaten (N_e) plotted against the initial prey density (N) - fitted with the Random Predator Equation using the parameters obtained by the least squares best fit to the functional response ($a = 0.00817/\text{min.}$, $T_h = 7.185 \text{ min.}$).

The number eaten (N_e) plotted as the mean \pm S.E. of the mean.

3.3.4 Prediction of predation with both prey types present

Both models used to describe the functional response to type I prey (Section 3.3.2) will be used, with the Random Predator Equation for the response to type II prey (Section 3.3.3), to predict predation when both types are present. This was done using a modified version of the computer programme PREDICT (see Appendix Section A1.5). The resultant predictions, together with the observed predation are shown in Figs. 3.10 & 3.11. Figure 3.10 shows that the predictions based on the two-regression model of the response to type I prey give a good fit to the observed predation ($\chi^2 = 0.69$, $df = 7$, $P > 0.99$). The prediction based on the HLB model (Fig. 3.11) clearly is not such a good fit ($\chi^2 = 1.49$, $df = 7$, $0.95 < P < 0.99$). The number of prey type I eaten is consistently overestimated, whilst the number of prey type II is consistently underestimated. Examination of the figure of $N_e/N_e' \times N/N'$ (Murdoch's model) (Fig. 3.12) shows that the two regression model gives a good fit to the observed ratios, whereas the HLB model predicts a switch in preference from type II to type I, which is clearly a very poor fit of the observed preference. These two apparently similar models of the sigmoid response give very different predictions when combined with a normal type II functional response to predict predation with both prey types present.

The explanation for this difference lies in the variations of a and T_h incorporated into the model. The HLB model assumes a constant handling time and a search efficiency defined by the initial prey density. The two-regression model for most of the range of prey densities considered involves a constant search efficiency and a negative value for the handling time. At the highest densities of prey type I considered there is a switch in parameters to a higher search efficiency and a small positive handling time. A negative handling time means that for each prey found, the time available for searching is increased by the 'handling time'. Since the experiments are of fixed duration this can not be the literal explanation. This apparent increase in searching time could be interpreted as an increase in activity (i.e. rate of search), as stimulation of appetite, or as some similar mechanism which could be measured as a negative handling time.

The important differences between these two models become apparent when predictions of predation are made for the situation with both prey types present. In both models the search efficiency increases over a range of increasing densities of prey type I. In the case of the two-regression model the search efficiency for both prey types is effectively increased as a result of the sigmoid response to prey type I. This is the result of search efficiency being defined as 'negative handling time' which leads to an increase in the time available for searching and handling both prey types. In the HLB model, however, the effect of varying the search efficiency is restricted to the one prey type due to the way it is incorporated into the model. In a simple experimental arena, as used here, where the prey are mixed together, it is to be expected that an increase in the search efficiency for one prey type will effectively also cause an increase in search efficiency for the other. In a more complex arena, where different techniques are used to search for different prey types, or where the prey types occur in different parts of the environment, one would expect the search efficiencies to be independent of each other (see Chapter 5). This difference would have to be considered whenever forms of the Random Predator Equation (or other predator prey models) involving varying parameters are combined to predict predation with two or more prey types present.

Ne & Ne'

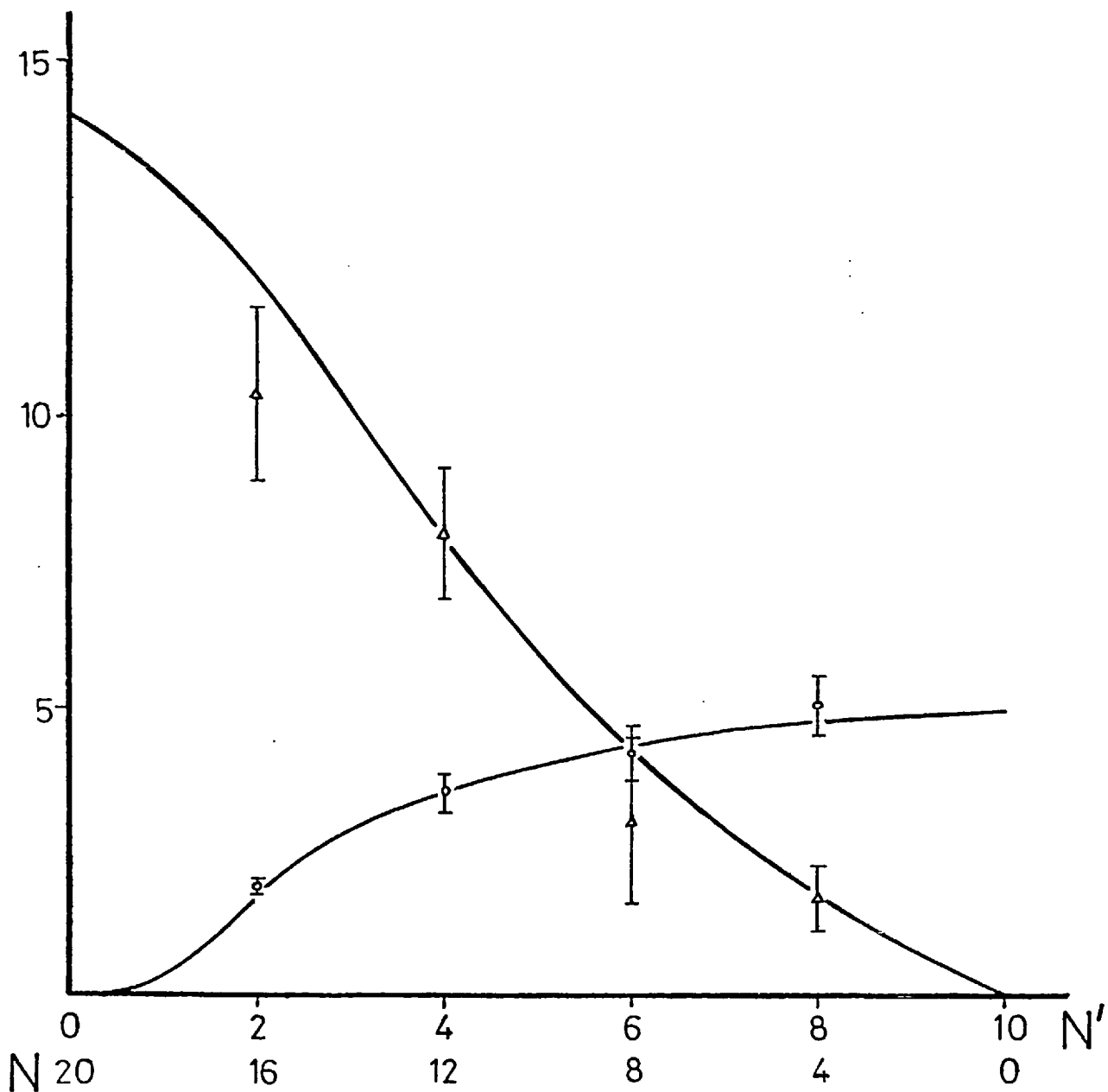


FIGURE 3.10

Predation of C. septempunctata with both types of B. brassicae present - the number of each prey type eaten (Ne & Ne') plotted against the combination of the initial prey densities (N & N' - arranged such that $2N + N' = 20$) - predicted predation calculated using the two regression model of the functional response to type I prey and the Random Predator Equation for the response to type II. Symbols used: Δ - number of type I eaten, \circ - number of type II eaten.

The numbers eaten (Ne & Ne') are plotted as the mean \pm S.E. of the mean.

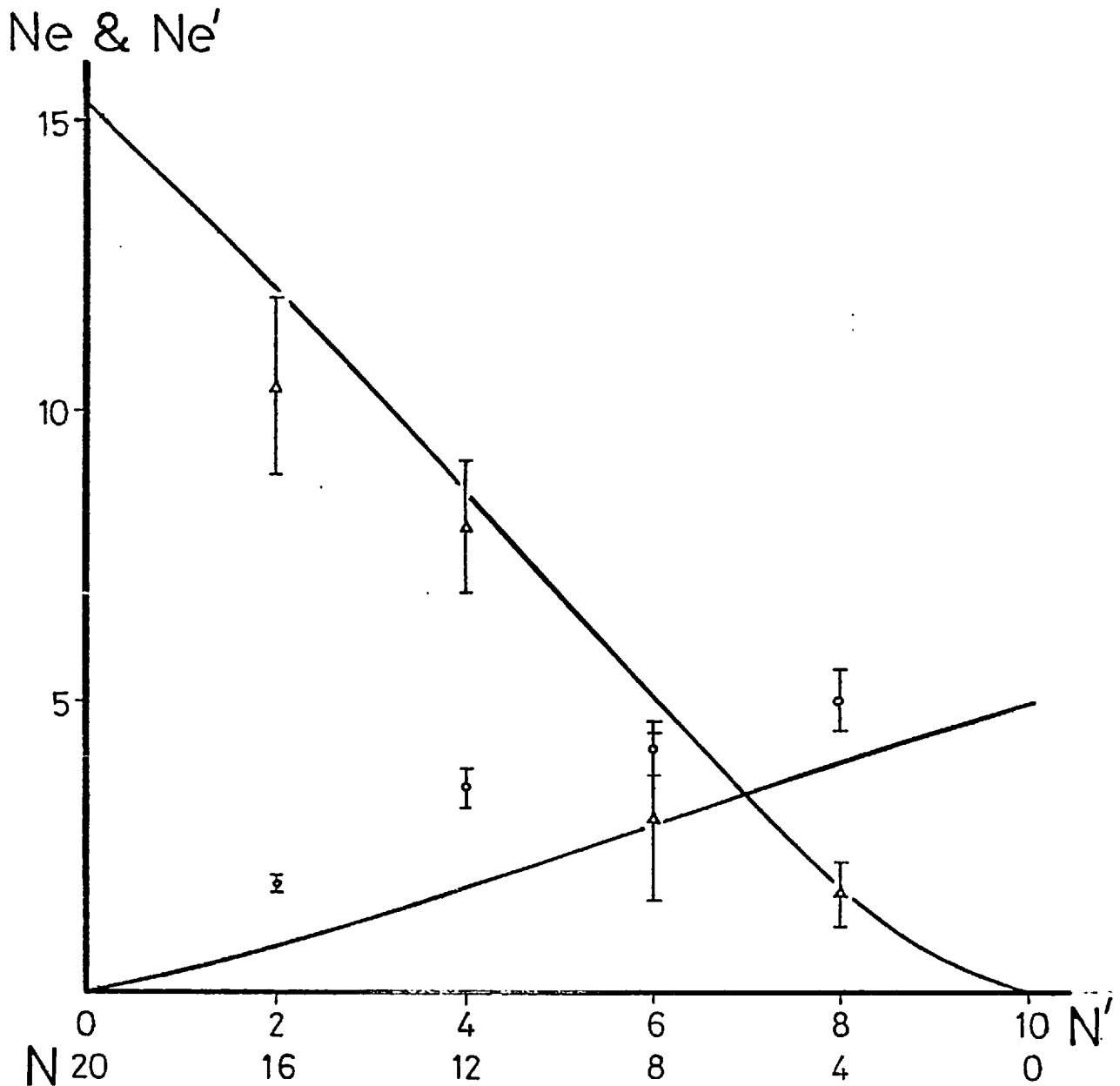


FIGURE 3.11 Predation of C. septempunctata with both types of E. brassicae present - the number of each prey type eaten (N_e & N_e') plotted against the combination of the initial prey densities (N & N' - arranged such that $2N + N' = 20$) - predicted predation calculated using the HLB model of the functional response to type I prey and the Random Predator Equation for the response to type II prey. Symbols used: Δ - number of type I eaten, \circ - number of type II eaten.

The numbers eaten (N_e & N_e') are plotted as the mean \pm S.E. of the mean.

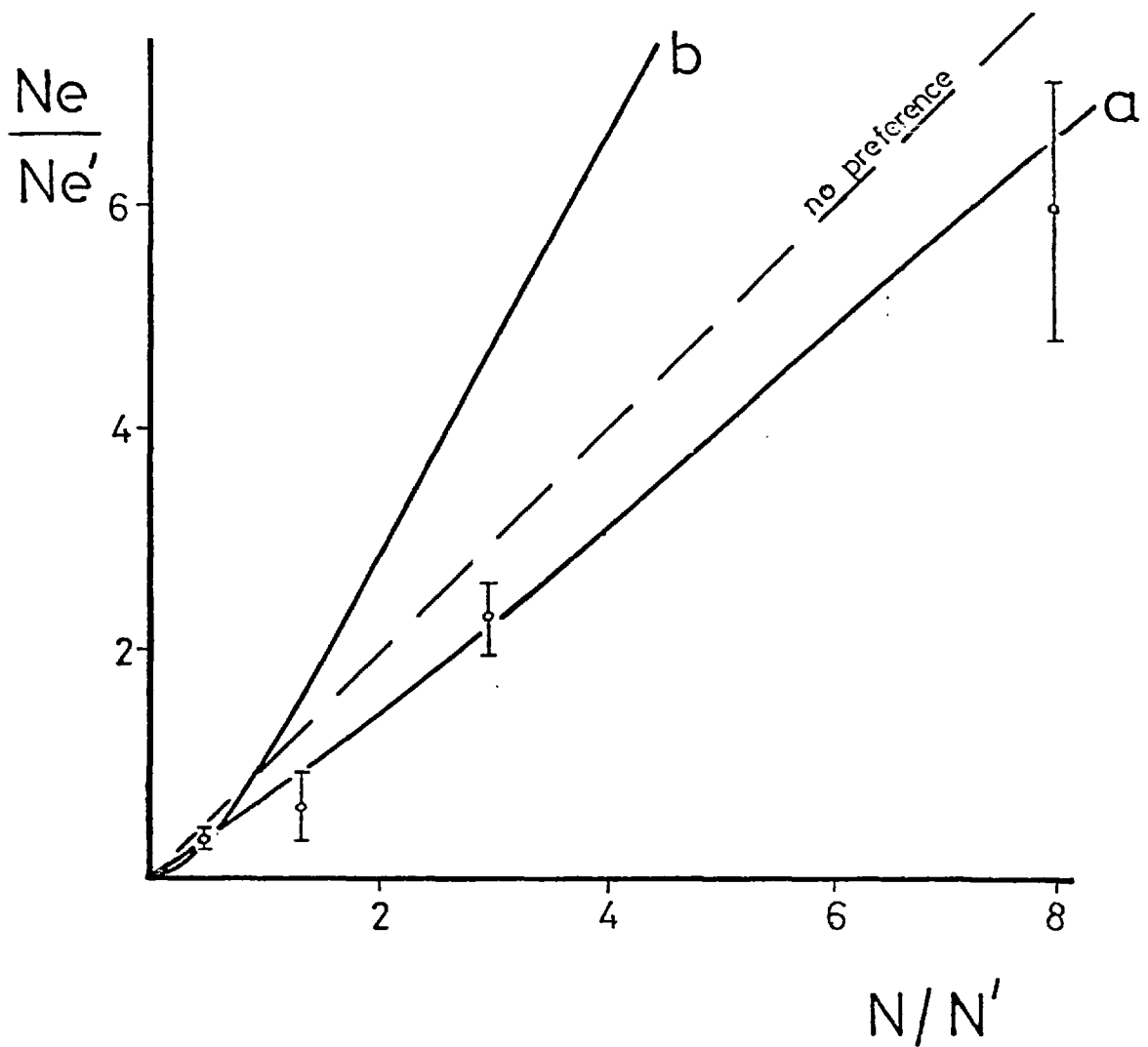


FIGURE 3.12 Predation by C. septempunctata when both prey types of B. brassicae are present - graph of the ratio of the two prey types eaten (Ne/Ne') plotted against the ratio of their initial densities (N/N'). Line a shows the predicted predation based on the two regression model of the functional response to type I B. brassicae, and line b shows the prediction using the HLB model of the functional response to type II prey. Both predictions use the Random Predator Equation to describe the functional response to type II B. brassicae.

The ratio Ne/Ne' is plotted as the mean ratio \pm S.E. of the mean.

3.3.5 'Over-predation' at low prey densities

In analysing the functional responses of C. septempunctata feeding on the two size classes of B. brassicae, a significant deviation from the Random Predator Equation was found. At low prey densities the coccinellids found and ate more prey than would be expected on the basis of the search efficiency and handling time evident from the predation at higher prey densities. If the graph of $\ln S \times N_e$ is examined, this shows up as increasingly large negative values of $\ln S$ as N_e (and hence N) decreases. This is particularly clear in the response to type II prey (Figs. 3.8 & 3.14) and is present, although complicated by a sigmoid response, in the figure for type I prey (Fig. 3.3). At first, this was thought to be an unusual case, but examination of other data showed several other examples which had not previously been commented upon. Two examples are shown in Fig. 3.13 from the work of Mogi (1969) and Fernando (pers. comm.). Other examples were found in the work of Hokyo & Kawauchi (1975) and Reeve (pers. comm.). This phenomenon is referred to in this work as 'over-predation' at low prey densities.

To obtain a non-biological description of this 'over-predation' the linear form of the Random Predator Equation:

$$\ln S = - a T + a Th Ne, \quad . . . 3.6$$

can be modified by an additional term which causes the value of $\ln S$ to tend to minus infinity as N_e tends to zero. The term $(c \ln S)/N_e$ was found to be suitable, when c has positive values. Incorporating this term into Eqn. 3.6 gives:

$$\ln S = - a T + a Th Ne + (c \ln S)/N_e, \quad . . . 3.7$$

where c is a constant representing some measure of the degree of curvature of the relationship. This can be rearranged to give the functional response equation:

$$N_e = N \left[1 - \exp \left(\frac{- a Ne(T - Th Ne)}{Ne - c} \right) \right]. \quad . . . 3.8$$

In order to abstract the parameters of such a model, Eqn. 3.7 can be treated as a multiple regression equation (of the form $y = a x + b y/x + c$). Multiple regression analysis of the data on C. septempunctata feeding on type II aphid prey (Table 3.3) yielded the parameters used in Fig. 3.14, where it can be seen that the data is well described ($F = 97.0$, $df = 2,4$, $P < 0.001$). However, such an approach is, strictly speaking, not correct for the same reasons noted for the linear regression technique in Section 2.2. A least squares technique similar to that suggested for the Random Predator Equation could be used (using function XNEWTO, Appendix Section A1.2), but since the low values of the number of prey eaten at low prey densities have little effect upon the result, the approach is, in this case, unresolvable.

Although a description of this phenomenon is readily obtained, an explanation is not so easily found. It was initially thought that a normal distribution of search efficiency values would, if used to calculate functional response data, yield such an effect. Accordingly, in collaboration with Dr D. J. Rogers, such an approach was tried using a simple computer programme. However, the results obtained did not differ significantly from the Random Predator Equation.

In examining examples of this phenomenon, it was noted that one factor in common for all experimental arrangements was the relatively small size of the arenas used. Thus, Fernando (pers. comm.) used leaf discs of 16 sq cm for mites, the work in this chapter uses nine cm diameter petri dishes for coccinellids, Reeve (pers. comm.) used buckets for Notonecta, and Hokyo & Kawauchi (1975) used the pentatomid bug, Podisus maculiventris Say, in small arenas of 8.5 cm diameter and larger arenas of 15 cm diameter. The results of Hokyo & Kawauchi (1975) show that this effect is more pronounced in the small arenas. Therefore, this phenomenon appears to be connected with the small sizes of the arenas used. A possible explanation, however, lies in the derivation of the Random Predator Equation rather than the arena itself. When the Poisson distribution is used to describe the distribution of encounters with prey (see Section 1.2.2 and Eqns. 1.2.1 & 1.2.2), an approximation is made (Stoy, 1932). This approximation assumes that the number of prey present is large, and hence the number of prey eaten is considerably less, and,

therefore, the area available is only partially searched. This assumption applies to the Random Predator Equation, and so, using small arenas and low prey densities such that all the prey may be eaten, it is violated, and deviations such as that observed might be found.

In order to elucidate this situation, the approach used will be the same as that used in Section 2.4.3 on the models of dome shaped functional responses. Accordingly observations were made of the handling time for successive prey when individual coccinellids were offered ten type I prey under experimental conditions. These observations include as 'handling time', such elements as the digestive pause, post ingestion grooming, and movement during which the coccinellid rejected all prey encountered. By making observations every 20 seconds, a number of interactions could be monitored simultaneously. The results, together with the mean for each prey eaten and the overall mean are given in Table 3.5. The mean for each successive prey eaten gives somewhat inconsistent results, but the overall mean (i.e. \bar{T}_h , see Section 2.4) gives a smooth curve (Fig. 3.15A) which is well described ($F = 523$, $df = 1,8$, $P < 0.001$) by an equation of the form:

$$\bar{T}_h = a N_e / (1 + a b N_e), \quad \dots 3.9$$

with the parameters a (1.753) and b (0.03655) obtained by a least squares technique. This equation can be used to calculate \bar{T}_h and, by substitution into the Random Predator Equation, values for \bar{a} can be obtained:

$$\bar{a} = \ln S / (T - \bar{T}_h N_e).$$

However, since \bar{a} can not be evaluated when N_e exceeds 10.75 (as this causes $\bar{T}_h N_e$ to exceed T), only five points are available for Fig. 3.15 of \bar{a} plotted as a function of N_e . In order to describe these five points an equation of the form:

$$\bar{a} = \exp(c \ln N_e + d) + g \quad \dots 3.10$$

was used and, when the parameters c (- 1.209), d (- 3.988) and g (0.003992) were obtained by a least squares technique,

a reasonably good fit to the calculated values of \bar{a} was obtained ($F = 30.3$, $df = 2,2$, $P < 0.05$). Equations 3.9 and 3.10 can be substituted into the Random Predator Equation:

$$\begin{aligned} N_e &= N(1 - \exp(-\bar{a}(T - \bar{T}_h N_e))) \\ N_e &= N(1 - \exp(-(\exp(c \ln N_e + d) + g)(T - \\ &\quad a N_e^2 / (1 + a b N_e)))) \quad . . . 3.11 \end{aligned}$$

and used to calculate the functional response using subroutine XNEWTC (Appendix Section A1.2.6). The resultant figure of the functional response (Fig. 3.16A - line A) shows that, although a good fit to the data is obtained at low prey densities, the fit diverges, and overall it is not significant ($F = 2.64$, $df = 4,2$, $P > 0.05$). The $\ln S \times N_e$ figure (Fig. 3.16B - line A) shows a similar situation, although the fit here is significant ($F = 32.6$, $df = 4,2$, $P < 0.05$). The inadequate fit obtained is due to the upper asymptote of 10.75 defined by the parameters of Eqn. 3.8. Accordingly, the parameter b which largely defines this asymptote was varied, and the best value found by a least squares technique (using programme BESTFIT and subroutine XNEWTC - Appendix Sections A1.3 and A1.2.5). This resulted in a best value for b of 0.1375, and the resultant functional response (Fig. 3.16A - line B) provides a reasonable fit to the data ($F = 19.2$, $df = 4,2$, $P = 0.05$), while the $\ln S \times N_e$ relationship is a rather better fit ($F = 43.7$, $df = 4,2$, $P < 0.05$).

Thus, the $\ln S \times N_e$ figure (Fig. 3.16B) shows two phases of behaviour: (1) an initial high search efficiency and low handling time, followed by (2) reduced search efficiency and increased handling time. This means that the prey consumption rate as a function of time will be similar to the relationship shown in Fig. 3.15B - initially rapid consumption decreases to a steady slow rate. This, effectively, is a model of satiation. The coccinellid, initially starving, rapidly consumes two or three aphids, and then reduces its consumption rate to accommodate the rate at which food is passed through its gut.

This explanation may not suffice to explain the 'over-predation' observed in other cases; in particular it is unlikely to apply to the functional response of C. septempunctata to type I aphid prey (Section 3.3.2) where, in order to alleviate starvation, rather more first instar aphids would need to be consumed.

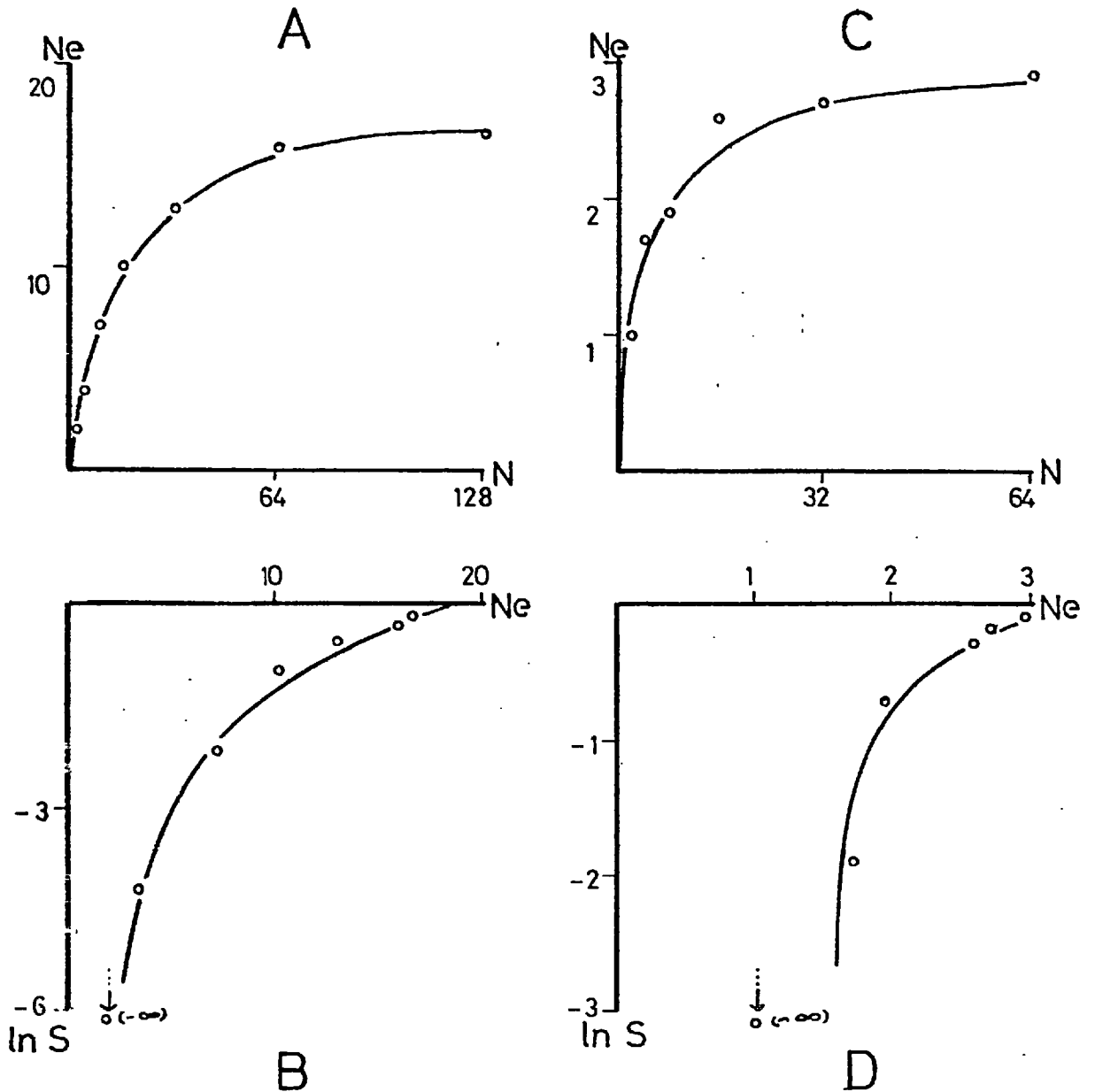


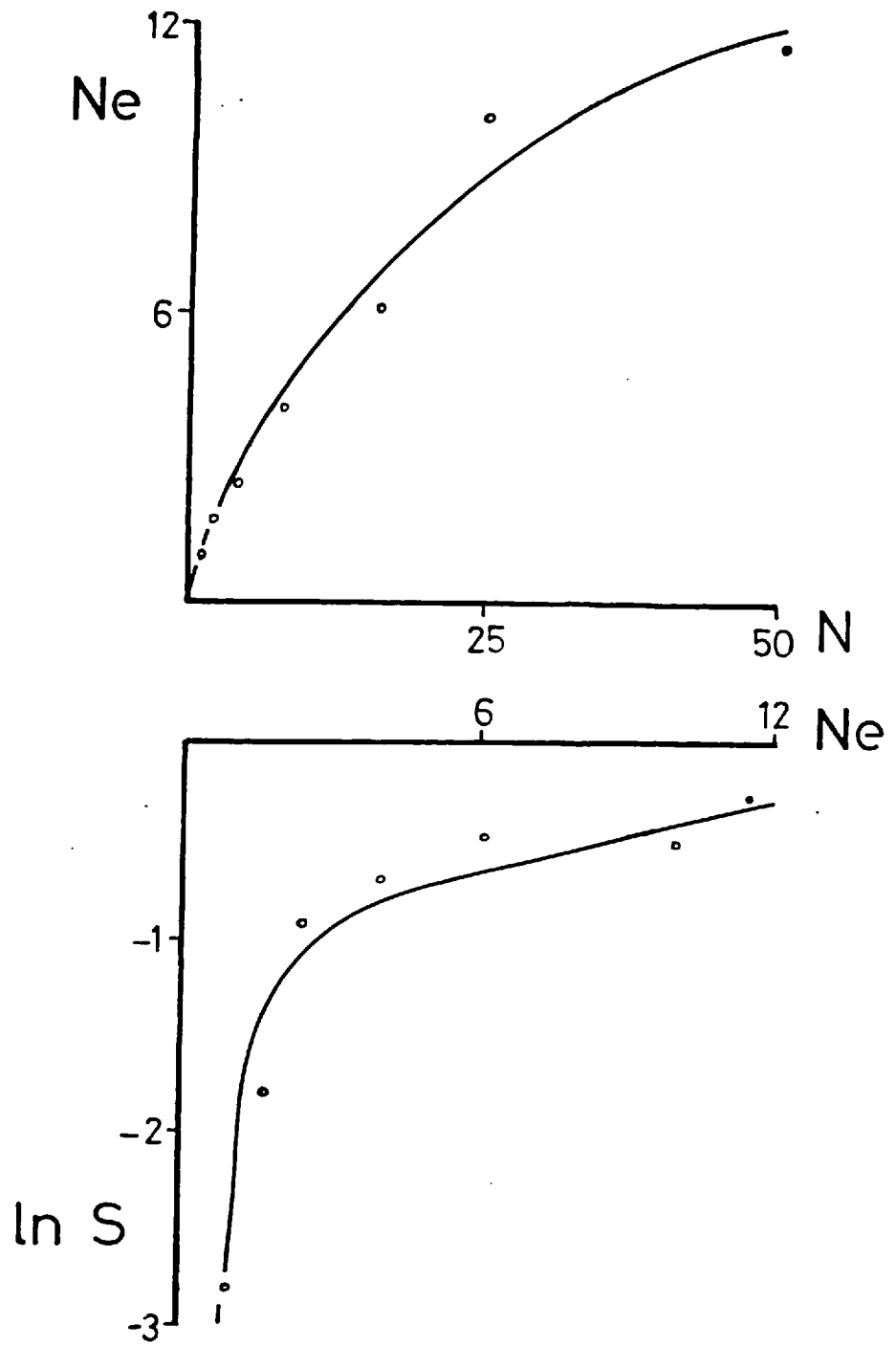
FIGURE 3.13 Examples of 'over-predation' at low prey densities: (A) - functional response and (B) - $\ln S \times Ne$ figure of the predation of third instar Harmonia axyridis Pallas (Coccinellidae) feeding on the aphid, Aphis craccivora Koch, (data from Mogi (1969)). (C) - functional response and (D) - $\ln S \times Ne$ figure from data of Fernando (pers. comm.) on the predation of protonymphs of Phytoseilus persimilis Athias-Heriot feeding on deutonymphs of Tetranychus urticae Koch (arena a 16 sq cm disc of bean leaf, time period 24 hours).

The data is given as the means only; the lines were fitted by eye.

FIGURE 3.14 Predation of C. septempunctata on type II B. brassicae fitted with the descriptive model of 'over-predation' at low prey densities (Eqns. 3.7 & 3.8).

- (A) - functional response - the number of prey eaten plotted against the initial prey density (N). Parameters of fitted functional response obtained from (B); $F = 97$, $df = 2,4$, $P < 0.001$.
- (B) - $\ln S \times N_e$ figure - the logarithm of the mean proportion of prey surviving ($\ln S$) plotted against the number of prey eaten (N_e). Model fitted by multiple regression analysis of Eqn. 3.7 (this relationship): $a = 0.0072$, $c = 0.70$, $Th = 7.11 \text{ min.}$; $F = 54$, $df = 2,4$, $P < 0.01$.

Data (from Table 3.4) given as the means only - see Figs. 3.8 & 3.9 for the S.E. of the mean.



	F E E D N U M B E R								
	1	2	3	4	5	6	7	8	9
Replicates	1.33	0.33	8.33	1.33	8.33	13.00	4.67	28.67	14.00
	2.00	9.33	7.67	17.00	24.33	6.67	15.33	12.33	12.33
	1.00	5.00	13.67	2.67	4.33	3.33	10.33	4.00	
	2.00	1.00	1.00	1.33	23.67	6.33	14.00		
	1.33	1.67	4.00	1.67	3.33	29.33	10.00		
	1.67	7.00	0.67	1.33	10.33	16.33	21.33		
	1.00	6.33	6.67	7.33	3.00	7.67	10.00		
	1.00	9.33	3.00	13.33	12.33	19.67			
	0.33	5.33	10.00	4.33	24.33	19.67			
	0.33	11.33	4.00	6.33	30.33				
	3.00	6.00	2.33	5.33					
	0.33	0.33	1.33	7.00					
	0.33		17.33	14.00					
	1.00		19.33						
	0.67								
0.33									
Number of replicates	16	12	14	13	10	9	7	3	2
Mean	1.10	5.25	7.10	6.38	14.43	13.56	12.24	15.00	13.17
Running mean	1.10	3.17	4.48	4.96	6.85	7.97	8.58	9.38	9.80
Calculated running mean	1.62	3.07	4.38	5.57	6.64	7.63	8.53	9.36	10.13

TABLE 3.5 C. septempunctata feeding on type II prey: observations of handling times (in minutes, to the nearest 20 sec.), under experimental conditions. The calculated running mean was obtained by fitting Eqn. 3.8 to the data and substitution.

FIGURE 3.15 Predation of C. septempunctata on type II B. brassicae - results from continuous observations.

- (A) - The observed mean handling time (\bar{T}_h) plotted as a function of the number of prey eaten (N_e). Equation 3.9 ($\bar{T}_h = a N_e / (1 + a b N_e)$) is fitted to the data using the least squares best fit technique: $a = 1.753$, $b = 0.03655$; $F = 523$, $df = 1,8$, $P < 0.001$.
- (B) - The calculated mean search efficiency (\bar{a}) plotted against the number of prey eaten (N_e). Equation 3.10 ($\bar{a} = \exp(c \ln N_e + d) + g$) is fitted to the data using the least squares best fit technique: $c = -1.209$, $d = -3.988$, $g = 0.003992$; $F = 30$, $df = 2,2$, $P < 0.05$.

Data (from Table 3.5) given as the mean only.

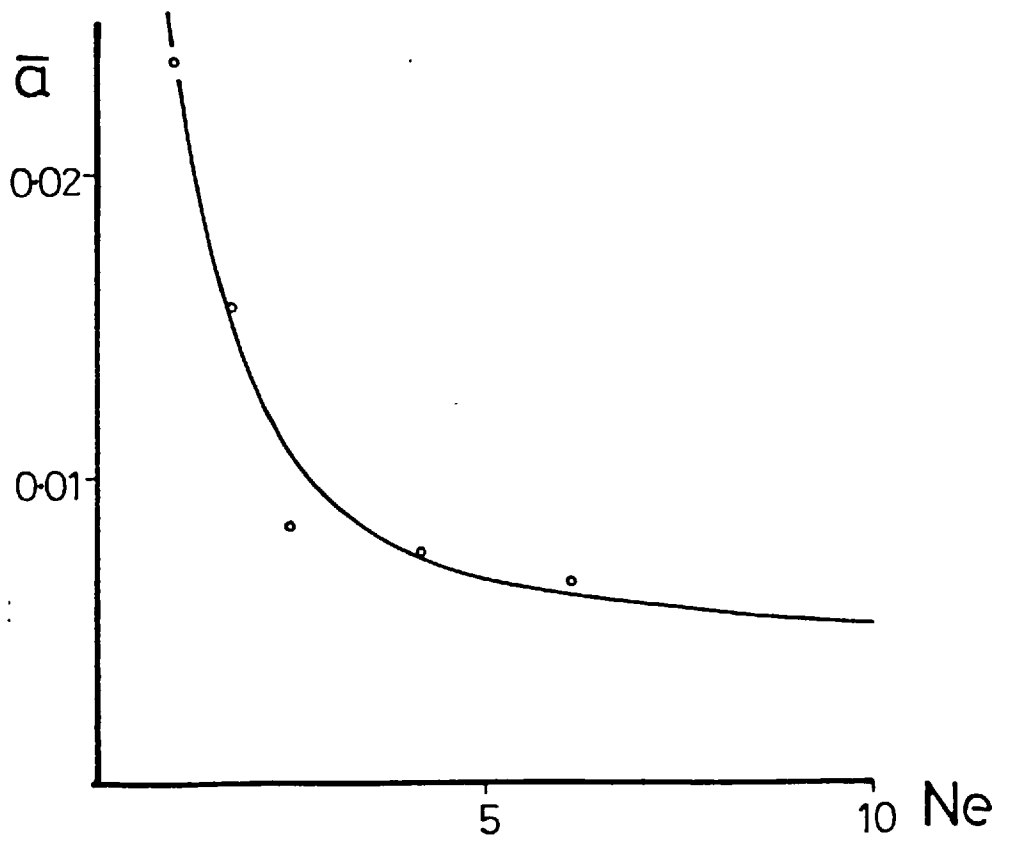
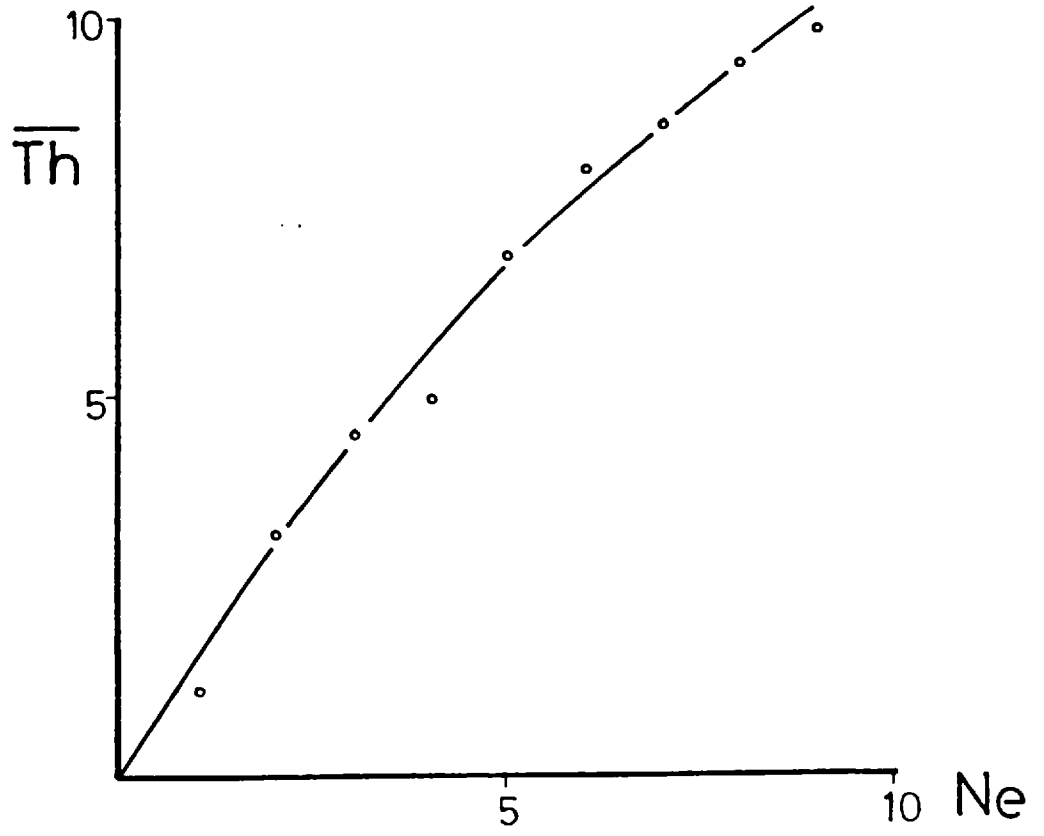


FIGURE 3.16 Predation of C. septempunctata on type II B. brassicae - fitting the satiation model to predation data.

(A) - functional response - the number of prey eaten (N_e) plotted against the initial prey density (N) - fitted with the satiation model based on Eqns. 3.9 & 3.10, as described in the text.
Line a - calculated functional response using the parameters obtained in Fig. 3.15: $F = 2.6$, $df = 2,4$, $P > 0.05$.

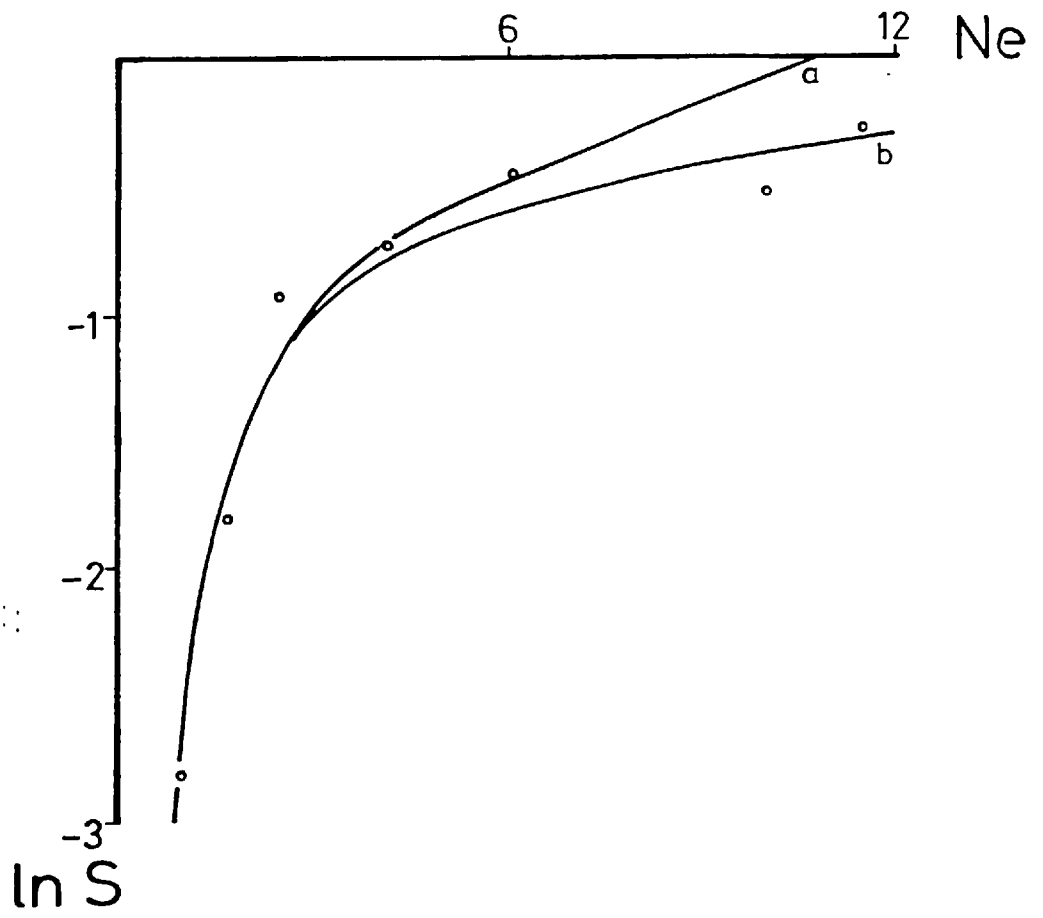
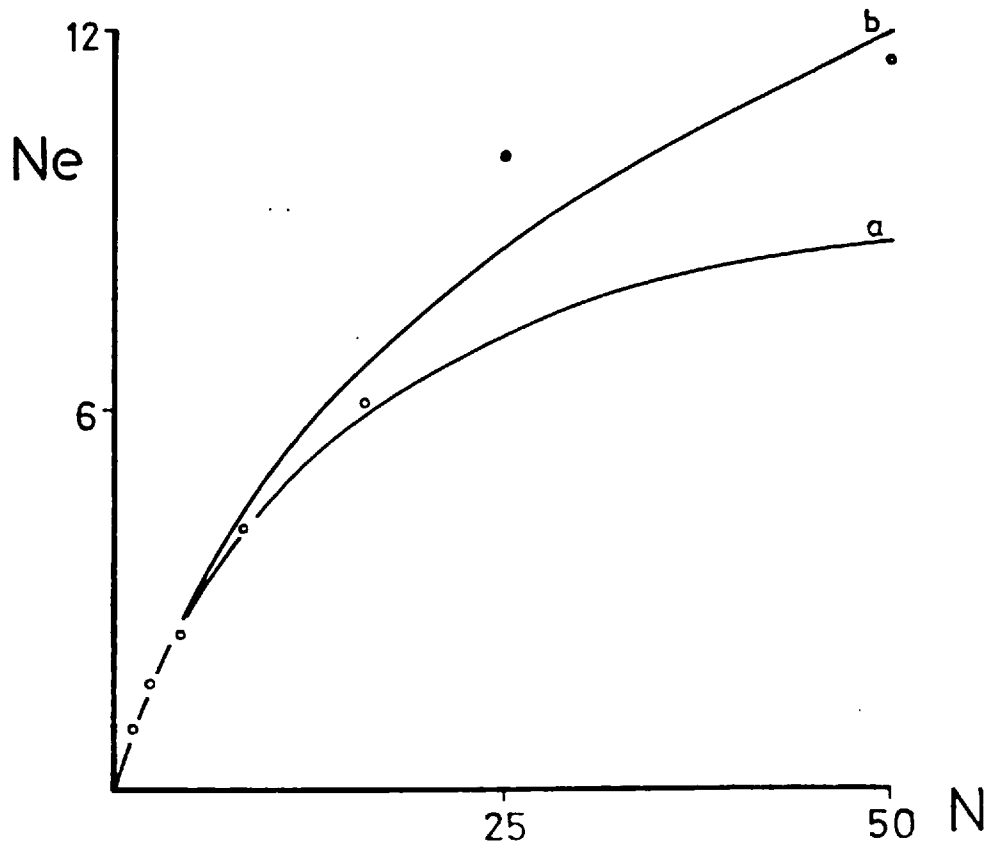
Line b - parameter b estimated by the least squares best fit to the functional response with the other parameters held constant:
 $b = 0.1375$; $F = 19.2$, $df = 3,3$, $P < 0.05$.

(B) - $\ln S \times N_e$ figure - the logarithm of the proportion of prey surviving ($\ln S$) plotted against the number of prey eaten (N_e) - fitted with the satiation model.

Line a - as for (A): $F = 32.6$, $df = 2,4$, $P < 0.01$.

Line b - as for (A): $F = 43.7$, $df = 3,3$, $P < 0.01$.

Data (from Table 3.4) given as the mean only - see Figs. 3.8 & 3.9 for the S.E. of the mean.



3.4 DISCUSSION AND CONCLUSIONS

When offered a choice between large and small B. brassicae, C. septempunctata clearly show a preference for the large aphids (Fig. 3.2). Examination of predicted prey consumption when both types are present (Figs. 3.10 & 3.12) shows that this preference can be defined by the functional responses to the individual prey types. It is clearly shown that this preference (Fig. 3.12) is the result of a greater search efficiency for the larger prey. This conclusion can almost certainly be extended to other coccinellids and their aphid prey.

The word 'preference', as generally used and defined, has connotations of deliberate choice (for example, the Shorter Oxford English Dictionary gives: the act of preferring i.e. to set or hold (one thing) before another in favour or esteem; to choose rather; to like better): in the case of a predator-prey interaction, the less preferred prey being rejected or the more preferred deliberately selected. Murdoch's mathematical description (Murdoch, 1969; Murdoch, Avery & Smyth, 1975) really includes two components, only one of which is in accordance with the normal use of the word preference. The first component is the definition of the ratio of the prey encounter rates in terms of the ratio of the prey densities:

$$N_{enc}/N_{enc'} = f(N/N')$$

where N_{enc} and $N_{enc'}$ are the encounter rates for the two prey types. This relationship has already been defined in terms of the functional responses to the two prey types (Section 1.3.3) and, for the Holling Disc Equation, takes the form:

$$N_{enc}/N_{enc'} = a/a' \cdot (N/N'),$$

whilst for the Random Predator Equation it takes the form:

$$N_{enc}/N_{enc'} = \frac{1 - \exp(- a T_s)}{1 - \exp(- a' T_s)} \cdot (N/N').$$

The second component of preference involves the definition of the ratio of the prey types eaten in terms of the ratio of the prey encounter rates:

$$N_e/N_{e'} = f'(N_{enc}/N_{enc'}) .$$

In the simplest case, analagous to Murdoch's model, the relationship is proportional:

$$N_e/N_{e'} = K . (N_{enc}/N_{enc'}) ,$$

where K is a preference constant. This component involves selection or rejection of prey, and is in accordance with the dictionary definition of preference. The first component is entirely due to the different search efficiencies and should not be included as 'preference' on the basis of the dictionary definition. It is, therefore, useful to distinguish between 'searching' or 'automatic' preference (first component present; ratio of prey types eaten equal to the ratio of the encounter rates) and 'selective' or 'deliberate' preference (second component present; preference due to deliberate rejection or selection of prey encountered). To state this mathematically, 'automatic' preference is defined by the situation:

$$N_e/N_{e'} = N_{enc}/N_{enc'} = f(N/N') ,$$

and 'deliberate' preference is defined by:

$$N_e/N_{e'} = f'(N_{enc}/N_{enc'}) = f'(N/N') .$$

If the search efficiencies for the two prey types are equal, there will be no 'automatic' preference, whilst if all prey encountered are eaten, there will be no 'deliberate' preference. Depending upon the presence or absence of these two components, four combinations can occur when a predator-prey interaction is examined for preference. These four combinations and examples of each are tabulated as Table 3.6.

In Chapter 1 (Section 1.3.5) two hypotheses of the foraging strategies of birds were described. Tinbergen (1960) put forward the idea of a 'searching image' to account for the

PREFERENCE :		DEFINITION	PREFERENCE ACCORDING TO MURDOCH (1969)	EXAMPLES
'AUTO-MATIC'	'DELIBERATE'			
-	-	$N_e/N_{e'} = N_{enc}/N_{enc'} = N/N'$	No	Murdoch & Marks (1973)
+	-	$N_e/N_{e'} = N_{enc}/N_{enc'} = f(N/N')$	Yes	This work (Chapter 3) Royama (1970)
-	+	$N_e/N_{e'} = f'(N_{enc}/N_{enc'}) = f'(N/N')$	Yes	Murdoch (1969) - final experiments Murton (1971) - ?
+	+	$N_e/N_{e'} = f'(N_{enc}/N_{enc'}) = f'(f(N/N'))$	Yes	This work (Chapter 5) Lawton, Beddington & Bonser (1974) Tinbergen (1960)

TABLE 3.6 The four combinations of the presence or absence of 'automatic' and 'deliberate' preference (as introduced in this chapter). Since encounter rates are not available from some of the literature, a probable example is listed with a question mark next to it.

variable preference shown towards certain food types by birds. The deliberate selection of a prey type, perhaps due to a 'searching image', has since been demonstrated by Murton (1971). Royama (1970) put forward an alternative hypothesis that predators can intensify their searching in areas where energy intake is maximized. The effect of this upon preference would be similar to the effects of the 'searching image'. This has been demonstrated by Smith and Sweatman (1974). The resultant preference for a food type is caused by the different prey encounter rates, and not by selection or rejection of the prey by the predator. These two hypotheses, however, are not incompatible. Tinbergen's hypothesis describes 'deliberate' preference, whilst that of Royama describes 'automatic' preference. As noted above, both types of preference can occur together; a predator can restrict its search to the most rewarding part of the available habitat, and use a 'searching image' to maximize its efficiency within that area.

In Chapter 5, an experimental arrangement is examined in which a predator can show preference for part of its habitat, and hence show 'automatic' preference for the prey type in that area.

* * * * *

Comparison of the functional response figures with the corresponding $\ln S \times N_e$ plots (Figs. 3.5 & 3.3, prey type I; Figs. 3.9 & 3.8, prey type II) clearly show how much more informative the latter figures can be. The 'over-predation' at low prey densities is apparent in the $\ln S \times N_e$ plots for both prey types. That for prey type I (Fig. 3.3) clearly indicates a sigmoid response, in contrast to the conventional functional response figure (Fig. 3.5). This useful approach to examining deviations from the type II functional response is discussed in Section 2.3.

The differences between the predictions based on the two models of the response to type I prey have been discussed in Section 3.3.4. The predicted relationships in Figs. 3.10 and 3.11 both show an interesting result. The predicted response for the numbers of prey type II eaten shows a concave shape over part of the range of prey densities. This phenomenon is predicted for prey densities up to eight using the HLB model, and up to two

using the two-regression model, and results in the response to the density of prey type II being of a sigmoid shape. Therefore, a normal, type II functional response can be transformed to a sigmoid, type III response by using an alternative prey. To obtain this result, two conditions were necessary. Firstly, the functional response to the alternative prey was sigmoid in shape. The functional response of a predator to a less preferred prey is frequently sigmoid (Hassell, Lawton & Beddington, 1977), and so this situation must often arise. Secondly, as one prey type increased in density, the other decreased, and vice versa. If both conditions are met, a sigmoid functional response to the preferred prey will result. Murdoch & Oaten (1975) consider sigmoid functional responses to be important stabilizing factors, although Hassell, Lawton & Beddington (1977), point out how this importance can frequently be reduced or masked by circumstances. It is of interest to see how a sigmoid response can arise for a preferred prey where it is not normally observed.

In conclusion, it has been shown that suitable models of the functional responses to two prey types can be used to predict, with some accuracy, the predation which occurs when both are present.

CHAPTER 4

THE EFFECTS OF THE DISTRIBUTION OF EGGS OF PIERIS BRASSICAE (L.) UPON THE FUNCTIONAL RESPONSE OF ANTHOCORIS NEMORUM (L.)

4.1 INTRODUCTION

In this chapter the variation of the functional response of a predator due to aggregation of the prey is examined. The predators used are adults of Anthocoris nemorum (L.) and the prey are eggs of Pieris brassicae (L.). Anthocorids have recently been extensively studied (Anderson, 1961; Dixon & Russell, 1973; Evans, 1973, 1976a,b,c) and much has been recorded of their ecology and behaviour. Anthocorids eat a wide variety of prey, most of which are mobile. However, it is necessary to use an immobile prey in order to establish the effects of prey distribution. Mobile prey can be glued down (Dimetry, 1976), but this is not practical on the scale used here. Amongst the possible immobile prey types, lepidopterous eggs are suitable, and hence the use of P. brassicae eggs here.

Evans (1973), observing the searching behaviour of A. confusus Reuter in 20 x 20 cm perspex arenas, found that the anthocorid's search track, after feeding, became more tortuous and, as a consequence, small clumps of prey (aphids) were readily exploited. If no further prey were found, the path became less tortuous and returned to normal over a period of five minutes. He also found that, subsequent to feeding, the anthocorids tended to turn successively in the same direction, resulting in circling movements around the prey's location.

In view of previous observations on anthocorid searching behaviour, it, therefore, seems likely that a greater proportion of prey will be eaten as the prey become more clumped. Ivlev (1961), working on fishes, predicted and found that prey consumption depends upon an index of aggregation in a curvi-linear manner. Accordingly, in this chapter the functional responses to four different distributions will be examined. The distributions will cover a range of aggregation from random to regularly arranged clumps of ten eggs. It is to be expected that the efficiency of the anthocorids will increase as the aggregation of the prey increases. The results of this work will form a basis for comparison with the simulation studies of Chapter 6, and will be used to determine the intra-habitat distribution of prey for Chapter 5.

4.2 EXPERIMENTAL METHOD

4.2.1 The Arenas

Square perspex trays with fitted lids were used as arenas. They were of internal measurement 20.2 cm and had sides 1.3 cm in height. Glued to the base was a piece of 15 x 15 cm graph paper leaving around it a 2.6 cm margin. This margin and the sides of the tray were coated with fluon.

4.2.2 The Prey: *Pieris brassicae* eggs

The functional responses were obtained for four distributions of *P. brassicae* eggs: random, using the negative binomial distribution with values for K of 1.0 and 0.01, and regularly arranged clumps of ten. In this chapter the first three distributions will be collectively referred to as 'scattered' and the last as 'clumped'.

The random distribution of prey was obtained by using random number tables. In obtaining the negative binomial distributions, the graph paper on the base of the arena was divided into 225 units of one square centimetre. The frequency with which the densities per unit occurred was calculated using programme PUT (described and listed in Appendix Section A1.4). Using the value for K of 1.0 to generate the frequencies, a good fit to the distribution was obtained. Due to the small number of units available, the fit using the value for K of 0.01 was not so good. However, bearing in mind that the true value of K in this case is greater than 0.01, the generated distribution is intermediate between that based on the negative binomial with the value for K of 1.0 and the most aggregated distribution involving the regularly arranged clumps of ten eggs glued adjacent to each other.

The eggs were individually glued to the graph paper using gum tragacanth. Since eggs of constant age were not easily supplied, their age in the experiments was variable, and this may be one source of error in the results.

4.2.3 The Predators: Anthocoris nemorum Adults

Since Evans (1973) states that A. nemorum can not be bred in the laboratory for more than one generation, no attempt was made to maintain a culture. Instead, adults and large nymphs were collected from the field and kept in the laboratory until used for experiments. They were fed on Acyrosyphon pisum (Harris) and kept in rearing containers, as used and described by Anderson (1961). Evans used A. confusus for his practical work, and was able to maintain them in culture. However, at Silwood Park during the period of study, A. confusus was too scarce to rely on for maintaining a culture, and hence obtaining A. nemorum from the field was considered more dependable. In 1976, perhaps due to the drought conditions, A. nemorum was scarce, but sufficient were obtained to complete the experimental programme.

Anthocorids are less reliable experimental animals than coccinellids, and between a quarter and a half of the experimental runs made were failures, due to the anthocorids failing to feed or dying. This, coupled with the difficulty of culture and time-consuming culture methods, makes them a difficult experimental animal for general studies.

4.2.4 Experimental Procedure

Anderson (1961) states that anthocorids do not immediately attack on the first encounter with a new prey type. Several encounters are necessary before they recognise the prey and begin to feed. The level of this encounter threshold will be affected by hunger, and thus anthocorids of standard starvation have been used in this work. To achieve standard starvation, the experimental animals were isolated in individual $\frac{1}{2}$ dram vials at 15.00 h on the day previous to each run. Before each run, the anthocorids were examined and any with missing or broken appendages were discarded. The anthocorids were introduced to the arenas at 13.00 h and the eggs which had been eaten were counted at 14.00 h, 15.00 h and 09.00 h the next morning. The runs were conducted at 20°C and 60% R.H.. Apart from a period of eight hours darkness overnight, the arenas were subject to constant illumination from fluorescent tubes.

Eggs which had been attacked could be distinguished by their deflated appearance caused by the loss of liquid. The eggs' colouring is due to the fluid content; the egg walls being colourless. Therefore when an anthocorid consumed all the contents of an egg, a colourless deflated shell remained. However, more frequently it occurred that only some of the egg contents were consumed by the anthocorid and this resulted in the yellow colour remaining. Over the course of a few hours, evaporation causes the egg walls to collapse leaving a yellow deflated shell. This means that only some prey were totally eaten, and so the number attacked was recorded. Furthermore, since a pierced egg takes a few hours to deflate, it can be attacked more than once. Thus, in the short term, this situation is more characteristic of a host-parasitoid interaction than of a predator-prey interaction. Of necessity, in applying the Random Predator Equation to the results, the number of deflated prey is taken as the number eaten, and the possibility of a prey being attacked more than once is overlooked.

4.3 RESULTS AND ANALYSIS

The numbers of eggs attacked are tabulated as Tables 4.1 - 4.4.

Figures 4.1 - 4.3 show the functional responses for each of the three time intervals. It can be seen that in all cases there are no marked deviations from the normal, type II functional response. This is confirmed by the examination of the $\ln S \times N_e$ figures (Figs. 4.4 - 4.7) (logarithm of the proportion of prey surviving plotted against the number of prey eaten - see Sections 2.2 & 2.3); all the relationships are reasonably linear. Accordingly, the technique of the least squares best fit to the functional response (Section 2.2, Appendix Section A1.3) has been used to find the parameters used in the figures. The parameters have also been calculated by the normal regression technique (Rogers, 1972) and by finding the best fit linear relationship using programme 22 in Davies (1969) (see Section 2.2). The results from these three methods are given in Table 4.5. It can be seen that there is no consistent trend for one method to yield higher or lower estimates of the parameters in comparison with the others, but the least squares best fit technique does consistently yield the best fit to the data. The difference between the estimates is sometimes as high as 50%, and so the importance of using the best method of parameter extraction can be seen.

TIME	DENSITY	NUMBER EATEN	\bar{N}_e	S.E.	$\ln \bar{S}$	$\overline{\ln S}$	S.E.
one hour	2	0 1 0 0 1	0.4	0.2	- 0.223	- 0.277	.170
	4	2 0 1 1 0	0.8	0.4	- 0.223	- 0.254	.127
	8	3 2 0 0 1	1.2	0.6	- 0.163	- 0.178	.089
	16	1 3 0 2 2	1.6	0.5	- 0.105	- 0.108	.036
	32	4 2 3 1 3	2.6	0.5	- 0.085	- 0.085	.018
	64	3 4 4 2 3	3.2	0.4	- 0.051	- 0.051	.007
two hours	2	0 2 1 0 2	1.0	0.4	- 0.693	*	
	4	3 1 2 3 1	2.0	0.4	- 0.693	- 0.808	.248
	8	3 3 1 2 4	2.6	0.5	- 0.393	- 0.411	.094
	16	4 6 1 3 3	3.4	0.8	- 0.239	- 0.248	.067
	32	6 5 4 4 5	4.8	0.4	- 0.163	- 0.163	.013
	64	4 5 5 3 5	4.4	0.4	- 0.071	- 0.071	.007
twenty hours	2	2 2 1 1 2	1.6	0.2	- 1.609	*	
	4	4 3 3 3 4	3.4	0.2	- 1.897	*	
	8	5 7 7 5 6	6.0	0.4	- 1.386	- 1.501	.248
	16	8 12 5 7 8	8.0	1.1	- 0.693	- 0.745	.170
	32	9 16 13 15 16	13.8	1.3	- 0.564	- 0.574	.069
	64	12 19 18 9 24	16.4	2.7	- 0.296	- 0.302	.056

TABLE 4.1 Predation of A. nemorum on eggs of P. brassicae arranged at random. Results given of the number of prey eaten in each replicate, the mean number eaten (\bar{N}_e), the logarithm of mean S ($\ln \bar{S}$), and the mean of the logarithmic values of S ($\overline{\ln S}$). The symbol * is used to denote a value of $\overline{\ln S}$ which can not be evaluated due to total predation in one or more replicates.

TIME	DENSITY	NUMBER EATEN	\bar{N}_e	S.E.	$\ln \bar{S}$	$\overline{\ln S}$	S.E.
one hour	2	0 0 0 0 1	0.2	0.2	- 0.105	- 0.139	.139
	4	0 1 0 2 0	0.6	0.4	- 0.163	- 0.196	.136
	9	1 0 3 0 2	1.2	0.6	- 0.143	- 0.155	.078
	16	2 1 3 4 0	2.0	0.7	- 0.134	- 0.139	.051
	31	3 4 1 3 4	3.0	0.5	- 0.102	- 0.103	.020
	63	2 4 3 4 4	3.4	0.4	- 0.055	- 0.056	.007
two hours	2	2 1 0 2 1	1.2	0.4	- 0.916	*	
	4	1 1 2 3 2	1.8	0.4	- 0.600	- 0.670	.201
	9	3 1 4 2 2	2.4	0.5	- 0.310	- 0.323	.080
	16	5 3 4 4 2	3.6	0.5	- 0.255	- 0.258	.040
	31	4 4 3 4 5	4.0	0.3	- 0.138	- 0.138	.011
	63	4 5 3 5 4	4.2	0.4	- 0.069	- 0.069	.007
twenty hours	2	2 2 2 2 1	1.8	0.2	- 2.303	*	
	4	3 4 4 4 2	3.4	0.4	- 1.897	*	
	9	7 7 5 6 6	6.2	0.4	- 1.168	- 1.203	.134
	16	7 10 7 9 11	8.8	0.8	- 0.799	- 0.824	.114
	31	25 19 5 12 17	15.6	3.4	- 0.700	- 0.810	.246
	63	12 17 24 8 15	15.2	2.7	- 0.276	- 0.283	.058

TABLE 4.2 Predation of A. nemorum on eggs of P. brassicae arranged using the negative binomial (K = 1.0). Results given of the number of prey eaten in each replicate, the mean number eaten (\bar{N}_e), the logarithm of mean S ($\ln \bar{S}$), and the mean of the logarithmic values of S ($\overline{\ln S}$). The symbol * is used to denote a value of $\overline{\ln S}$ which can not be evaluated due to total predation in one or more replicates.

TIME	DENSITY	NUMBER EATEN	\bar{N}_e	S.E.	$\ln \bar{S}$	$\overline{\ln S}$	S.E.
one hour	3	1 1 0 1 0	0.6	0.2	- 0.223	- 0.243	.098
	4	2 0 0 2 0	0.8	0.5	- 0.223	- 0.277	.170
	11	1 0 3 2 2	1.6	0.5	- 0.157	- 0.163	.054
	16	2 3 1 1 4	2.2	0.6	- 0.148	- 0.152	.042
	22	2 4 3 1 2	2.4	0.5	- 0.116	- 0.117	.027
	37	4 3 2 3 4	3.2	0.4	- 0.090	- 0.091	.011
	64	2 0 4 4 4	2.8	0.8	- 0.045	- 0.045	.013
two hours	3	2 1 0 2 3	1.6	0.5	- 0.762	*	
	4	3 2 0 4 1	2.0	0.7	- 0.693	*	
	11	3 2 4 5 2	3.2	0.6	- 0.344	- 0.379	.069
	16	3 3 4 2 5	3.4	0.5	- 0.239	- 0.242	.040
	22	4 4 5 4 3	4.0	0.3	- 0.201	- 0.201	.018
	37	6 3 4 5 4	4.4	0.5	- 0.127	- 0.127	.016
	64	3 5 4 6 5	4.6	0.5	- 0.074	- 0.075	.009
twenty hours	3	3 2 1 3 3	2.4	0.4	- 1.609	*	
	4	4 3 3 4 2	3.2	0.4	- 1.609	*	
	11	7 6 8 9 4	6.8	0.8	- 0.963	- 1.051	.215
	16	8 7 10 6 11	8.4	0.9	- 0.744	- 0.777	.130
	22	11 9 7 13 8	9.6	1.1	- 0.573	- 0.590	.092
	37	18 15 9 12 13	13.4	1.5	- 0.450	- 0.458	.065
	64	8 14 17 16 13	13.6	1.6	- 0.239	- 0.241	.031

TABLE 4.3 Predation of A. nemorum on eggs of P. brassicae arranged using the negative binomial ($K = 0.01$). Results given of the number of prey eaten in each replicate, the mean number eaten (\bar{N}_e), the logarithm of mean S ($\ln \bar{S}$), and the mean of the logarithmic values of S ($\overline{\ln S}$). The symbol * is used to denote a value of $\overline{\ln S}$ which can not be evaluated due to total predation in one or more replicates.

TIME	DENSITY	NUMBER EATEN	\bar{N}_e	S.E.	$\ln \bar{S}$	$\overline{\ln S}$	S.E.
one hour	10	0 0 3 1 4	1.6	0.8	- 0.174	- 0.195	.102
	20	2 4 0 0 3	1.8	0.8	- 0.094	- 0.098	.044
	30	0 0 4 3 4	2.2	0.9	- 0.076	- 0.078	.033
	40	0 3 4 2 4	2.6	0.7	- 0.067	- 0.068	.020
	60	4 3 2 2 4	3.0	0.5	- 0.051	- 0.051	.008
	80	4 3 4 2 4	3.4	0.4	- 0.039	- 0.039	.005
two hours	10	4 0 6 5 7	4.4	1.2	- 0.580	- 0.665	.203
	20	4 7 0 8 5	4.8	1.4	- 0.274	- 0.290	.089
	30	0 5 8 7 7	5.4	1.4	- 0.198	- 0.205	.055
	40	4 5 7 4 8	5.6	0.8	- 0.151	- 0.152	.024
	60	5 5 6 4 7	5.4	0.5	- 0.094	- 0.094	.011
	80	5 5 4 7 6	5.4	0.5	- 0.062	- 0.062	.006
twenty hours	10	9 8 10 7 10	8.8	0.6	- 2.120	*	
	20	7 16 15 19 10	13.4	2.2	- 1.109	- 1.423	.449
	30	9 18 15 19 17	15.6	1.8	- 0.734	- 0.761	.113
	40	12 10 16 12 22	16.2	2.0	- 0.519	- 0.533	.085
	60	15 11 18 17 21	16.4	1.7	- 0.319	- 0.322	.038
	80	17 11 16 14 26	16.8	2.5	- 0.207	- 0.209	.036

TABLE 4.4 Predation of A. nemorum on eggs of P. brassicae arranged in regularly distributed clumps of ten eggs. Results given of the number of prey eaten in each replicate, the mean number eaten (\bar{N}_e), the logarithm of mean S ($\ln \bar{S}$), and the mean of the logarithmic values of S ($\overline{\ln S}$). The symbol * is used to denote a value of $\ln S$ which can not be evaluated due to total predation in one or more replicates.

TABLE 4.5

Abstracted parameters of the functional responses of A. nemorum to eggs of P. brassicae. Results from three methods of estimating the parameters of the Random Predator Equation (a = search efficiency; Th = handling time). Method 1: linear regression analysis of $\ln S \times N_e$ after Rogers (1972). Method 2: best fit linear relationship of $\ln S \times N_e$ after Davies (1969). n refers to the number of points dropped due to total predation resulting in $\ln S$ values which can not be evaluated. Method 3: least squares best fit to the functional response (Section 2.2).
The results of these three methods are examined in Sections 2.2 & 4.4.

PREY DIS- TRIBUTION	TIME IN HOURS	M E T H O D 1					M E T H O D 2					M E T H O D 3					
		ABSTRACTED PARAMETERS		GOODNESS OF FIT			ABSTRACTED PARAMETERS		GOODNESS OF FIT			ABSTRACTED PARAMETERS		GOODNESS OF FIT			
		a	Th	F	df	P	n	a	Th	F	df	P	a	Th	F	df	P
random	1	.00411	15.6	210	1,4	<.001	0	.00498	17.3	97	1,4	<.001	.00350	14.3	306	1,4	<.001
	2	.00741	23.1	84	1,4	<.001	1	.00898	23.8	74	1,4	.001	.00765	23.6	87	1,4	<.001
	20	.00159	64.0	209	1,4	<.001	2	.00171	67.2	157	1,4	<.001	.00125	58.2	313	1,4	<.001
negative binomial K = 1.0	1	.00252	7.8	42	1,4	<.01	0	.00310	10.0	101	1,4	<.001	.00364	12.5	256	1,4	<.001
	2	.00896	27.0	113	1,4	<.001	1	.00884	27.4	109	1,4	<.001	.00755	26.0	140	1,4	<.001
	20	.00185	65.4	99	1,4	<.001	2	.00105	39.2	16	1,4	<.05	.00170	63.5	101	1,4	<.001
negative binomial K = 0.01	1	.00428	12.6	32	1,5	<.01	0	.00530	15.7	85	1,5	<.001	.00542	16.3	89	1,5	<.001
	2	.00949	25.3	297	1,5	<.001	2	.00741	23.6	270	1,5	<.001	.00854	24.5	382	1,5	<.001
	20	.00155	76.8	276	1,5	<.001	2	.00135	71.4	341	1,5	<.001	.00134	72.3	345	1,5	<.001
'clumped'	1	.00382	15.7	46	1,4	<.01	0	.00380	15.5	45	1,4	<.01	.00330	14.8	52	1,4	<.01
	2	.01780	20.8	20	1,4	<.05	0	.01722	20.7	19	1,4	<.05	.02085	21.1	23	1,4	<.01
	20	.00347	66.0	299	1,4	<.001	1	.00567	69.3	151	1,4	<.001	.00399	67.4	420	1,4	<.001

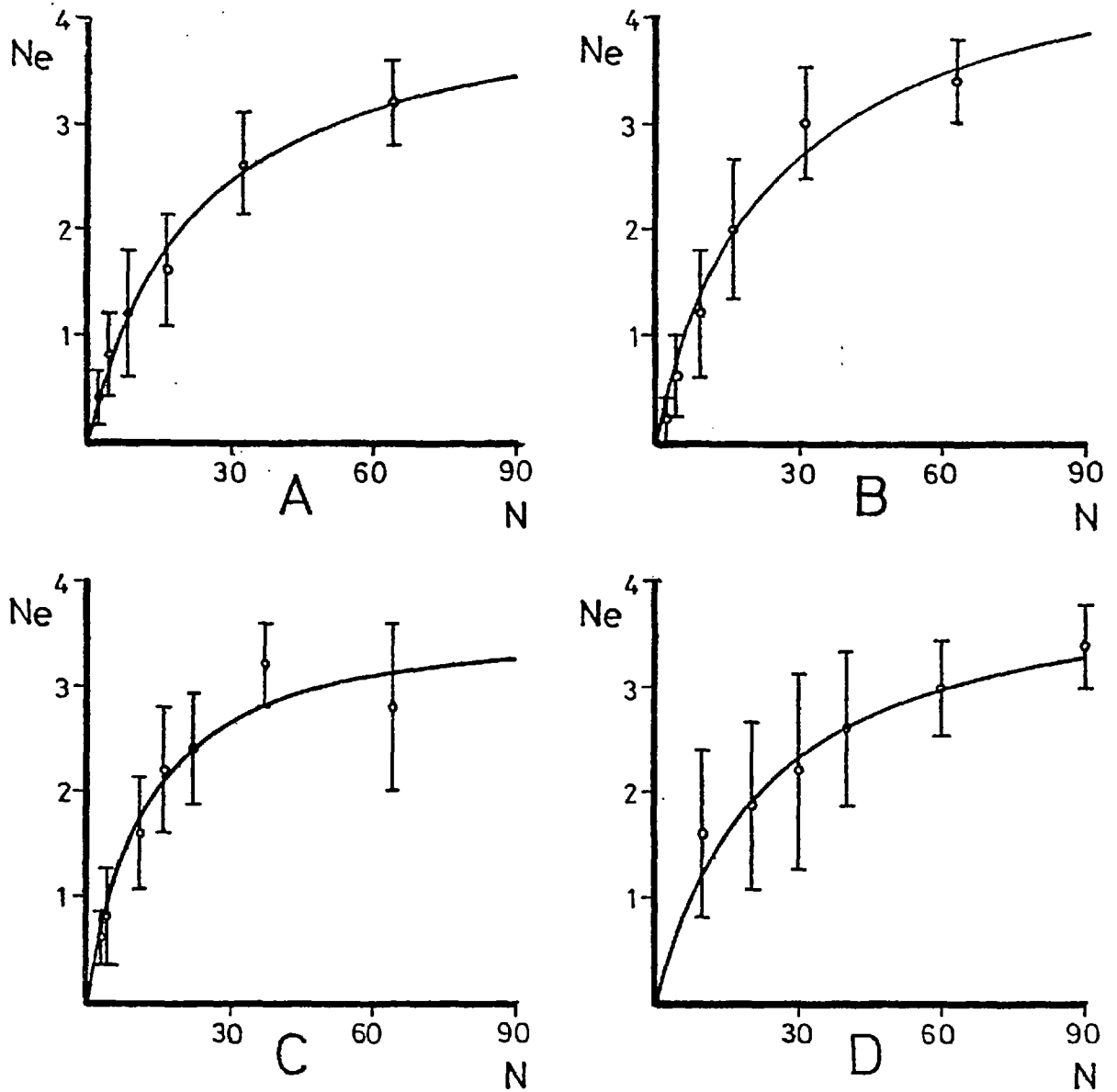


FIGURE 4.1 Functional responses of A. nemorum to eggs of P. brassicae after one hour - the number eaten (Ne) plotted against the prey density (N). The Random Predator Equation is fitted by the method of the least squares best fit to the functional response.

(A) - eggs arranged at random; $a = 0.00350/\text{min.}$, $Th = 14.27 \text{ min.}$

(B) - eggs arranged using the negative binomial ($K = 1.0$); $a = 0.00364/\text{min.}$, $Th = 12.47 \text{ min.}$

(C) - eggs arranged using the negative binomial ($K = 0.01$); $a = 0.00542/\text{min.}$, $Th = 16.26 \text{ min.}$

(D) - eggs arranged in regularly distributed clumps of ten; $a = 0.00330/\text{min.}$, $Th = 14.84 \text{ min.}$

Number eaten plotted as the mean \pm S.E. of mean.

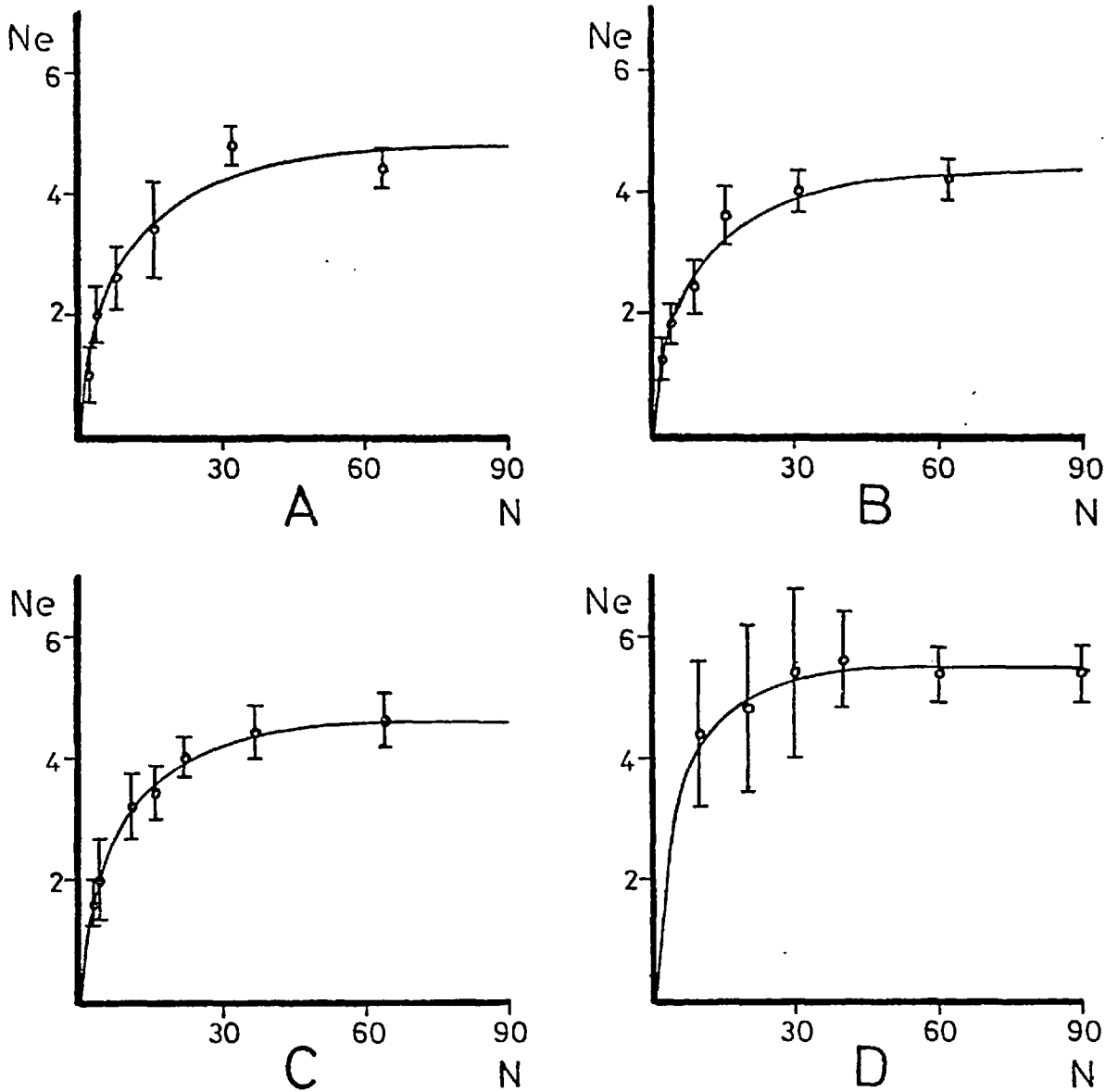


FIGURE 4.2 Functional responses of A. nemorum to eggs of P. brassicae after two hours - the number eaten (Ne) plotted against the prey density (N). The Random Predator Equation is fitted by the method of the least squares best fit to the functional response.

(A) - eggs arranged at random; $a = 0.00765/\text{min.}$, $T_h = 23.62 \text{ min.}$

(B) - eggs arranged using the negative binomial ($K = 1.0$); $a = 0.007553/\text{min.}$, $T_h = 25.97 \text{ min.}$

(C) - eggs arranged using the negative binomial ($K = 0.01$); $a = 0.00854/\text{min.}$, $T_h = 24.46 \text{ min.}$

(D) - eggs arranged in regularly distributed clumps of ten; $a = 0.00854/\text{min.}$, $T_h = 21.12 \text{ min.}$

Number eaten plotted as the mean \pm S.E. of mean.

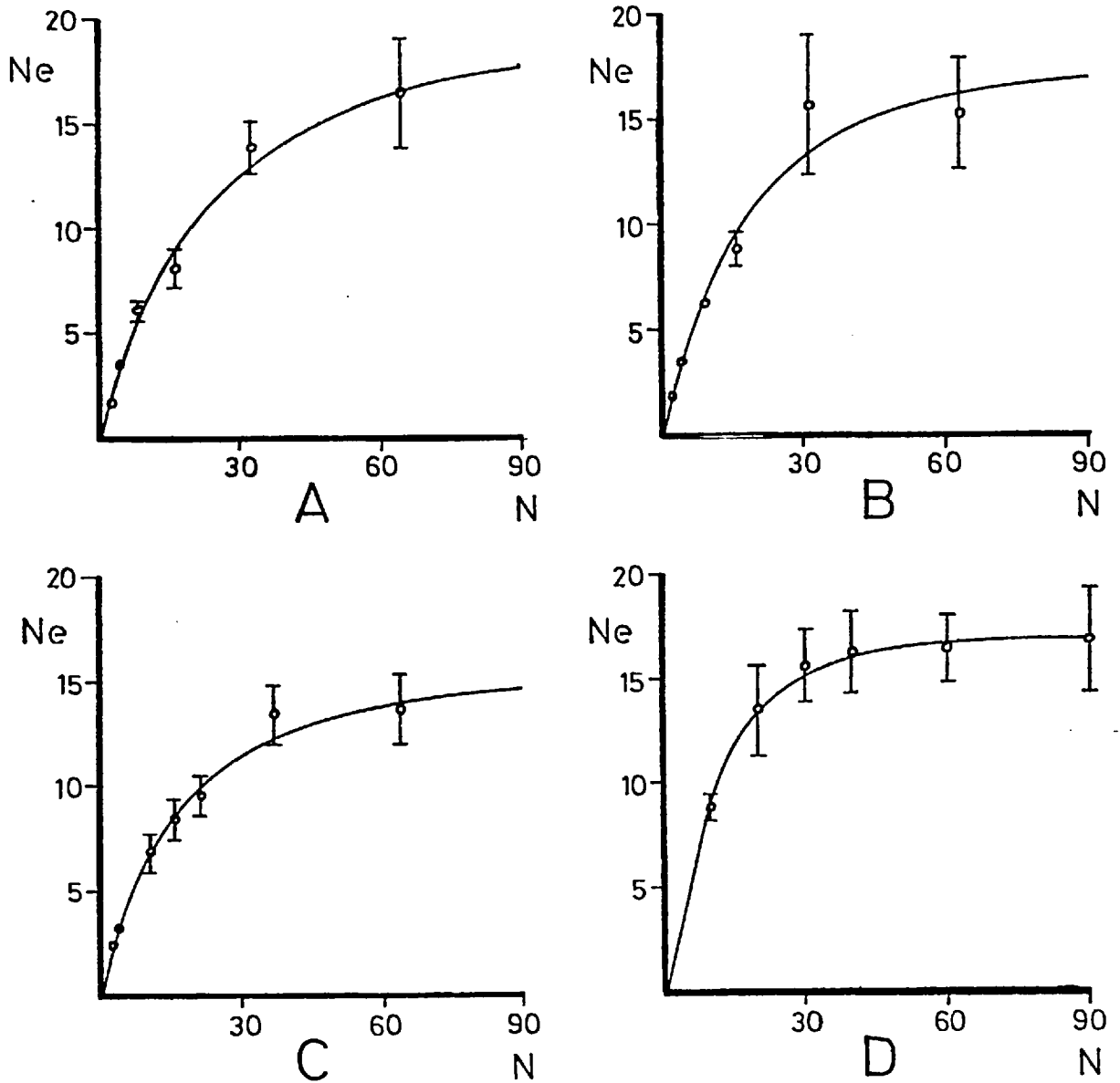


FIGURE 4.3 Functional responses of *A. nemorum* to eggs of *P. brassicae* after twenty hours 6 the number eaten (N_e) plotted against the prey density (N). The Random Predator Equation is fitted by the method of the least squares best fit to the functional response.

(A) - eggs arranged at random; $a = 0.00125/\text{min.}$, $T_h = 58.22 \text{ min.}$

(B) - eggs arranged using the negative binomial ($K = 1.0$); $a = 0.00170/\text{min.}$, $T_h = 63.48 \text{ min.}$

(C) - eggs arranged using the negative binomial ($K = 0.01$); $a = 0.00134/\text{min.}$, $T_h = 72.28 \text{ min.}$

(D) - eggs arranged in regularly distributed clumps of ten; $a = 0.00399/\text{min.}$, $T_h = 67.37 \text{ min.}$

Number eaten plotted as the mean \pm S.E. of mean.

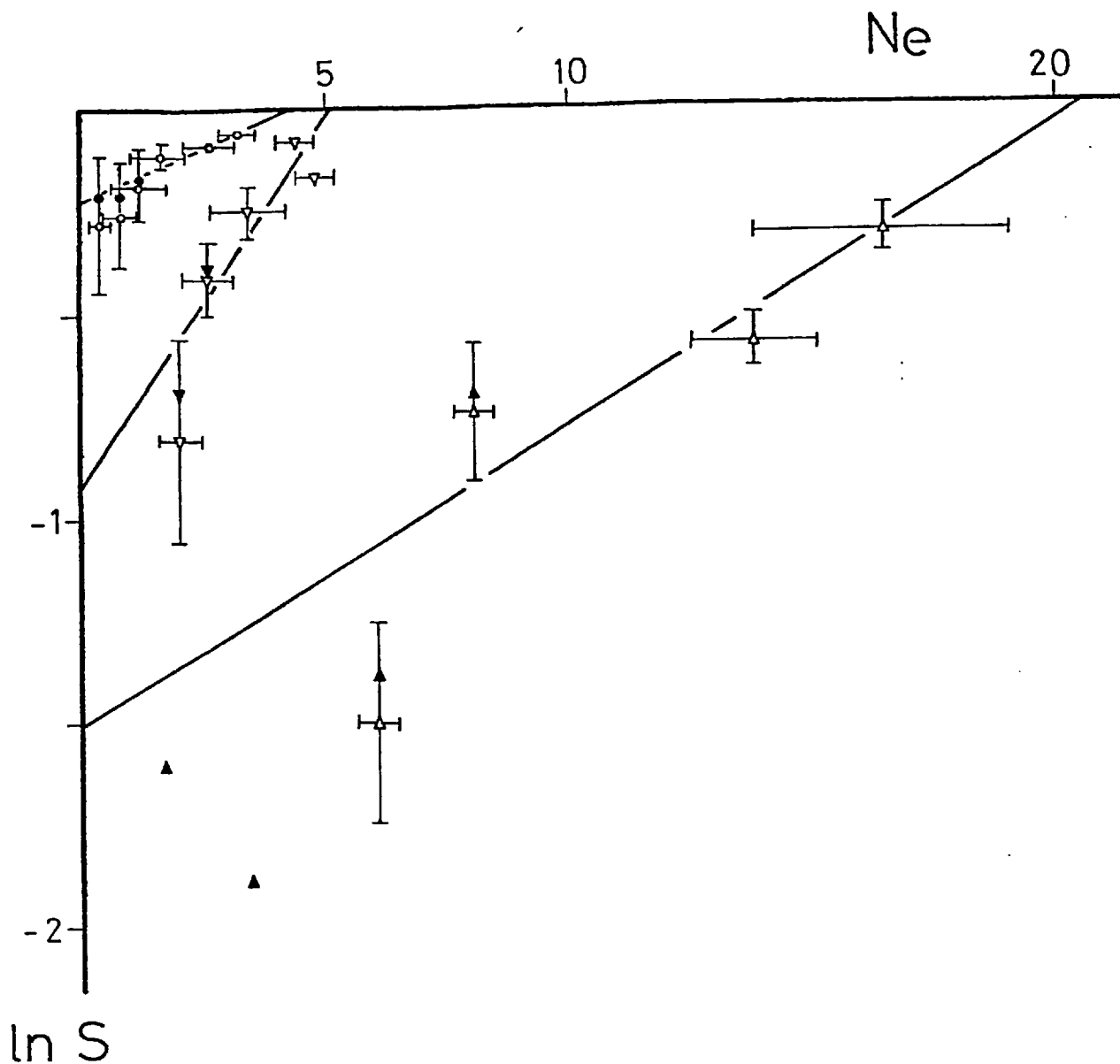


FIGURE 4.4 Predation of A. nemorum on eggs of P. brassicae arranged at random. - logarithm of the proportion of prey surviving ($\ln S$) plotted against the number eaten (Ne). The results after all three time intervals are shown. The fitted lines were obtained by the least squares best fit to the functional response (see Table 4.6). Symbols used are: \circ - after one hour; ∇ - after two hours; \triangle - after twenty hours; solid symbols are used for the values of $\ln \bar{S}$ where these are significantly different from $\overline{\ln S}$.

Number eaten and $\ln S$ plotted as the mean \pm S.E. of the mean.

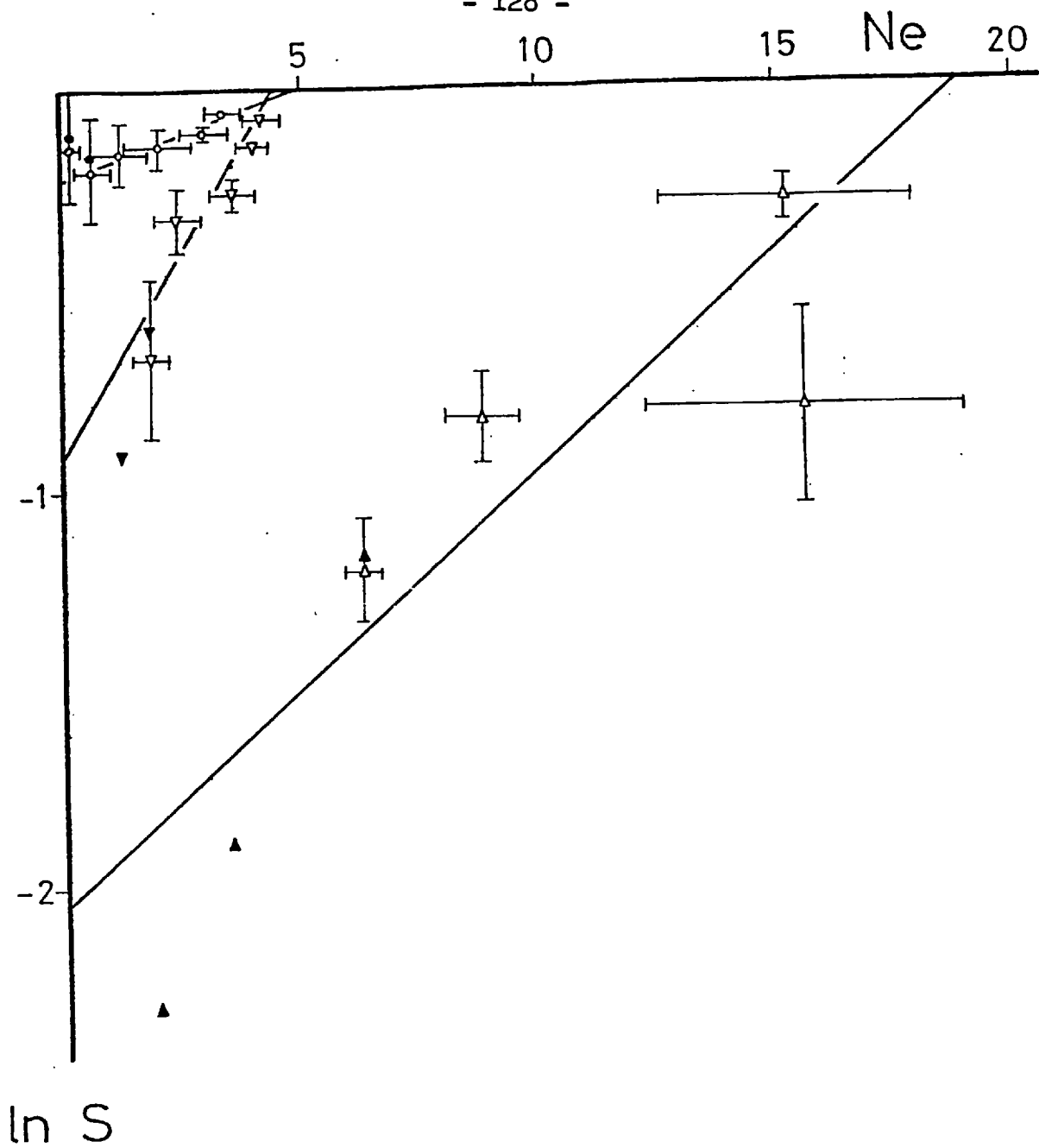


FIGURE 4.5

Predation of A. nemorum on eggs of P. brassicae arranged using the negative binomial distribution ($K = 1.0$) - logarithm of the proportion of prey surviving ($\ln S$) plotted against the number eaten (N_e). The results after all three time intervals are shown. The fitted lines were obtained by the least squares best fit to the functional response (see Table 4.6). Symbols used are: \circ - after one hour; ∇ - after two hours; Δ - after twenty hours; solid symbols are used for values of $\ln \bar{S}$ where these are significantly different from $\overline{\ln S}$. Number eaten and $\ln S$ plotted as the mean \pm S.E. of the mean.

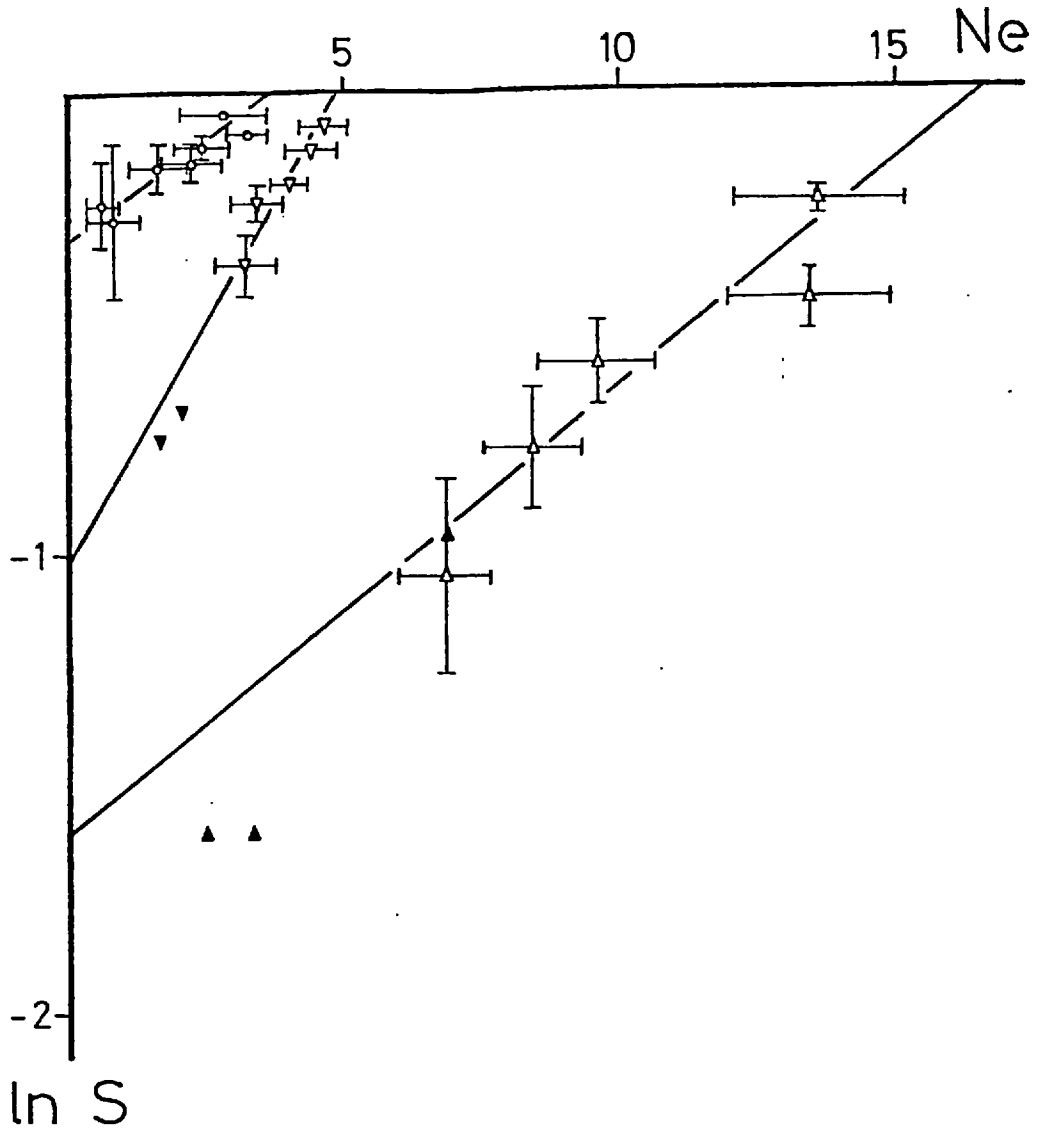


FIGURE 4.6 Predation of A. nemorum on eggs of P. brassicae arranged using the negative binomial distribution ($K = 0.01$) - logarithm of the proportion of prey surviving ($\ln S$) plotted against the number eaten (Ne). The results after all three time intervals are shown. The fitted lines were obtained by the least squares best fit to the functional response (see Table 4.6). Symbols used are: \circ - after one hour; ∇ - after two hours; \triangle - after twenty hours; solid symbols are used for values of $\ln \bar{S}$ where these are significantly different from $\overline{\ln S}$.
Number eaten and $\ln S$ plotted as the mean \pm S.E. of the mean.

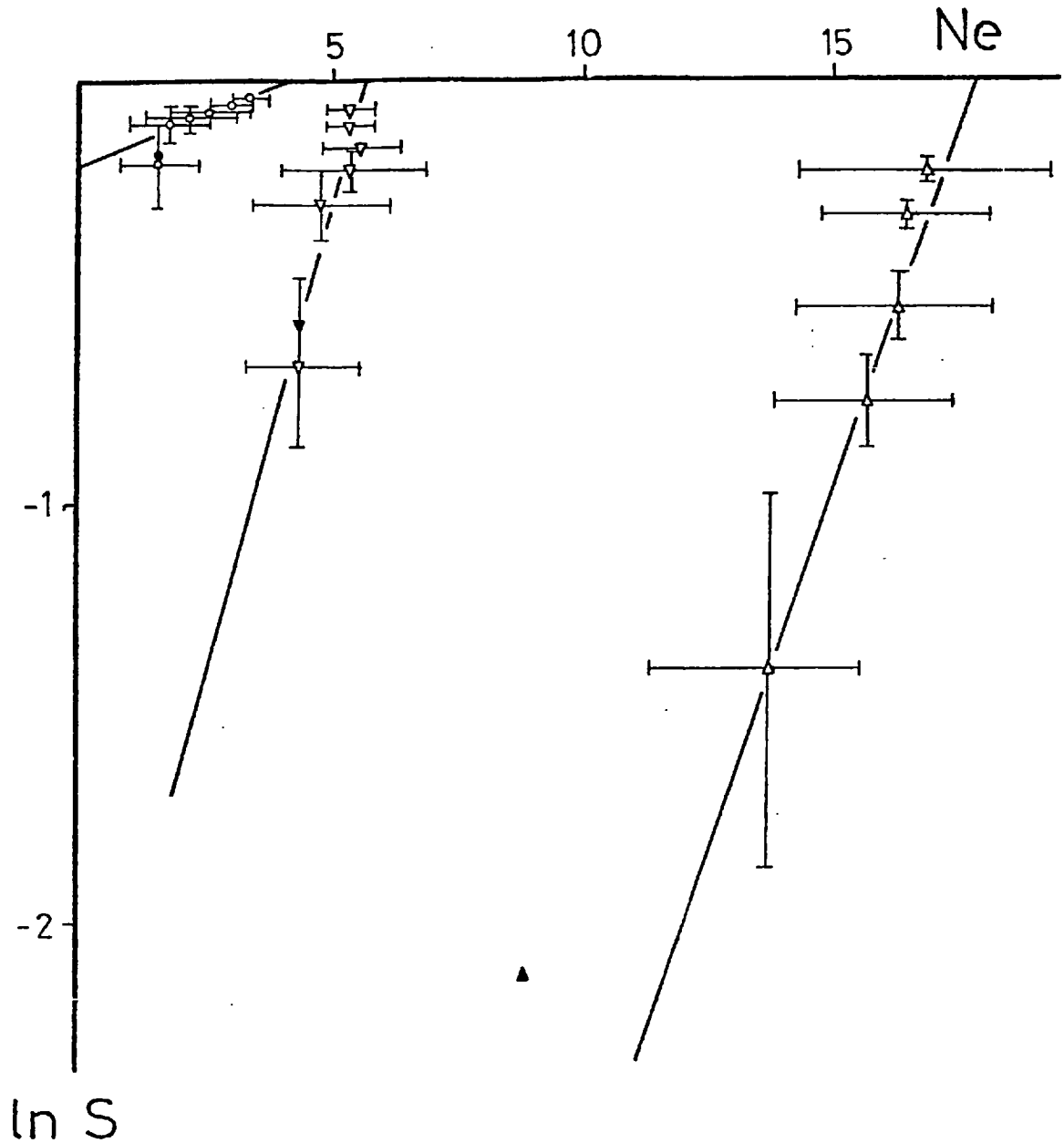


FIGURE 4.7 Predation of A. nemorum on eggs of P. brassicae arranged in regularly distributed clumps of ten - logarithm of the proportion of prey surviving plotted against the number eaten (N_e). The results after all three time intervals are shown. The fitted lines were obtained by the least squares best fit to the functional response (see Table 4.6). Symbols used are; \bullet - after one hour; ∇ - after two hours; \blacktriangle - after twenty hours; solid symbols are used for values of $\ln \bar{S}$ where these are significantly different from $\overline{\ln S}$.

Number eaten and $\ln S$ plotted as the mean \pm S.E. of the mean.

4.4 DISCUSSION AND CONCLUSIONS

The premises leading to the Random Predator Equation (Rogers, 1972) include the assumption that the search efficiency and handling time of a predator searching at random for a given prey type are constant over time. In the experiments considered here, this would result in the search efficiency and handling time estimates for the functional responses being constant, irrespective of the time intervals and prey distribution. Examination of Table 4.6 shows that this is not the case. The estimated search efficiencies and handling times are largely unaffected by the prey distribution, but are different for each time interval.

The mean estimated handling time after two hours is approximately double that obtained after one hour. This results from the $\ln S \times N_e$ plots (Figs. 4.4 - 4.7) showing a common intercept on the N_e axis, implying a common maximum prey consumption of approximately five. This is due to temporary satiation of the anthocorid after eating five prey. Thus, if the prey density were sufficiently high, on average five prey would be eaten in the first hour, and the satiated anthocorid would not feed again during the second hour. After twenty hours, the estimated handling time is considerably higher, and this is due to one or more long periods of inactivity or rejection of prey. The data obtained after twenty hours can be fitted to a modified Random Predator Equation of the form:

$$N_e = N(1 - \exp(- a(T - T_w - T_h N_e))) \quad . . . 4.1$$

where T_w is the time wasted or period of rejection of prey. The value of T_w can be varied to obtain the required values for the search efficiency or handling time. Thus, if T_w is twelve hours, the handling times obtained are comparable with those obtained after two hours; whilst if T_w is 16 hours, the estimated handling times are comparable with those after one hour. Since the estimated handling times after one hour are consistent with those observed (Chapter 5), this latter estimate of T_w seems reasonable. This means that over the twenty hour period, anthocorids search and feed for about four hours only.

TIME IN HOURS	DISTRIBUTION	a	a	Th	Th
one	random	.00350	.00399	14.27	14.48
	K = 1.0	.00364		12.47	
	K = 0.01	.00542		16.26	
	'clumped'	.00330		14.84	
two	random	.00765	.00791	23.62	23.29
	K = 1.0	.00755		25.97	
	K = 0.01	.00854		24.46	
	'clumped'	.02085		21.12	
twenty	random	.00125	.00143	58.22	65.34
	K = 1.0	.00170		63.48	
	K = 0.01	.00134		72.28	
	'clumped'	.00399		67.37	

TABLE 4.6

Predation of A. nemorum on a range of distributions of eggs of P. brassicae at three time intervals - summary of the estimated parameters (a = search efficiency; Th = handling time) of the Random Predator Equation obtained by the least squares best fit to the functional response. Mean values are given where the parameters are consistent.

It can be seen (Table 4.6) that the estimates of the search efficiency for the 'scattered' distributions differ from those for the 'clumped' distribution. Therefore, the 'clumped' distribution will be considered separately below. Considering the 'scattered' distributions, it can be seen that compared with the estimates after one hour, the estimates after two hours are higher, and after twenty hours, lower. This initial increase is caused by the time taken to recognise the prey before feeding is initiated (Anderson, 1961). From the original data (Tables 4.1 - 4.3) it can be seen that about one quarter of the anthocorids do not commence to feed until the second hour; insufficient encounters being made during the first hour to initiate feeding. This delay results in the higher estimated search efficiency after two hours. The decrease found after twenty hours is a reflection of the long period of rejection of prey. Table 4.6 shows that, for the first two hours, the search efficiency for the prey arranged according to the negative binomial distribution ($K = 0.01$) is greater than that for the other 'scattered' distributions. This tendency is lost by twenty hours, and may not be significant. Comparison of the functional response figures after one hour (Fig. 4.1) with those after two hours (Fig. 4.2) and twenty hours (Fig. 4.3) shows that an initially high variance is soon lost. This again is caused by the time lag for the recognition of the prey; some anthocorids do not feed during the first hour (leading to high variance) but most have started to feed by the end of the second (leading to reduced variance).

In the case of the 'clumped' prey, the estimates of the search efficiency after two hours and twenty hours are higher than those obtained for the 'scattered' distributions of prey (Table 4.6). Furthermore, examination of the functional response figures shows that the high variance found after one hour for the 'scattered' distributions (Fig. 4.1) is still present for the 'clumped' distribution after two hours (Fig. 4.2), but reduced after twenty hours (Fig. 4.3). These differences are due to the compact distribution of the eggs. A clump of ten eggs will be encountered less frequently than ten 'scattered' eggs. Hence, 'scattered' distributions will cause more encounters, and feeding will be initiated more rapidly. However, once an anthocorid 'recognises' a clump of eggs, it stays by that clump and its search efficiency

is greatly increased. These two effects cancel each other out during the first hour, leading to results similar to those obtained for the 'scattered' distributions. At the end of two hours, however, the increased search efficiency has the greater effect and this is reflected in the estimated parameters. Since the effects of the longer time necessary to recognise the prey are exaggerated by the increased search efficiency once the clump is found, the high variance still occurs after the second hour. The greater search efficiency is still evident after twenty hours, but the variance is reduced.

From this discussion, it can be seen that the parameters of the Random Predator Equation do not remain constant. The effects of any time lag for recognition, satiation, periods of inactivity and aggregative behaviour in response to a clump of prey are all measured in terms of the two parameters search efficiency and handling time. These two parameters, therefore, should be considered as an amalgamation of searching behaviour, and not just the simple constants originally defined.

CHAPTER 5

PREDATION OF ANTHOCORIS NEMORUM (L.) UPON PIERIS BRASSICAE (L.) EGGS ARRANGED ON BEAN PLANTS

5.1 INTRODUCTION

In this chapter, the searching behaviour of A. nemorum upon bean plants will be examined. This topic has not received a great deal of attention in the past. Anderson (1961) and Evans (1973) have both noted that starved anthocorids will probe plant tissues and drink from water droplets; in view of this, it seems likely that anthocorids searching on plants are more likely to survive the experimental period, than those used in the dry, perspex arenas described in Chapter 4.

Steer (1929) noted that A. nemorum nymphs searching for red spider mites and their eggs (Oligonychus ulmi Koch and Tetranychus telarius L.) search systematically on the underside of leaves of Rubus spp. They were observed to walk the length of a vein and probe carefully on either side i.e. where most of the mites and their eggs were to be found.

Dixon & Russell (1972) studied the searching behaviour of adult A. nemorum and A. confusus Rtr. on sycamore leaves. They recorded the search paths of the anthocorids on the underside of the leaves, and found that they spent disproportionately more time on the main veins. The experiments implied that negligible time is spent searching on the upper surface of leaves. The authors consider that 18 hours per day are spent searching and feeding; they do not mention long periods of inactivity. Long 'digestive pauses' are included as handling time in their approach, but do not seem to be considered of any importance. They

also found that the speed of movement when the anthocorids were on the petioles was greater than when they were on the leaves.

Evans (1973) also made more detailed observations on the searching behaviour of first and second instar nymphs of A. nemorum on bean plants. He found that the nymphs spent 48% of the available time at rest on the petiole or base of the leaves. Of the remaining time, 15% was spent on the upper surface. Of the time spent searching on the undersurface of the leaves, first instar nymphs spent 42% on the veins and 45% on the edges of leaves, while second instar nymphs spent 18% and 79% respectively in these areas. The greatest distance travelled was on the edge of the leaves, and along the veins; he found the speed of movement to be greatest upon the leaves.

Brunner & Burts (1975) examined the behaviour of A. nemoralis (F.) nymphs searching for Pear Psylla (Psylla pyricola Forster) upon individual pear leaves, and found differences in behaviour depending upon the satiation of the anthocorid. Starved anthocorids moved slowly (5.7 cm/min) with a high turning rate (68° turn/cm); when a prey was found, they increased their rate of turn and decreased their speed (the time for which this occurred is not mentioned). The search paths of the starved nymphs showed a high correlation with the distribution of immature prey; thus, the predator spent 71% of the time on the lower leaf surface, where 74% of the immature pear psylla occurred and 48% of the time on the midribs where 64% of the immature prey were to be found. Satiated individuals, in contrast, had a relatively higher speed (7.2 cm/min) and a reduced rate of turn (30° turn/cm). The primary route was around the leaf periphery and repeated attempts were made to leave the leaf; the authors conclude that such behaviour is the action of satiated individuals searching for a resting place.

Thus, Dixon & Russell (1972) working with adult anthocorids on sycamore leaves, Evans (1973) working with nymphal A. nemorum on bean leaves and Brunner & Burts (1975) working with nymphal A. nemoralis on pear leaves, all found that anthocorids spend most time searching on the veins and edges of the underside of leaves. It will be seen, from observations in this

chapter (Section 5.6), that adults of A. nemorum search on bean plants in a manner different to that described above.

In this chapter, two arrangements of P. brassicae eggs are used: individual eggs on the edges of the leaves and clumps on the centre of the uppersurface. The functional responses to these two arrangements (Section 5.3) are used to predict predation when both arrangements are used (Section 5.4). The distributions of attacks between leaves or clumps of eggs are recorded (Section 5.5), and continuous observation of the searching behaviour and allocation of time are made for each prey arrangement (Section 5.6).

5.2 EXPERIMENTAL METHOD

5.2.1 The Arenas

For this work, the arena consisted of an individual plant of miniature broad beans, Vicia fabae (L.), planted in a pot. The plants used were seedlings old enough to have four leaves; the central axil and any bracts were pinched off, leaving the stem and the four leaves. The stem was bound with cello tape to bring the bases of the leaves together. The crevice between the two pairs of leaves was blocked with a small wad of damp cotton wool to prevent anthocorids becoming stuck down this gap or upon the cello tape. The bean seedling was then planted in a plastic pot of diameter 12.6 cm, the soil level coming to within about two cm of the top of the pot. A thin layer of fine, dry sand was then spread on top of the soil, preventing the anthocorids hiding in the soil, and making them readily visible when upon the surface. A plastic propagator top was placed on top of the pot. The top of the propagator lid had been removed and replaced with fine mesh netting, allowing ventilation and preventing condensation within the arena. The inside of the bottom of the propagator top was coated with fluon, in order to prevent the anthocorids climbing upon the side and top of the propagator. This experimental arrangement is shown in Fig. 5.1.

5.2.2 The Prey: P. brassicae eggs

As in the last chapter, the eggs were glued down using gum tragacanth. Two arrangements of prey were used: firstly, clumps of ten eggs were glued in the centre of the upper surface of the leaves and secondly, individual eggs were glued at regular intervals around the edge of the leaves, again upon the upper surface. These two arrangements will be referred to as 'clump' eggs and 'edge' eggs in this work.

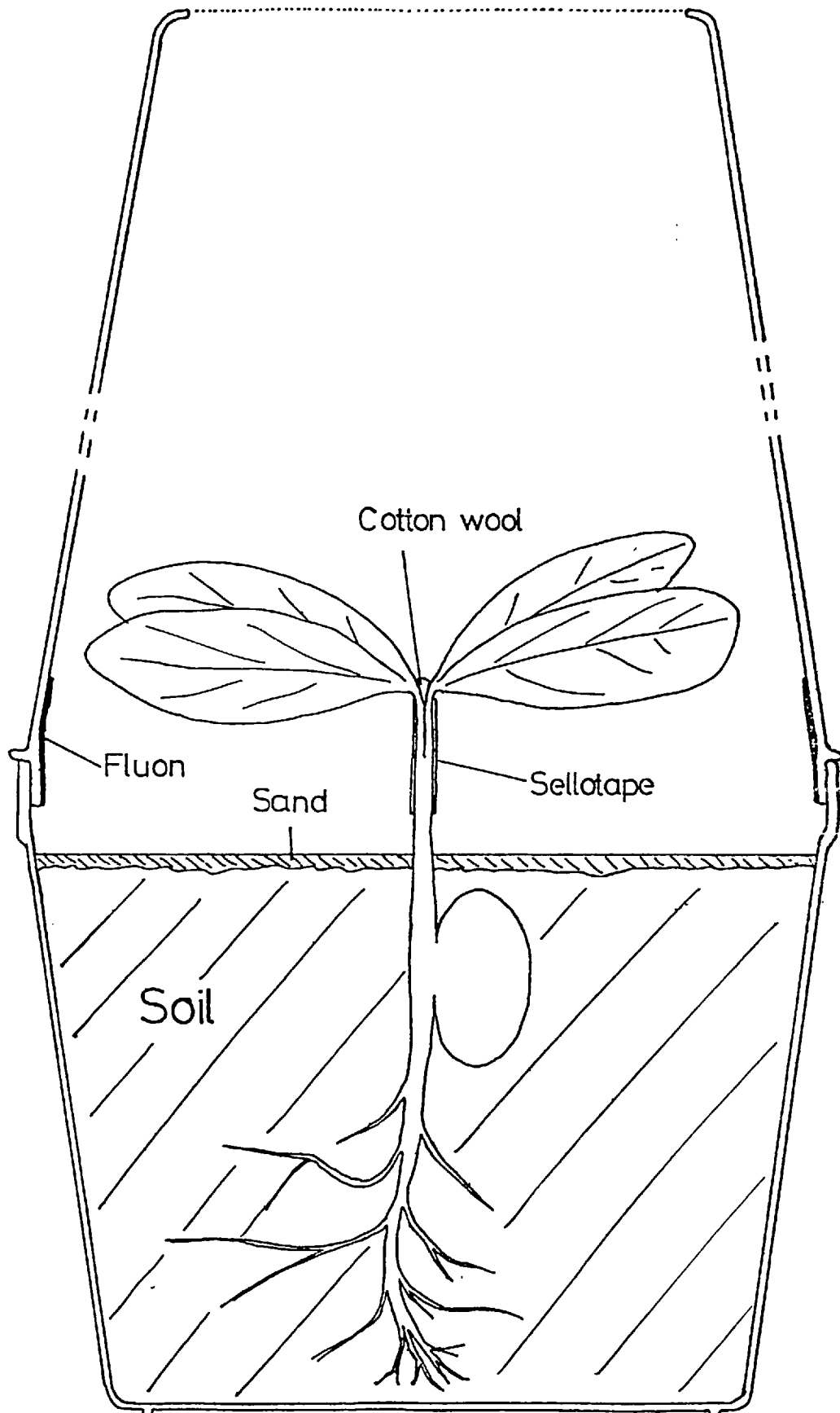


FIGURE 5.1 A sectional view of the arena used in the work of Chapter 5, as described in Section 5.2.1. Approximately x 1.

5.2.3 The Predators: *A. nemorum* adults

In order to obtain anthocorids of standard starvation, they were treated in a manner similar to that used for the work with square, perspex arenas (Section 4.2.3).

5.2.4 Experimental Procedure

The procedure used was basically the same as that used in Chapter 4 (Section 4.2.4). Predation was recorded after one, two and twenty hours. The distribution of attacks was also recorded; in the case of 'clump' eggs, the number attacked in each clump was recorded, while for 'edge' eggs, the number attacked on each leaf was recorded. By using an eight track event recorder, observations were made of the anthocorid's behaviour during the second hour and the final hour of one replicate of each arrangement of eggs.

It was found that mortalities during the course of experiments were lower than those obtained in the work with the square, perspex arenas described in Chapter 4. This is due to a combination of the availability of moisture from the plants, and the presence of hiding or resting places in the arena leading to reduced activity.

5.3 FUNCTIONAL RESPONSES TO INDIVIDUAL PREY ARRANGEMENTS

5.3.1 Introduction and Methods

Predation was scored in the same way as for the work with square, perspex arenas described in Chapter 4. Once again, due to the deflation of punctured eggs, the number of eggs attacked, rather than the number consumed, was recorded.

5.3.2 Results and Analysis

The predation of 'edge' and 'clump' prey and the corresponding $\ln S$ values (logarithm of proportion of eggs surviving) are set out in Tables 5.1 ('clump') and 5.2 ('edge'). The resultant functional responses and $\ln S \times N_e$ plots (see Sections 2.2 and 2.3) are shown in Figs. 5.2 (one hour), 5.3 (two hours) and 5.4 (twenty hours). The $\ln S \times N_e$ plots show linear relationships, and so the Random Predator Equation has been fitted to the functional responses by the least squares best fit technique (Section 2.2, Appendix Section A1.3), and the parameters obtained are tabulated in Table 5.3. A significantly good fit is obtained in all cases.

5.3.3 Discussion

The functional responses obtained (Figs. 5.2-5.4) differ according to the egg arrangement and the time interval.

The responses after one hour (Fig. 5.2) show that the search efficiency and the maximum consumption rate are less for 'clump' prey than they are for 'edge' prey. This can be explained by a difference in encounter rates, similar to that suggested in Chapter 4 to account for the difference between 'scattered' and 'clumped' distributions after one hour. In that case, it was suggested that, if scattered individual eggs and clumped eggs are present at equal densities, scattered eggs will

be more frequently encountered, and so recognition of the eggs as prey, and hence initiation of feeding, will occur sooner. In view of the results of Section 5.6, this phenomenon is likely to be even more pronounced due to the greater proportion of time spent searching on the edges of leaves. Therefore, if the time lag for recognition is less for 'edge' prey, the anthocorids will spend more time searching for and feeding upon 'edge' prey, and hence, have a greater search efficiency and maximum consumption rate.

Due to the greater rate of feeding once 'clump' eggs are found (as described in Chapter 4), the maximum consumption rates after two hours are similar. However, because of the larger proportion of time being spent searching the edges of leaves, the anthocorids still show a greater search efficiency for 'edge' prey.

After twenty hours, however, the two responses are very different. The search efficiency for 'edge' prey is much greater than for 'clump' prey. This is still due to the tendency of the anthocorids to search the edges of leaves; thus, at low densities, most of the 'edge' eggs are likely to have been encountered by most of the anthocorids. The maximum consumption rate, however, is much greater for 'clump' eggs than for 'edge' eggs. This is caused by the anthocorids puncturing several eggs within a clump, without necessarily feeding much on them (Section 4.2). Thus, the actual maximum consumption of eggs is likely to be similar for both arrangements,

When the standard errors of the points of the graphs at the three time intervals are compared, it can be seen that these are large after one and two hours, the results only becoming reasonably consistent after twenty hours. This high, initial variance was also found in the work of Chapter 4, and again, is because some individuals do not start feeding until after the second hour (see Tables 5.1 & 5.2). This may be due to the time lag needed for recognition of the prey, but is accentuated by the more heterogeneous arena providing resting sites where the anthocorids remain inactive for long periods without searching for food (see Section 5.6).

TIME	N	NUMBER EATEN (Ne)	\bar{N}_e	S.E.	$\ln S$	S.E.
One	10	0 0 0 3 0	0.6	0.60	- .071	.071
	20	0 0 2 3 0	1.0	0.63	- .054	.034
	30	2 0 0 0 4	1.2	0.80	- .042	.028
	40	0 1 1 2 3	1.4	0.51	- .036	.013
	80	0 2 3 3 0	1.6	0.60	- .018	.008
Two	10	3 0 0 3 0	1.2	0.73	- .143	.087
	20	4 0 2 7 0	2.6	1.33	- .152	.081
	30	2 0 2 5 6	3.0	1.10	- .109	.041
	40	0 4 2 5 5	3.2	0.97	- .085	.026
	80	3 2 4 3 4	3.2	0.37	- .041	.005
Twenty	10	3 0 2 3 5	2.6	0.81	- .326	.113
	20	6 8 2 12 2	6.0	1.26	- .399	.151
	30	5 4 2 8 12	6.2	1.74	- .243	.078
	40	7 7 10 14 5	8.6	1.57	- .247	.052
	80	10 8 9 6 15	9.6	1.50	- .129	.022

TABLE 5.1 Predation of A. nemorum upon 'clump' eggs of P. brassicae. The first of each series of replicates was used in the continuous observations of Section 5.6.

TIME	N	NUMBER EATEN (Ne)	Ne	S.E.	ln S	S.E.
One	4	0 1 0 0 1	0.4	0.24	- .115	.070
	8	1 2 0 0 1	0.8	0.37	- .111	.053
	16	2 3 0 0 1	1.2	0.58	- .081	.040
	32	3 0 3 0 4	2.0	0.84	- .066	.028
	64	1 3 5 0 2	2.2	0.86	- .035	.014
Two	4	0 3 0 0 4	1.4	0.87	- .431	*
	8	2 2 0 2 2	1.6	0.40	- .960	.145
	16	2 4 0 4 3	2.6	0.75	- .183	.054
	32	5 3 5 0 4	3.4	0.93	- .114	.032
	64	2 3 5 4 6	4.0	0.71	- .065	.012
Twenty	4	1 4 0 2 4	2.2	0.80	- .799	*
	8	5 3 5 6 5	4.8	0.49	- .960	.145
	16	5 4 7 6 4	5.2	0.58	- .399	.055
	32	9 5 5 3 8	6.0	1.10	- .211	.043
	64	4 5 7 6 6	5.6	0.51	- .092	.009

TABLE 5.2 Predation of A. nemorum upon 'edge' eggs of P. brassicae. The first of each series of replicates was used in the continuous observations of Section 5.6. (* - ln of mean S given due to total predation in one replicate.)

PREY ARRANGEMENT	TOTAL TIME	ABSTRACTED PARAMETERS		GOODNESS OF FIT		
		a	Th	F	df	P
'clumps'	One	.00161	28.9	270	1,4	<.01
	Two	.00251	29.3	17	1,4	<.05
	Twenty	.000447	91.5	43	1,4	<.01
'edge'	One	.00239	19.6	135	1,4	<.01
	Two	.00362	26.4	100	1,4	<.01
	Twenty	.00197	192.1	11	1,4	<.05

TABLE 5.3 Abstracted parameters of the Random Predator Equation for the functional responses of A. nemorum to 'clump' and 'edge' eggs of P. brassicae (Figs. 5.2 - 5.4), obtained by the least squares best fit to the functional response (Section 2.2) from the data of Tables 5.1 & 5.2.

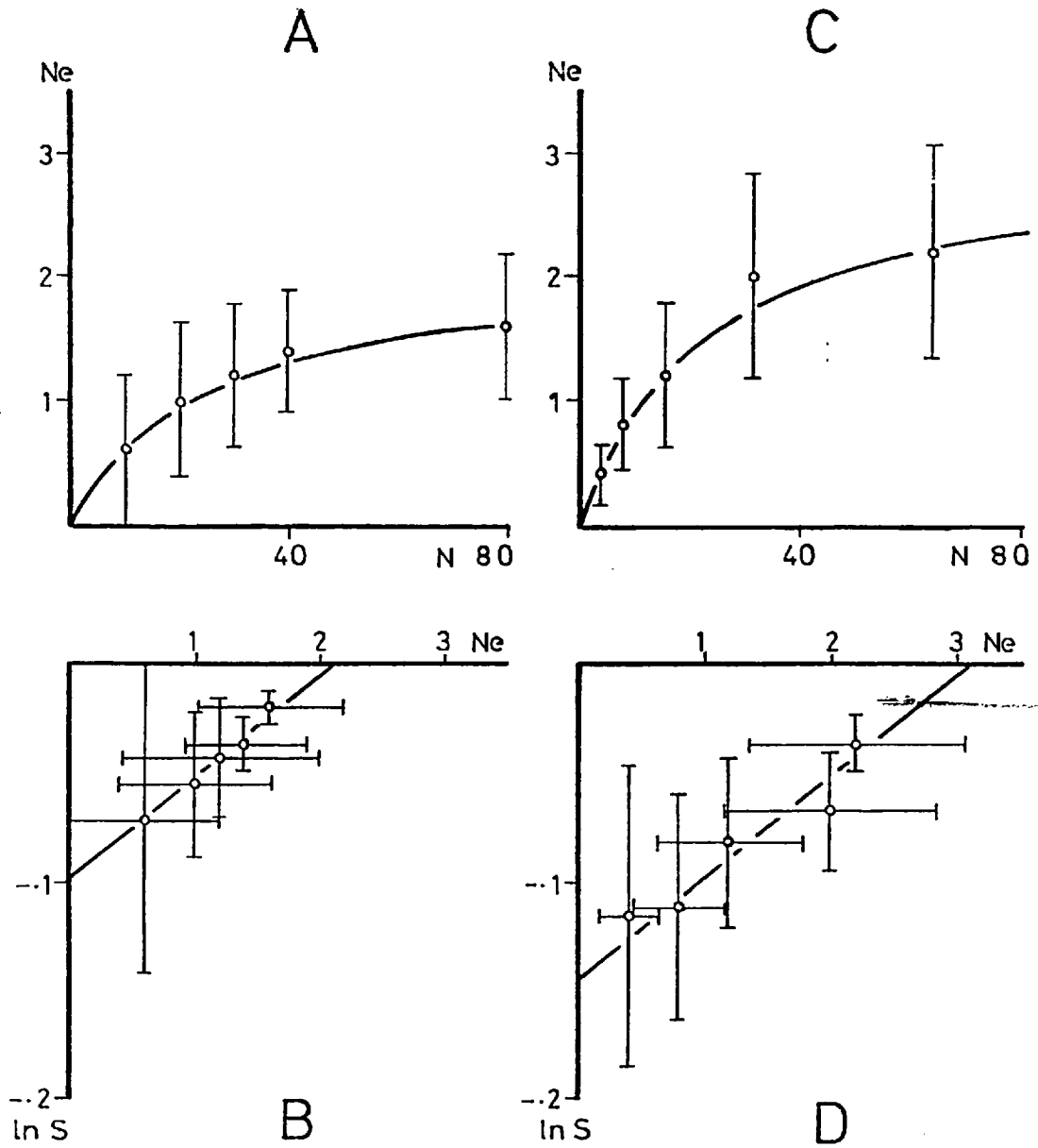


FIGURE 5.2 Predation of A. nemorum upon eggs of P. brassicae - functional responses and $\ln S \times Ne$ plots for 'clump' (A & B) and 'edge' (C & D) eggs after one hour. The Random Predator Equation is fitted using the parameters given in Table 5.3. Number eaten (Ne) and $\ln S$ plotted as mean \pm S.E. of mean.

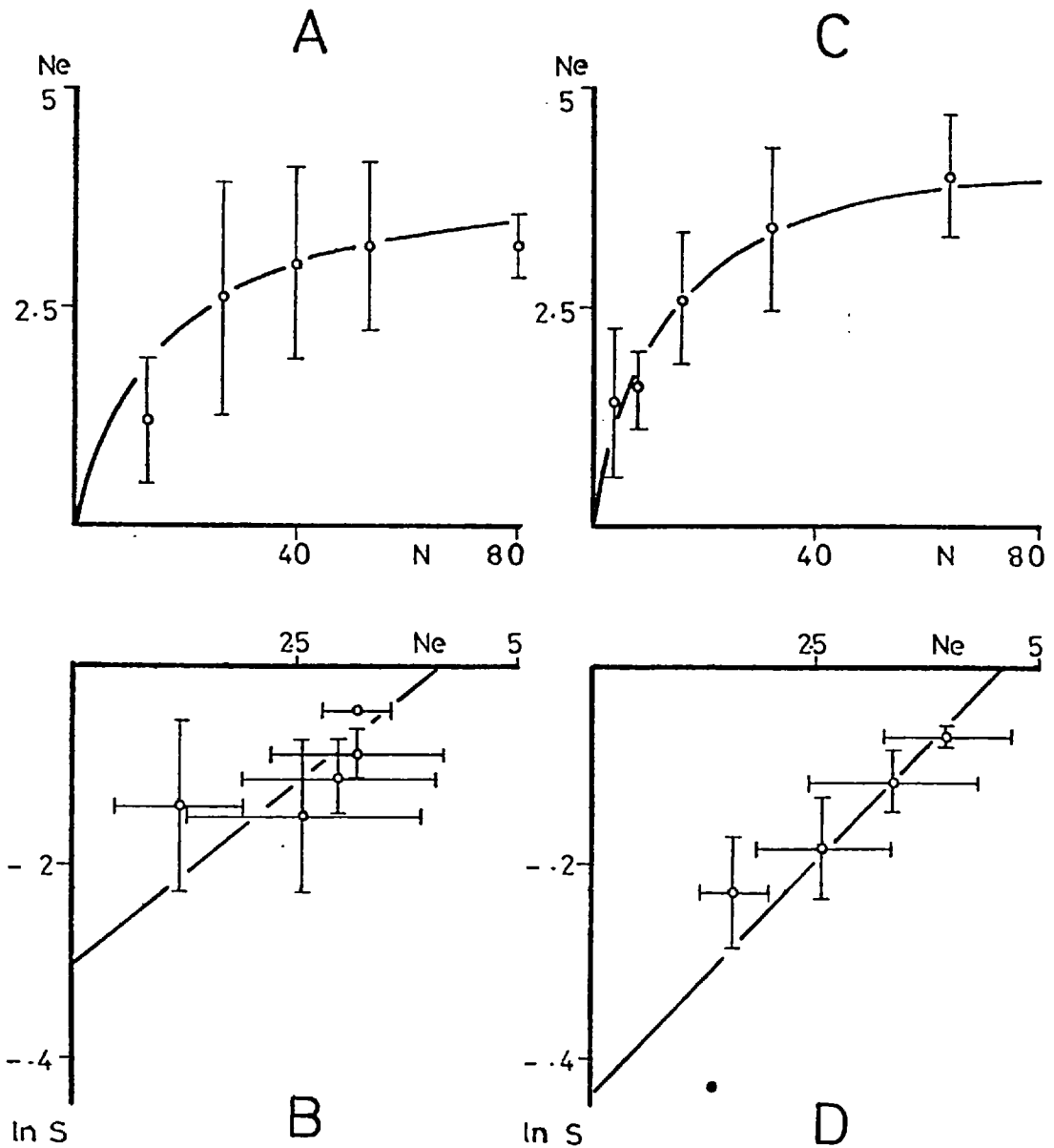


FIGURE 5.3 Predation of A. nemorum upon eggs of P. brassicae - functional responses and $\ln S \times Ne$ plots for 'clump' (A & B) and 'edge' (C & D) eggs after two hours. The Random Predator Equation is fitted using the parameters given in Table 5.3. The symbol • is used to denote a value of \ln mean S, as opposed to mean $\ln S$.

Number eaten (Ne) and $\ln S$ plotted as mean \pm S.E. of mean.

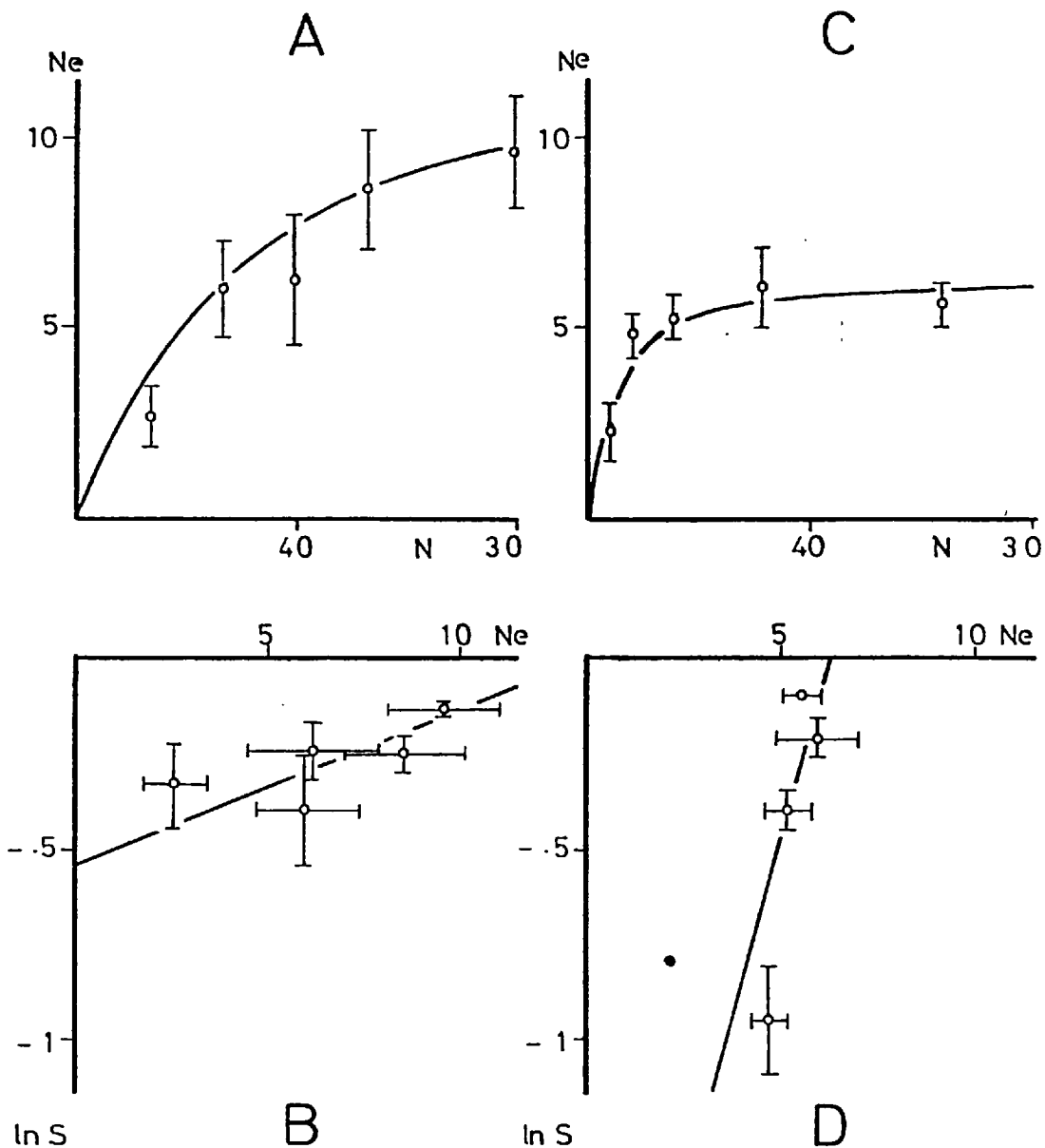


FIGURE 5.4 Predation of A. nemorum upon eggs of P. brassicae - functional responses and $\ln S \times Ne$ plots for 'clump' (A & B) and 'edge' (C & D) eggs after twenty hours. The Random Predator Equation is fitted using the parameters given in Table 5.3. The symbol \bullet is used to denote a value of \ln mean S , as opposed to mean $\ln S$.

Number eaten (Ne) and $\ln S$ plotted as mean \pm S.E. of mean.

5.4 PREDATION ON MIXED ARRANGEMENTS OF EGGS

5.4.1 Introduction and Methods

The functional responses to two prey types (or arrangements) presented separately can be used to predict predation at all combinations of densities when both are present, assuming that no 'deliberate' preference is shown (Section 3.5). Thus, a three dimensional figure ($N_e \times N \times N'$, where N_e = the number of prey eaten and N and N' are the densities of the two prey types) is obtained, as is shown, for example, in Lawton, Beddington & Bonser (1974). In Chapter 3, using coccinellids feeding on two size classes of aphid prey, a section through this three dimensional graph was considered, such that $2N + N' = 20$. In this section using anthocorids, nine combinations of the densities of the two prey arrangements will be used, in an attempt to cover the range of the relationship defined by the two functional responses.

5.4.2 Results and Analysis

The predation which occurred at the nine combinations of egg densities is given in Table 5.4.

In Figs. 5.5 (one hour), 5.6 (two hours) and 5.7 (twenty hours), the predictions based on the Random Predator Equation for the separate prey arrangements are fitted to the predation results. The adaptation of the Random Predator Equation to two prey types is given in Section 1.3.3; the computer programme PREDICT (Appendix Section A1.5) was used to solve the resultant equations using the parameters given in Table 5.3. The data is presented as three sections of the three dimensional relationship ($N_e \times N \times N'$; the number eaten x density of 'edge' eggs x density of 'clump' eggs) with the number of 'clump' eggs (N') constant at 10, 40 or 80 in each section.

5.4.3 Discussion

Examination of Figs 5.5-5.7 shows that, on the whole, the predictions based on the functional responses give a poor fit when compared with the accuracy obtained in Chapter 3 using coxichelids.

The predictions after one hour provide a good fit to the observed data ($\chi^2 = 1.103$, $df = 8$, $P > .99$). However, due to the large variance in the data after one hour for both the separate functional responses and for this mixed prey experiment, not too much reliance can be placed on this result.

The figure for two hours (Fig. 5.6) does not show such a good fit to the data ($\chi^2 = 8.9$, $df = 8$, $.05 < P < .95$). In particular, the results when 80 'clump' prey are present are not fitted by the predictions. In this case the consumption of 'clump' prey is underestimated. The consumption when 64 'edge' prey are present also seems to be underestimated when there are 40 and 80 'clump' prey.

After twenty hours, this tendency has become clearer. In all cases the consumption of 'clump' prey is underestimated; in all except one, the consumption of 'edge' prey is overestimated. The variance after twenty hours is still high; examination of Table 5.3 shows the reason for this. There is a tendency for the anthocorids to concentrate on the eggs of one arrangement. Thus, when 40 'clump' and 64 'edge' prey are available, two anthocorids eat mainly 'clump' eggs, two eat mainly 'edge' eggs, and one eats both in equal numbers. This tendency to concentrate on one prey arrangement is present after one and two hours, and it seems likely that the feeds of the first few hours determine the subsequent behaviour during the experiment.

TIME IN HOURS	DENSITY CLUMP/ EDGE	PREDATION OF 'CLUMP' EGGS					PREDATION OF 'EDGE' EGGS								
		NUMBER EATEN					Ne	S.E.	NUMBER EATEN					Ne	S.E.
One	10 / 4	0	0	2	0	2	0.8	0.49	1	0	0	0	1	0.4	0.24
	10 / 16	0	0	1	2	0	0.6	0.40	1	0	0	1	2	0.8	0.37
	10 / 64	0	0	0	2	0	0.4	0.40	0	3	4	3	1	2.2	0.73
	40 / 4	2	1	0	3	0	1.2	0.58	0	0	1	0	0	0.2	0.20
	40 / 16	1	0	0	0	4	1.0	0.77	1	0	1	1	2	1.0	0.32
	40 / 64	0	0	2	3	0	1.0	0.63	3	2	0	0	2	1.4	0.60
	80 / 4	0	3	0	2	4	1.8	0.80	0	0	0	0	0	0.0	0.00
	80 / 16	3	0	4	0	0	1.4	0.87	0	2	0	1	0	0.6	0.46
	80 / 64	0	0	2	4	0	1.2	0.80	3	3	1	0	0	1.4	0.68
Two	10 / 4	0	0	4	0	2	1.2	0.80	3	0	0	2	3	1.6	0.68
	10 / 16	0	0	5	2	0	1.4	0.98	4	0	0	2	3	1.8	0.80
	10 / 64	2	0	0	2	0	0.8	0.49	2	5	4	4	3	3.6	0.51
	40 / 4	2	1	4	5	3	3.0	0.71	0	0	1	0	0	0.2	0.20
	40 / 16	2	3	0	1	9	3.0	1.58	1	1	3	2	2	1.8	0.37
	40 / 64	2	1	4	3	2	2.2	0.58	5	5	0	0	3	2.6	1.12
	80 / 4	3	3	6	9	4	5.0	1.14	0	0	0	0	0	0.0	0.00
	80 / 16	7	0	5	3	6	4.2	1.24	0	4	0	1	0	1.0	0.79
	80 / 64	5	0	4	7	5	4.2	1.16	3	7	3	1	4	3.6	0.98
Twenty	10 / 4	0	5	4	4	4	3.4	0.87	3	0	0	2	3	1.6	0.68
	10 / 16	0	0	5	4	2	2.2	1.02	6	4	2	2	3	3.4	0.75
	10 / 64	2	0	0	2	0	0.8	0.49	4	7	6	5	4	5.2	0.58
	40 / 4	12	4	7	10	15	9.6	1.91	0	1	1	0	0	0.4	0.24
	40 / 16	4	5	0	1	13	4.6	2.29	1	1	5	3	2	2.4	0.75
	40 / 64	2	1	8	7	3	4.2	1.39	8	9	1	0	3	4.2	1.83
	80 / 4	4	8	17	13	4	9.2	2.56	1	0	0	0	0	0.2	0.20
	80 / 16	12	4	8	14	10	9.6	1.72	0	7	0	2	1	2.0	1.30
	80 / 64	10	3	19	7	6	9.0	2.74	3	11	3	1	12	6.0	2.28

TABLE 5.4 Predation of A. nemorum upon mixtures of 'clump' and 'edge' eggs of P. brassicae. The first of each series of replicates was used in the continuous observations of Section 5.6.

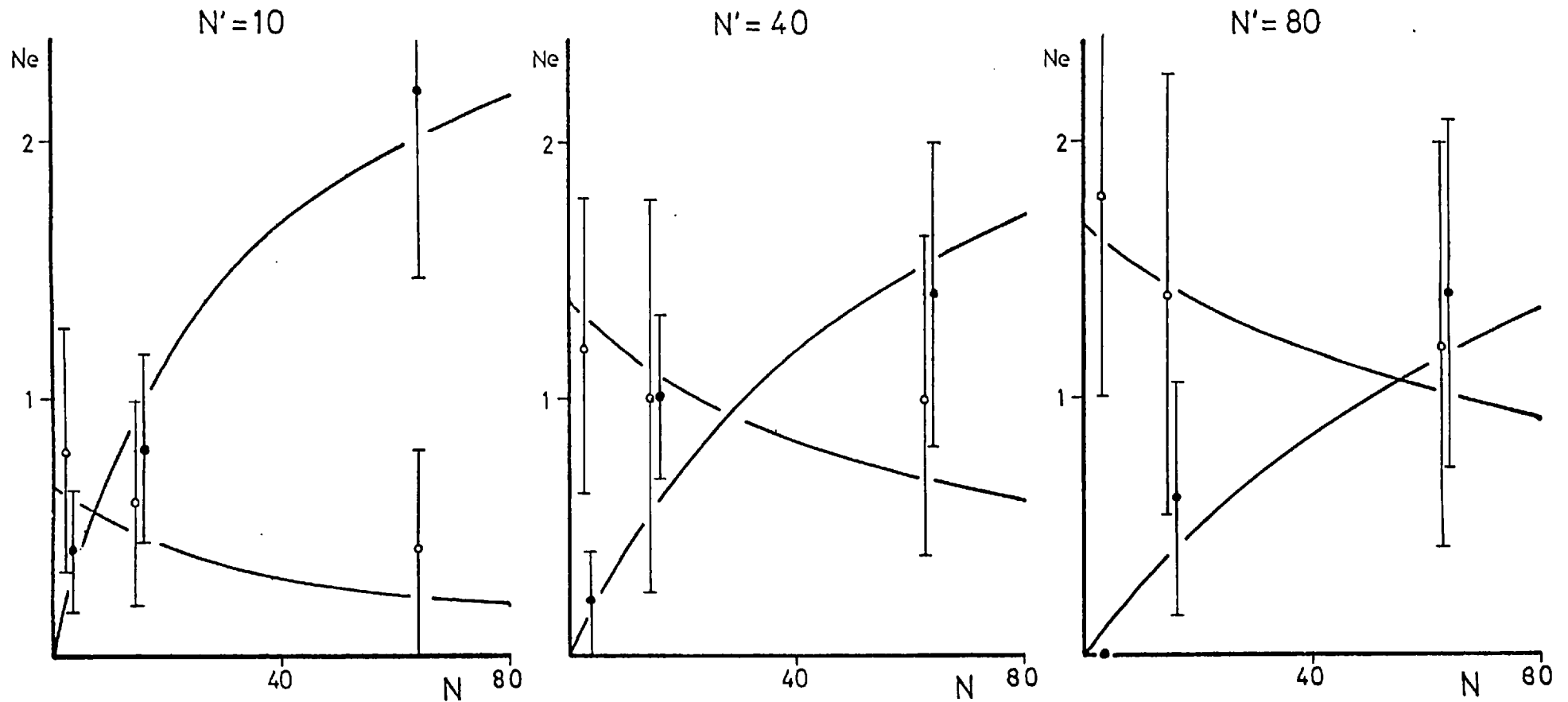


FIGURE 5.5 Predation after one hour of *A. nemorum* upon mixtures of 'clump' and 'edge' eggs of *P. brassicae*. Solid lines show predictions from the individual functional responses (Table 5.3), (goodness of fit $\chi^2=1.1, df=8, P>.99$). In each figure, the number of 'clump' eggs (N') is held constant, while the number of 'edge' eggs (N) is varied. Symbols used are \circ for 'clump' eggs and \bullet for 'edge' eggs. Number eaten (N_e) plotted as mean \pm S.E. of mean.

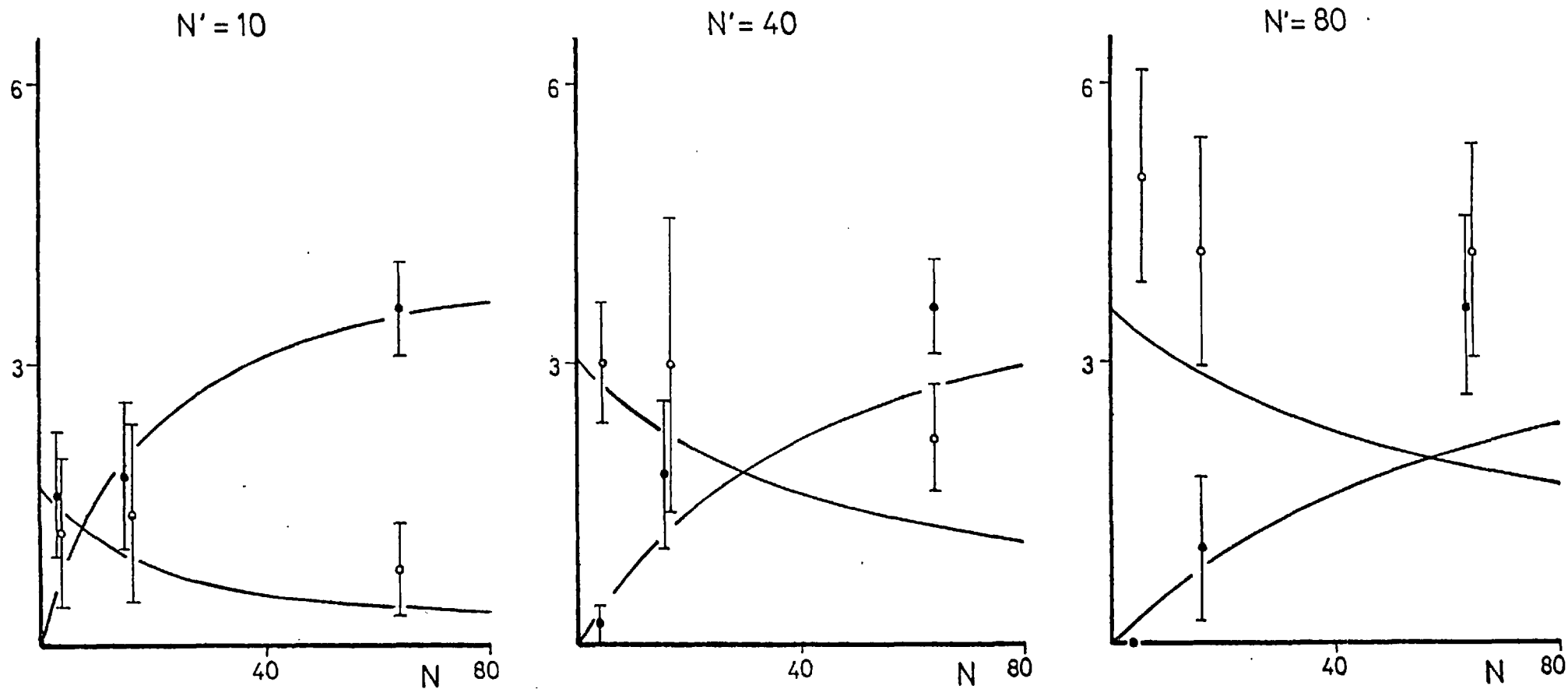


FIGURE 5.6 Predation, after two hours, of A. nemorum upon mixtures of 'clump' and 'edge' eggs of P. brassicae. Solid lines show predictions from the individual functional responses (Table 5.3), (goodness of fit $\chi^2=8.9, df=8, .05 < P < .95$). In each figure, the number of 'clump' eggs (N') is held constant, while the number of 'edge' eggs (N) is varied. Symbols used are \circ for 'clump' eggs and \bullet for 'edge' eggs. Number eaten plotted as mean \pm S.E. of mean.

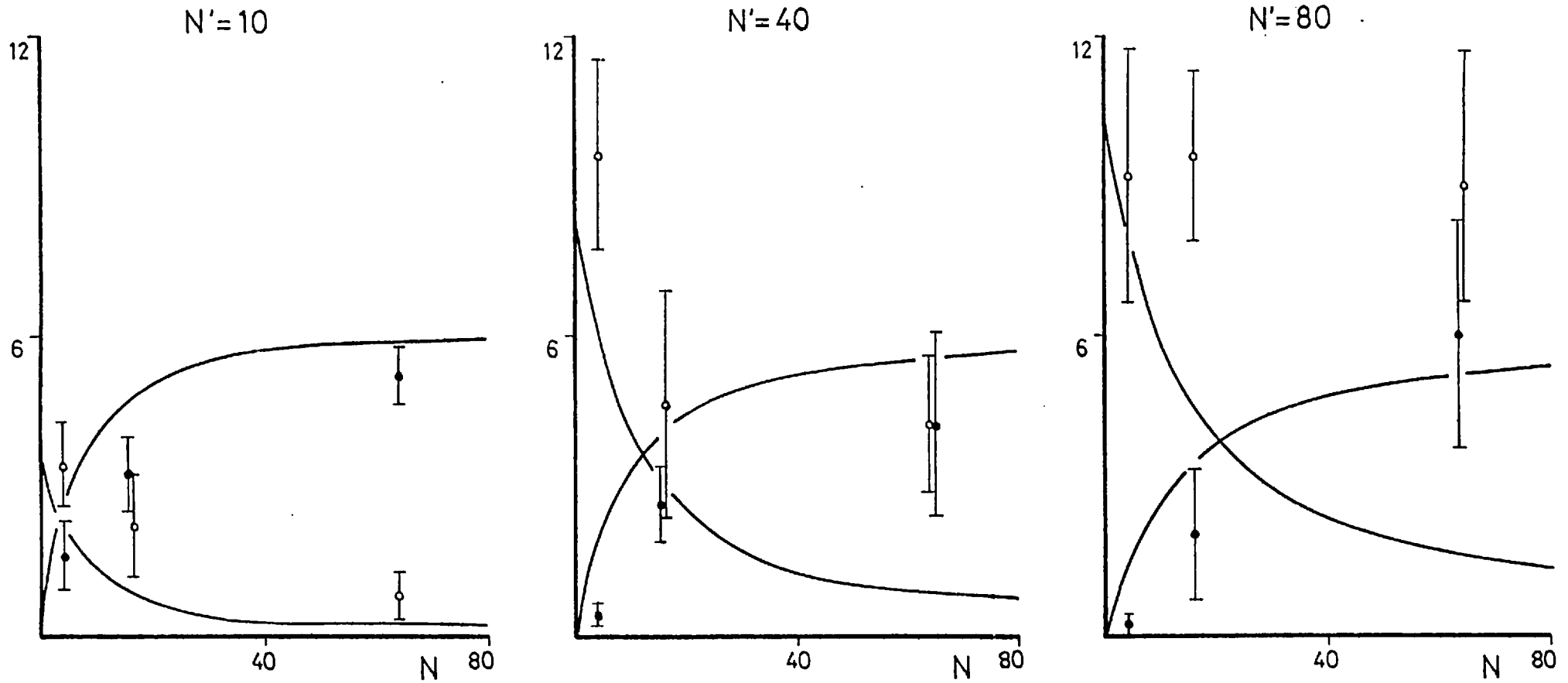


FIGURE 5.7 Predation, after twenty hours, of *A. nemorum* upon mixtures of 'clump' and 'edge' eggs of *P. brassicae*. Solid lines show predictions from the individual functional responses (Table 5.3), (goodness of fit $\chi^2=70.7, df=8, P<.001$). In each figure, the number of 'clump' eggs (N') is held constant, while the number of 'edge' eggs (N) is varied. Symbols used are \circ for 'clump' eggs and \bullet for 'edge' eggs. Numbers eaten (N_e) plotted as mean \pm S.E. of mean.

5.5 DISTRIBUTION OF ATTACKS

5.5.1 Introduction and Method

In order to have a more complete picture of the searching behaviour of anthocorids in these arenas, it is necessary to observe them searching on the plants. The results of such continuous observations are described in the next section (5.6), whilst here the distribution of attacks between clumps or leaves are recorded for each replicate, since this will be a reflection of where the anthocorids searched.

When the predation was scored, the distribution of attacks was also recorded. For the 'clump' prey, the number eaten from each clump was recorded, and for the 'edge' prey, the number eaten from each leaf.

5.5.2 Results and Analysis

The distributions of attacks are given as Tables 5.5 ('edge' eggs), 5.6 ('clump' eggs), 5.7 (both arrangements together; distribution of attacks amongst the 'edge' eggs) and 5.8 (both arrangements together; distribution of attacks amongst the 'clump' eggs).

The variance/mean ratio provides a simple method of assessing how the attacks are distributed. When the ratio equals unity, the distribution is random; increasing values greater than unity show increasing aggregation, and decreasing values less than unity show increasing regularity. These ratios for each egg arrangement and the pooled totals for each time interval are given in Table 5.9.

5.5.3 Discussion

It can be seen from the data of the distributions of attacks (Tables 5.5-5.8) and the resultant variance/mean ratios (Table 5.9), that the anthocorids distribute their attacks differently depending upon the arrangements of the eggs. Thus, when 'clump' eggs are considered, the attacks are distributed in an aggregated manner, whilst for the 'edge' eggs, the attacks tend to be regularly distributed. This effect is also present when both prey arrangements are used.

These distributions of attacks must be a reflection of the method of search used by the anthocorids. The edges of the leaves are, therefore, to some extent searched systematically; at the higher densities attacks are made in each leaf (Table 5.5). In the case of 'clump' prey, however, the attacks are localized, several attacks being made in the same clump, and frequently some clumps are not attacked at all (Table 5.6).

TIME	N	NUMBER OF ATTACKS MADE ON EACH LEAF				
One	8	0 1 0 0	1 0 0 0	—	—	1 0 0 0
	16	0 1 0 1	0 1 1 1	—	—	0 0 1 0
	32	0 0 2 2	—	1 1 1 0	—	0 1 1 1
	64	1 0 0 0	1 1 0 1	1 2 1 1	—	0 1 0 1
Two	8	0 1 1 0	1 0 1 0	—	1 0 1 0	1 0 1 0
	16	0 1 0 1	0 2 1 1	—	1 2 0 1	0 0 1 2
	32	0 0 2 2	0 2 0 1	1 2 1 1	—	2 1 1 1
	64	1 1 0 0	1 1 0 1	1 2 1 1	0 1 1 2	1 1 2 2
Twenty	8	2 1 1 1	1 0 1 1	2 2 0 1	2 3 1 0	2 1 1 1
	16	1 2 1 1	0 2 1 1	0 3 3 1	3 2 0 1	0 1 1 2
	32	0 2 4 2	3 0 2 0	1 2 1 1	0 2 1 0	4 1 1 3
	64	1 1 0 2	1 3 0 1	1 2 2 2	1 1 1 3	1 1 2 2

TABLE 5.5 The distribution of attacks by A. nemorum on 'edge' eggs of P. brassicae. The first of each series of replicates was used in the continuous observations of Section 5.6. The symbol — denotes that no predation took place in that replicate.

TIME	N	NUMBER OF ATTACKS MADE IN EACH CLUMP				
One	20	—	—	2 0 - -	3 0 - -	—
	30	2 0 0 -	—	—	—	0 4 0 -
	40	—	1 0 0 0	0 0 0 1	0 2 0 0	0 1 2 0
	80	—	0 0 0 0 2 0 0 0	0 1 2 0 0 0 0 0	0 2 1 0 0 0 0 0	—
Two	20	4 0 - -	—	2 0 - -	7 0 - -	—
	30	—	—	0 2 0 -	—	—
	40	—	3 0 0 1	0 0 0 2	0 5 0 0	0 3 2 0
	80	0 0 0 0 0 0 3 0	0 0 0 0 2 0 0 0	0 1 1 0 0 2 0 0	0 2 1 0 0 0 0 0	0 1 2 1 0 0 0 0
Twenty	20	4 2 - -	5 3 - -	2 0 - -	8 4 - -	2 0 - -
	30	2 3 0 -	0 1 3 -	0 2 0 -	4 1 3 -	0 6 6 -
	40	0 0 3 4	3 0 2 2	4 0 0 6	0 8 6 0	0 3 2 0
	80	0 0 0 0 7 0 3 0	0 0 2 0 6 0 0 0	0 4 1 2 0 2 0 0	0 0 0 0 3 2 1 0	0 1 2 1 3 0 6 2

TABLE 5.6 The distribution of attacks by A. nemorum on 'clump' eggs of P. brassicae. The first of each series of replicates was used in the continuous observations of Section 5.6. The symbol - denotes the absence of further clumps at that density, and — denotes that no predation took place in that replicate.

TIME IN HOURS	DENSITY 'EDGE'/ 'CLUMP'	NUMBER OF ATTACKS MADE ON EACH LEAF				
		FIVE REPLICATES :				
One	16 / 10	0 1 0 0	—	—	0 0 0 1	1 1 0 0
	16 / 40	1 0 0 0	—	—	0 1 0 0	—
	16 / 80	—	2 0 0 0	—	0 1 0 0	—
	64 / 10	0 1 2 0	—	3 1 0 0	0 1 1 1	0 0 0 1
	64 / 40	1 1 1 0	0 1 1 0	—	—	0 1 1 0
	64 / 80	1 2 0 0	0 1 1 1	0 1 0 0	—	—
Two	16 / 10	1 1 1 1	—	—	0 1 0 1	2 1 0 0
	16 / 40	1 0 0 0	1 0 0 0	0 1 2 0	1 0 0 1	0 0 2 0
	16 / 80	—	2 0 1 1	—	0 1 0 0	—
	64 / 10	0 3 2 0	0 2 0 0	3 1 0 0	0 1 2 1	0 1 0 2
	64 / 40	2 1 1 1	0 1 1 3	—	—	1 1 1 0
	64 / 80	1 2 0 0	1 2 2 2	2 1 0 0	0 0 0 1	1 2 0 1
Twenty	16 / 10	1 2 1 2	0 2 2 0	0 1 1 0	0 1 0 1	2 1 0 0
	16 / 40	1 0 0 0	1 0 0 0	1 1 2 1	1 0 1 1	0 0 2 0
	16 / 80	—	2 1 1 3	—	0 1 1 0	0 0 0 1
	64 / 10	1 3 3 0	0 2 0 2	3 1 2 0	1 1 2 1	1 1 0 2
	64 / 40	3 1 2 2	2 2 2 3	0 1 0 0	—	1 1 1 0
	64 / 80	1 2 0 0	4 2 2 3	2 1 0 0	0 0 0 1	4 6 1 1

TABLE 5.7 Distribution of attacks on 'edge' eggs of P. brassicae by A. nemorum, when mixtures of both arrangements are available. The first replicate of each series was used in the continuous observations of Section 5.6. — denotes that no predation took place in that replicate.

TIME IN HOURS	DENSITY 'EDGE'/ 'CLUMP'	NUMBER OF ATTACKS IN EACH CLUMP				
		FIVE REPLICATES :				
One	4 / 40	2 0 0 0	0 0 1 0	—	0 1 0 2	—
	16 / 40	1 0 0 0	—	—	—	0 2 2 0
	64 / 40	—	—	2 0 0 0	0 3 0 0	—
	4 / 80	—	0 3 0 0 0 0 0 0	—	1 0 0 0 1 0 0 0	0 0 0 0 0 0 0 4
	16 / 80	0 1 0 0 0 2 0 0	—	0 0 0 0 2 0 1 0	—	—
	64 / 80	—	—	2 0 0 0 0 0 0 0	0 0 2 0 0 2 0 0	—
	4 / 40	2 0 0 0	0 0 1 0	0 3 0 1	0 1 0 4	0 0 0 3
Two	16 / 40	1 0 1 0	0 0 3 0	—	0 0 0 1	0 2 7 0
	64 / 40	0 2 0 0	0 0 1 0	4 0 0 0	0 3 0 0	0 0 1 0
	4 / 80	0 2 1 0 0 0 0 0	0 3 0 0 0 0 0 0	0 0 0 0 6 0 0 0	1 0 0 0 4 0 4 0	0 0 0 4 0 0 0 0
	16 / 80	0 1 0 0 0 4 2 0	—	0 0 1 1 2 0 1 0	0 0 0 3 0 0 0 0	0 0 0 0 0 0 6 0
	64 / 80	0 1 0 0 4 0 0 0	—	4 0 0 0 0 0 0 0	1 1 2 0 0 2 0 1	0 0 0 0 0 5 0 0
	4 / 40	2 0 6 4	1 2 1 0	3 3 0 1	0 6 0 4	0 8 0 7
	Twenty	16 / 40	2 1 1 0	1 0 3 1	—	0 0 0 1
64 / 40		0 2 0 0	0 0 1 0	5 3 0 0	3 4 0 0	1 1 1 0
4 / 80		0 2 1 0 0 1 0 0	0 3 1 0 1 2 0 1	0 0 4 0 8 5 0 0	1 2 0 0 4 2 4 0	0 0 0 4 0 0 0 0
16 / 80		5 1 0 0 0 4 2 0	0 0 4 0 0 0 0 0	0 1 1 1 2 0 1 2	0 7 1 3 0 3 0 0	0 0 2 0 0 2 6 0
64 / 80		0 1 0 0 6 0 3 0	0 0 0 0 0 3 0 0	4 7 0 0 0 5 0 3	1 1 2 0 0 2 0 1	0 0 0 0 0 6 0 0

TABLE 5.8 Distribution of attacks by A. nemorum among 'clump' eggs of P. brassicae when mixtures of both arrangements are available. The first replicate of each series was used in the continuous observations of Section 5.6. — denotes that no predation took place in that replicate.

PREY ARRANGEMENT	PREY DENSITY 'EDGE' / 'CLUMP'	VARIANCE / MEAN RATIO OF THE DISTRIBUTION OF ATTACKS AFTER THE TIMES OF :		
		ONE HOUR	TWO HOURS	TWENTY HOURS
'clumps' only	- / 20	1.800		1.926
	- / 30	2.800		2.106
	- / 40	1.210	1.746	2.804 2.624
	- / 80	1.478		2.872
'edges' only	8 / -	0.818		0.491
	16 / -	0.545		0.737
	32 / -	0.618	0.635	1.088 0.696
	64 / -	0.527		0.481
mixture - 'clump' ratios :	4 / 40	1.273		2.868
	16 / 40	1.343		2.501
	64 / 40	2.257		2.253
	4 / 80	2.739	1.726	2.923 2.907
	16 / 80	1.210		2.744
	64 / 80	1.733		3.427
mixture - 'edge' ratios :	16 / 10	0.727		0.777
	64 / 10	1.109		0.818
	16 / 40	1.160		0.772
	64 / 40	0.455	0.903	0.784 1.143
	16 / 80	1.476		1.055
	64 / 80	0.776		1.860

TABLE 5.9 Variance / mean ratios of the distribution of attacks between leaves for 'edge' eggs and between clumps for 'clump' eggs. The ratio for each prey arrangement and time interval is given, together with the ratio of the pooled results for each type of arrangement and time interval. For actual data see Tables 5.5 - 5.8.

5.6 RECORDINGS OF ANTHOCORID ACTIVITY

5.6.1 Introduction and Method

To fill out the picture of anthocorid searching behaviour, and to try and confirm or reject some of the deductions made about their behaviour, the activity in one replicate of each prey arrangement was recorded.

This was done using an eight track event recorder, in which the tracks were used as follows:

1. off the plant / on the plant
2. on the stem / on the leaves
3. underside / upperside of the leaf
4. centre / edge of the leaf
5. not feeding / encounter with egg / feeding
6. not grooming / grooming
7. inactive / searching
8. a record of one minute intervals from a stop clock.

Anthocorid activity was recorded for the second hour and the final hour of the experiment.

5.6.2 Results and Analysis

The data from tracks 1, 5, 6 and 7 (above) are given in Tables 5.10 (1h - 2h) and 5.11 (19h - 20h), while the distribution of searching time upon the plants (tracks 2, 3, 4 and 7 above) is given in Tables 5.12 (1h - 2h) and 5.13 (19h - 20h). The latter two tables are repeated as percentages of the searching time (Table 5.14, 1h - 2h; Table 5.15, 19h - 20h).

5.6.3 Discussion

From the allocations of time given in Tables 5.10 (1h - 2h) and 5.11 (19h - 20h), a number of points become apparent. Firstly, the anthocorids spend long periods off the plant; this seems to be more frequent at the beginning of each experiment, and is one source of the high variance in the numbers eaten found after one and two hours. Secondly, a large amount of the time spent on the plant is spent in inactivity, this being more pronounced at the end of the experiment; this is in agreement with the long periods of inactivity suggested in the discussion of Chapter 4. Thirdly, a significant amount of time is spent in grooming. Fourthly, only a relatively small amount of time is spent searching; more time is spent searching at the end of the experiment than at the beginning. However, bearing in mind that considerably fewer attacks were made during the second recording (12 as compared with 44), it seems likely that this was not searching for food, but due to some other cause (looking for a mate, a site to rest, etc.). Fifthly, the number of encounters with eggs is considerably higher than the number of attacks; this is true of both recordings. Finally, an estimate of the handling time can be obtained; by taking each unfinished feed as half a feed, a value of 12'52" results.

In Tables 5.12 and 5.13, the time spent searching on the different parts of the plant is given, while in Tables 5.14 and 5.15, this data is given as percentages of the time spent searching. From these tables, a number of points arise. Perhaps the most obvious of these is the small proportion of the time spent searching on the centre of the underside of the leaf. This is at variance with the results of Dixon & Russell (1972) for adults searching on sycamore leaves and of Evans (1973) for nymphs searching on bean leaves (Section 5.1). The most likely explanation is that the adult anthocorids are unable to obtain a secure grip upon the underside of bean leaves. Evans found that second instar nymphs spend less time searching on the veins of the underside of leaves than do the first instar. Continuing this trend, the adults spend negligible time searching the centre of the undersides of leaves.

In a number of cases, a large percentage of the time is spent searching on the plant stem; generally however, most of the time searching is on the leaves. Examining the percentage distribution of time in Tables 5.14 and 5.15, a number of tendencies can be seen:

1. 1 - 2h 'clump' - more time was spent searching the edges of the leaves than was spent searching in the centre.
2. 19 - 20h 'clump' - this is reversed; by the end of the experiment more time was spent on the centre than on the edges of leaves.
3. 1 - 2h 'edge' - similar to 1 - 2h 'clump'.
4. 19 - 20h 'edge' - considerably more time was spent searching on the edges of leaves than on the centre.
5. 1 - 2h both - similar to 1 - 2h 'clump' and 1 - 2h 'edge'.
6. 19 - 20h both - the results here were varied. Some anthocorids spent more time searching on the edges (10/4, 10/16, 40/64)

which coincided with specialization on 'edge' eggs; others spent more time on the centre of the leaves (40/16, 80/64) and specialized on 'clump' eggs. Of the remainder, some spent more time on the edges of the leaves (40/4, 80/4, 80/16) and specialized on 'clump' eggs, while one (10/64) spent more time on the edges, and ate eggs of both arrangements.

DENSITY 'EDGE'/ 'CLUMP'	T I M E S P E N T :					NUMBER OF EN- COUNTERS	NUMBER OF FEEDS
	on the plant	in- active	groom- ing	active search	feed- ing		
- / 10	60.00	0.00	0.00	0.00	60.00	- / 43	- / 8*
- / 20	60.00	11.58	5.17	4.75	38.50	- / 15	- /*4*
- / 30	27.75	19.95	7.25	0.55	0.00	- / 0	- / 0
- / 40	36.55	1.50	25.83	9.22	0.00	- / 3	- / 0
- / 80	60.00	15.58	3.30	5.08	36.03	- / 52	- / 3*
4 / -	43.55	27.30	9.20	7.05	0.00	23 / -	0 / -
8 / -	21.75	0.87	3.38	1.75	15.75	12 / -	*1 / -
16 / -	60.00	29.33	13.67	17.00	0.00	32 / -	0 / -
32 / -	19.83	0.75	0.37	1.00	17.88	2 / -	*2 / -
64 / -	60.00	18.80	10.42	10.42	20.37	71 / -	1 / -
4 / 10	42.83	29.50	1.25	1.20	10.88	7 / 0	*2 / 0
16 / 10	60.00	17.00	0.63	7.13	35.87	14 / 0	*3 / 0
64 / 10	60.00	2.13	6.72	1.27	49.88	9 / 14	*2 / 2*
4 / 40	32.42	13.50	12.78	6.13	0.00	3 / 15	0 / 0
16 / 40	60.00	29.85	0.00	4.78	25.20	23 / 48	1 / 2*
64 / 40	60.00	6.88	7.33	3.72	42.07	6 / 24	*2 / 2*
4 / 80	57.33	12.67	4.58	21.08	19.00	34 / 132	0 / 2*
16 / 80	60.00	2.50	1.25	4.00	52.25	18 / 54	0 / 4
64 / 80	60.00	5.18	2.08	2.38	40.35	7 / 21	0 / 3

TABLE 5.10 The division of time and occurrence of predation and encounters by anthocorids searching during the second hour of the experiment. Continuous observations were made for one replicate of each combination of prey arrangements. The symbol * is used to indicate a feed which extends beyond the beginning or the end of the recording hour. The times are given in minutes.

DENSITY 'EDGE'/ 'CLUMP'	T I M E S P E N T :					NUMBER OF EN- COUNTERS	NUMBER OF FEEDS
	on the plant	in- active	groom- ing	active search	feed- ing		
- / 10	60.00	33.67	10.17	16.17	0.00	- / 47	- / 0
- / 20	60.00	54.83	1.87	3.30	0.00	- / 5	- / 0
- / 30	60.00	47.82	3.63	8.55	0.00	- / 39	- / 0
- / 40	60.00	43.75	5.63	2.13	8.48	- / 11	- / 1*
- / 80	41.80	8.50	20.80	12.50	0.00	- / 2	- / 0
4 / -	60.00	25.53	32.83	1.63	0.00	5 / -	0 / -
8 / -	47.50	39.55	8.25	1.70	0.00	4 / -	0 / -
16 / -	22.87	6.90	2.95	6.43	9.58	47 / -	*1 / -
32 / -	60.00	9.13	18.93	13.55	18.38	95 / -	*2 / -
64 / -	60.00	43.58	13.42	3.00	0.00	19 / -	0 / -
4 / 10	27.30	12.90	3.63	8.77	0.00	12 / 6	0 / 0
16 / 10	60.00	48.75	10.22	1.03	0.00	2 / 0	0 / 0
64 / 10	60.00	18.83	7.47	10.17	23.53	40 / 17	*1 / 0
4 / 40	60.00	11.03	5.32	2.57	41.08	10 / 34	0 / 2
16 / 40	60.00	25.53	1.50	4.30	28.67	7 / 30	0 / 1
64 / 40	60.00	25.13	16.87	10.95	7.05	22 / 108	0 / 1*
4 / 80	60.00	34.78	9.83	15.38	0.00	28 / 101	0 / 0
16 / 80	60.00	22.62	3.70	4.55	29.13	10 / 33	0 / 1*
64 / 80	60.00	18.25	9.62	10.85	21.28	36 / 115	0 / 2*

TABLE 5.11 The division of time and occurrence of predation and encounters by anthocorids searching during the final hour of the experiment. Continuous observations were made for one replicate of each combination of prey arrangements. The symbol * is used to indicate a feed which extends beyond the beginning or the end of the recording hour. The times are given in minutes.

DENSITY 'EDGE'/ 'CLUMP'	TOTAL TIME SEARCH- ING	TIME ON STEM	TIME ON THE LEAF UPPERSURFACE		TIME ON THE LEAF UNDERSURFACE	
			EDGE	CENTRE	EDGE	CENTRE
- / 10	0.00	-	-	-	-	-
- / 20	4.75	1.58	0.58	2.00	0.58	0.00
- / 30	0.55	0.38	0.05	0.00	0.08	0.00
- / 40	9.22	4.97	1.90	0.73	1.15	0.47
- / 80	5.08	0.60	2.35	0.75	0.88	0.50
4 / -	7.05	2.93	1.47	2.13	0.52	0.00
8 / -	1.75	0.00	0.62	0.35	0.65	0.13
16 / -	17.00	8.38	3.18	1.97	2.17	1.30
32 / -	1.00	0.00	0.67	0.08	0.25	0.00
64 / -	10.42	3.18	4.25	0.98	1.65	0.35
4 / 10	1.20	0.63	0.33	0.17	0.07	0.00
16 / 10	7.13	0.00	4.07	1.97	0.80	0.30
64 / 10	1.27	0.00	0.53	0.30	0.43	0.00
4 / 40	6.13	0.97	2.62	1.13	1.17	0.25
16 / 40	4.78	0.00	2.90	0.82	0.82	0.25
64 / 40	3.72	0.82	0.38	0.62	2.20	0.52
4 / 80	21.08	2.10	9.73	4.22	4.45	0.58
16 / 80	4.00	0.53	0.67	1.92	0.63	0.25
64 / 80	2.38	0.00	0.63	1.00	0.75	0.00

TABLE 5.12 The distribution of searching time by anthocorids during the second hour of the experiment. Continuous observations were made for one replicate of each combination of prey arrangements. The times are given in minutes.

DENSITY 'EDGE'/ 'CLUMP'	TOTAL TIME SEARCH- ING	TIME ON STEM	TIME ON THE LEAF UPPERSURFACE		TIME ON THE LEAF UNDERSURFACE	
			EDGE	CENTRE	EDGE	CENTRE
- / 10	16.17	0.93	2.88	8.98	2.42	0.95
- / 20	3.30	0.33	0.08	0.15	2.70	0.37
- / 30	8.55	0.70	1.30	2.90	3.12	0.50
- / 40	2.13	0.38	1.20	0.25	0.13	0.00
- / 80	12.50	7.70	1.20	2.00	0.90	0.70
4 / -	1.63	0.20	0.35	0.22	0.87	0.00
8 / -	1.70	0.75	0.28	0.00	0.67	0.00
16 / -	6.43	0.20	4.75	0.87	0.33	0.28
32 / -	13.55	0.92	7.37	1.67	3.47	0.13
64 / -	3.00	1.78	0.50	0.35	0.37	0.00
4 / 10	8.77	4.22	2.53	1.25	0.58	0.18
16 / 10	1.03	0.00	0.87	0.00	0.17	0.00
64 / 10	10.17	1.28	3.35	4.17	0.83	0.53
4 / 40	2.57	0.00	1.30	0.87	0.40	0.00
16 / 40	4.30	1.50	0.65	0.90	1.22	0.05
64 / 40	10.95	1.00	4.03	2.55	1.40	1.97
4 / 80	15.38	2.80	6.03	1.82	3.53	1.20
16 / 80	4.55	0.17	0.97	0.67	2.42	0.33
64 / 80	10.85	0.68	1.82	4.20	3.33	0.82

TABLE 5.13 The distribution of searching time by anthocorids during the final hour of the experiment. Continuous observations were made for one replicate of each combination of prey arrangements. The times are given in minutes.

DENSITY 'EDGE'/ 'CLUMP'	TOTAL TIME SEARCH- ING	% TIME ON STEM	% TIME ON LEAF UPPERSURFACE		% TIME ON LEAF UNDERSURFACE	
			EDGE	CENTRE	EDGE	CENTRE
- / 10	0.00	-	-	-	-	-
- / 20	4.75	33.3	12.3	42.1	12.3	0.0
- / 30	0.55	69.7	9.1	0.0	15.2	0.0
- / 40	9.22	53.9	20.6	8.0	12.5	5.1
- / 80	5.08	11.8	46.2	14.8	17.4	9.8
4 / -	7.05	41.6	20.8	30.3	7.3	0.0
8 / -	1.75	0.0	35.2	20.0	37.1	7.6
16 / -	17.00	49.3	18.7	11.6	12.7	7.6
32 / -	1.00	0.0	66.7	8.3	25.0	3.4
64 / -	10.42	30.6	40.8	9.4	15.8	3.4
4 / 10	1.20	52.8	27.8	13.9	5.6	0.0
16 / 10	7.13	0.0	57.0	27.6	11.2	4.2
64 / 10	1.27	0.0	42.1	23.7	34.2	0.0
4 / 40	6.13	15.8	69.8	18.5	19.0	4.1
16 / 40	4.78	0.0	60.6	17.1	17.1	5.2
64 / 40	3.72	22.0	10.3	16.6	59.2	13.9
4 / 80	21.08	10.0	46.2	20.0	21.1	2.8
16 / 80	4.00	13.3	16.7	47.9	15.8	6.3
64 / 80	2.38	0.0	26.6	42.0	31.5	0.0

TABLE 5.14 The distribution of searching time, expressed as percentages, by anthocorids during the second hour of the experiment. Continuous observations were made for one replicate of each combination of prey arrangements.

DENSITY 'EDGE'/ 'CLUMP'	TOTAL TIME SEARCH- ING	% TIME ON STEM	% TIME ON LEAF UPPERSURFACE		% TIME ON LEAF UNDERSURFACE	
			EDGE	CENTRE	EDGE	CENTRE
- / 10	16.17	5.8	17.8	55.6	15.0	5.9
- / 20	3.30	10.1	2.5	4.6	81.8	11.1
- / 30	8.55	8.2	15.2	33.9	36.5	5.8
- / 40	2.13	18.0	56.3	11.7	6.3	0.0
- / 80	12.50	61.6	9.6	16.0	7.2	5.6
4 / -	1.63	12.2	21.4	13.3	53.1	0.0
8 / -	1.70	44.1	16.7	0.0	39.2	0.0
16 / -	6.43	3.1	73.8	13.5	5.2	4.4
32 / -	13.55	6.8	54.4	19.7	25.6	1.0
64 / -	3.00	59.4	16.7	11.7	12.2	0.0
4 / 10	8.77	48.1	28.9	14.3	6.7	2.1
16 / 10	1.03	0.0	83.9	0.0	16.1	0.0
64 / 10	10.17	12.6	33.0	41.0	8.2	5.2
4 / 40	2.57	0.0	50.6	33.8	15.6	0.0
16 / 40	4.30	34.9	15.1	20.9	28.3	1.2
64 / 40	10.95	9.1	36.8	23.3	12.8	18.0
4 / 80	15.38	18.2	39.2	11.8	23.0	7.8
16 / 80	4.55	3.7	21.2	14.7	53.1	7.3
64 / 80	10.85	6.3	16.7	38.7	30.7	7.5

TABLE 5.15 The distribution of searching time, expressed as percentages of the time spent searching, by anthorids during the final hour of the experiment. Continuous observations were made for one replicate of each combination of prey arrangements. Total time spent searching given in minutes.

5.7 DISCUSSION AND CONCLUSIONS

In considering the results described in this chapter, one factor which should be borne in mind is the inconsistency of results after only one or two hours. Accordingly, of the overall predation results (Section 5.3 & 5.4) only those obtained after twenty hours are sufficiently consistent for much reliance to be placed upon them. On the other hand, the 'distribution of attacks' data (Section 5.5) and the continuous observations (Section 5.6) do provide a means of comparing the searching behaviour at the beginning of the experiment with that at the end.

These observations indicate that the searching behaviour of the anthocorids changes during the course of the experiment. The continuous observations showed that, when only one egg arrangement is used, the anthocorids initially spend more time searching on the edges of the leaf uppersurface than on the centre (Table 5.14), but that, by the end of the experiment, anthocorids offered 'clump' eggs search for more time on the centre than the edge, while those offered 'edge' eggs spent a greater proportion of time searching the leaf edges. This tendency suggests that the anthocorids, by selecting the most rewarding parts of the plant environment, can maximize the profitability of their searching time; this is the strategy suggested by Royama (1970) for great tits (Section 1.3.5).

In view of the classification of preference put forward in the discussion section of Chapter 3, there are three types of preference which may be acting here:

1. 'automatic' preference due to a difference in encounter rates caused by a difference in search efficiency for the eggs of the two arrangements.
2. 'automatic' preference due to a difference in encounter rates caused by habitat selection.
3. 'deliberate' preference for prey of one arrangement by the deliberate selection or rejection of one type when encountered.

The first possibility will occur, since the search efficiencies for the two arrangements differ. On this basis, there is an 'automatic' preference for 'edge' eggs. The observed predation after twenty hours (Fig. 5.7), however, shows a preference for 'clump' eggs -

i.e. some other behaviour is masking the effect of the 'automatic' preference based on search efficiencies.

The second possibility is an additional 'automatic' preference due to habitat selection. As described above, the anthocorids, by the end of the experiment, can select the most rewarding area of the plant. This, coupled with the selection of either 'edge' or 'clump' eggs found in Section 5.4, suggests an 'automatic' preference for either egg arrangement can occur by this mechanism.

The third possibility is that a 'deliberate' preference occurs. If the ratio at which the eggs of each arrangement are attacked is not equal to the ratio at which they are encountered, 'deliberate' preference can be considered to occur. From the continuous observations of Section 5.6, it was noted (Section 5.6.3) that there are considerably more encounters with eggs than feeds. This was not due to the initial time lag necessary to recognise the prey (Anderson, 1961), since in many cases the anthocorids had already fed. The large number of encounters may be due to the anthocorid walking over the plant in a temporarily satiated state. The stimulus of encountering eggs would reinitiate feeding, if above some threshold. The stimulus provided by a clump of eggs would be greater than that provided by an isolated egg, and this would result in the anthocorids selecting 'clump' eggs in a greater proportion than would be expected on the basis of the number of encounters with eggs of each arrangement. Thus, anthocorids could show 'deliberate' preference by selecting 'clump' eggs.

If such behaviour occurs, there should be some evidence for it from the encounters and feeds recorded by continuous observation in Section 5.6. Thus, during the second hour the ratio of the number of encounters with 'clump' eggs to the number with 'edge' eggs is 2.55, and the number of attacks on 'clump' eggs to the number on 'edge' eggs is 1.5; the corresponding values for the last hour are 2.65 and 7.0. Hence, bearing in mind that the number of encounters with clumps rather than with 'clump' eggs would be smaller, these results provide some support, at least from the last hour, for this explanation of 'deliberate' preference.

Therefore, all three possibilities are occurring in this situation; there is 'automatic' preference for 'edge' prey due to the difference in search efficiencies, 'automatic' preference for

eggs of the more rewarding arrangement due to habitat selection, and 'deliberate' preference for 'clump' eggs, perhaps due to the greater stimulus offered to a partially satiated anthocorid by a 'clump' of eggs.

The fact that the anthocorids can select the most rewarding part of the leaf suggests that switching may occur. However, examination of the figures for predation using both arrangements (Figs. 5.5 - 5.7) shows that at all ratios there is positive preference for 'clump' eggs. Therefore, a more extreme ratio than 10 'clump' to 64 'edge' would be necessary to demonstrate preference for 'edge' eggs.

CHAPTER 6

COMPUTER SIMULATIONS OF PREDATOR SEARCHING BEHAVIOUR

6.1 INTRODUCTION

The use of simulation models in studying predator-prey interactions goes back to Holling's 'disc experiment' (Holling, 1959b), in which a blindfolded human 'predator' searched, by tapping with a finger, for sandpaper discs pinned to a table (Section 1.2.2). Any strategy of search used (e.g. random, systematic etc.) is not mentioned, but it is implied by Holling's derivation of the Disc Equation that random search was used. The approach used in this work is basically similar, but, due to the use of computers, more sophisticated and rigidly controlled models can be developed, while results are more easily and rapidly obtained.

Murdie (1971) described a simple computer simulation model in which the prey were arranged in 150 quadrats (or units), each a matrix of 10 x 10. The inter-quadrat distribution of prey was determined using either the Poisson or the negative binomial distributions. (The expected frequencies were rounded off and, if necessary, extra quadrats were added to the densest figure to make up the number of quadrats to 150; cf. subroutine AGGPUT described below). Within each quadrat, the prey were distributed at random, or in adjacent squares to form a clump. The predator (described as a "bumbling idiot") starts at a random location in a quadrat selected at random, and has a random choice of moving into one of the eight adjacent squares, or remaining where it is (cf. subroutine DIR described below, in which the latter option is not available). Any prey encountered are eaten, and if no prey are found for twenty time units the predator is considered

to have starved to death. Two hundred predators are used in turn. Murdie found that this random walk was inefficient, and that the predator tended to get "boxed in" along the edges and in the corners of quadrats. He also found that more of the prey distributed at random were eaten; this is caused by the starvation of most predators looking for a single clump of prey. The extra twenty time units available for searching after a prey is found led to a density dependant effect, and the resultant figures of the number of prey eaten in response to prey density were initially exponential in shape, followed by a linear phase (cf. Section 6.6).

The computer simulation programme developed in this work is not dissimilar to that of Murdie (1971). This programme, however, only uses a single large two dimensional matrix for the arena, and is more sophisticated in that several methods of distributing the prey can be used, a range of search strategies are available for the predator, two prey types can be used, and both aggregative and functional response data can be generated.

The programme is described in the next section, whilst a listing can be found in Appendix Section A2.1. This chapter is subdivided to consider the following aspects using simulations:

- Section 6.3 the optimization of the aggregative walk,
- Section 6.4 the functional responses obtained using the various search strategies and prey distribution methods,
- Section 6.5 the production of sigmoid and dome shaped functional responses by varying the searching parameters,
- Section 6.6 the aggregative responses for the various search strategies and prey distribution methods,
- Section 6.7 the effects of using different giving up times upon the aggregative response,
- Section 6.8 the effects of alternative prey upon the aggregative response.

6.2 DESCRIPTION OF THE COMPUTER SIMULATION PROGRAMME

The computer simulation programme developed in this work involves the search by a hypothetical predator in a two dimensional arena. This arena is simulated by a large two dimensional matrix; for the bulk of this work, dimensions of 50 x 50 were used. The presence of prey at a given location (i.e. pair of co-ordinates) within the arena is indicated by a positive value, and absence by a zero value. In order to reduce the computer core space used by the arena, the value of each location is used to indicate the numbers of both prey types (A & B) present. Thus, the number of prey type B present at a location is indicated by:

$$\text{Number of type B} = \text{integer}(n/100),$$

where n is the value of that location. The number of type A is then given by:

$$\text{Number of type A} = n - \text{number of type B} \times 100.$$

As an empty location is searched, its value is set to minus one; if this location is re-encountered, it will be recognised as one previously searched, and so an estimate of the time wasted can be obtained. Four subroutines are available for different methods of prey distribution, and six search strategies are available in three subroutines. The encounter success rate and the handling time per prey may differ for the two prey types. The handling time can be defined as a function of the initial prey density or of the instantaneous number of prey eaten, whilst the encounter success rate may, depending upon the search strategy used, be similarly defined, or take different values for different searching behaviours. Either a fixed time limit can be used to generate functional response data, or a giving up time is used to obtain aggregative response data.

In the main programme (SIM) the parameters are read in; separate subroutines are used to distribute the prey and mimic the predators' activities. The results are printed out from the main programme.

There are four methods of distributing the prey, the method used being defined by a control option (ID). The strategies, subroutines and control option values are:

ID = 1: regular, subroutine REGPUT,

ID = 2: random, subroutine RANPUT,

ID = 3: using the negative binomial distribution, subroutine AGGPUT,

ID = 4: randomly distributed clumps, subroutine CLUPUT.

These distributions will be referred to as regular, random, aggregated and clumped respectively. In order to determine the prey type distributed, one of the subroutine arguments defines the value added to the relevant location of the arena (i.e. 1 or 100).

Subroutine REGPUT is used to arrange prey regularly. To obtain an even distribution, a perfect square is used for the prey density (if the input density is not a perfect square, it is rounded down to the nearest perfect square). This imposes an upper limit for the density of one prey in each location, before more than one prey are placed at some locations.

Subroutine RANPUT arranges prey at random by selecting random co-ordinates of the arena. There is no limit to the density which may be distributed using this subroutine.

Subroutine AGGPUT arranges prey using the negative binomial distribution, and is an improved version of programme PUT (Appendix Section A1.4) used to distribute prey for the work with square perspex arenas of Chapter 4. As for programme PUT, the arena is divided into a number of square units (625 for all simulations in this work). From the input values for the prey density and K of the negative binomial distribution, the expected frequencies of the densities of prey per unit are calculated. These are rounded off (varying the rounding off factor if necessary) to give the correct number of units (i.e. 625). Due to the finite number of units available, the resultant values for the prey density and K often differ markedly from the input values (as noted in Chapter 4). In this subroutine, an additional loop has been added to recalculate the frequencies using altered parameters if these differences are greater than 10%. The units are distributed at random within the arena, and the prey at random within each unit.

Subroutine CLUPUT distributes clumps of eight prey (arranged 2 x 2 with two prey in each position) in a random manner similar to that used in subroutine RANPUT. There is no limit to the density which can be arranged by this method, although it should be borne in mind that, at very high densities, the distribution will approach randomness. This is particularly apparent when the aggregative responses (Section 6.6) are considered. In Sections 6.3 & 6.4 an earlier version of this programme was used in which clumps of ten prey (arranged 3 x 3 with an extra prey in the central position) are distributed regularly in a manner similar to that used in subroutine REGPUT. Accordingly, for these two sections, the number of clumps distributed is a perfect square, and the input density value is adjusted if necessary. Since Sections 6.3 & 6.4 used an arena of 100 x 100, a density of up to 6,250 can be arranged before the clumps become adjacent. Clearly, as the density increases the distribution will become increasingly regular.

There are five options available for the predator's search strategy. One of these, the aggregative walk, also provides an extra, sixth option. The strategies of random search, random walk, and forward directed random walk are found in subroutine EAT123, the aggregative walk is subroutine AGGEAT, and subroutine CLUEAT contains the strategy of systematic local search in response to finding a prey. The strategy used is selected by an input control option (IS).

Subroutine EAT123 contains the first three search strategies. For the first option, (IS = 1) totally random search, locations are selected at random within the arena. The second option is a random walk: having searched one location, the predator moves at random into one of the eight adjacent locations, using subroutine DIR. The third option (IS = 3) is a forward directed or on-going walk such as that described by Smith (1974) for birds searching on a lawn. After searching each location, the predator moves using subroutine FDIR which selects, at random, one of the five adjacent squares which do not cause the predator to turn more than a right angle relative to its last direction of movement. Each location is searched in a similar manner for all the strategies. If the numerical value of the new location is minus one, this means

that it has been previously searched and one is added to the sum of the time wasted. If the value of the location is zero, no prey are present and the value of the location is set to minus one. If the location has a positive value, this means that at least one prey is present, and subroutine ENC is called. This subroutine, described below, determines the number of prey found, and adjusts the value of the location accordingly. The handling times for any prey eaten are added to the time spent and, if no prey remain, the location is set to minus one. When all the available time is used up, or the giving up time passes without any prey being found, the replicate terminates.

Subroutine AGGEAT is intended to mimic the aggregative behaviour shown by some predators (Banks, 1957; Murdie & Hassell, 1973; Thomas, 1975) in which, after finding a food item, the predator's search path becomes more tortuous (i.e. reduced step length and increased angle of turn) for a brief period. Thus, the normal search pattern consists of an input number of steps (LLS) in one direction using subroutine SDIR, followed by a turn using FDIR, and a further LLS steps in the new direction etc. If a prey is found, the search path changes to the random walk described under subroutine EAT123 using subroutine DIR. This behaviour persists for H time units (5 for all this work) after the last prey is found, whereupon the searching behaviour reverts to the normal phase (cf. Murdie & Hassell (1973) and Murdoch & Oaten (1975) as described in Section 1.4.3). This search strategy will be referred to as an aggregative walk. By setting the parameter H to zero, an on-going random walk of step length LLS is obtained. Locations are searched in the same manner as described for subroutine EAT123. In this and the next strategy (CLUEAT), the encounter success rate is defined separately for each searching phase.

Subroutine CLUEAT is an attempt to maximize predator search efficiency for feeding upon clumped prey. The normal searching behaviour is the forward directed random walk. When a prey is found, an area of 3 x 3 centred upon the prey is systematically searched at an expense of TC time units. For Sections 6.3 & 6.4 the area searched is 5 x 5. After searching this area, the predator takes a step of length LB (input) and reverts to the forward directed random walk. Again, locations are searched as

described for subroutine EAT123. The encounter success rates are separately defined for each searching phase.

Thus, three subroutines are available for taking steps within the arena. Subroutine DIR takes a step of length L (one for all of this work) in a random direction (i.e. into one of the eight adjacent squares). If such a step causes the predator to move beyond the boundary of the arena, further random directions are selected until the predator remains within the arena. Subroutine FDIR takes a step of length L in one of the eight directions used in subroutine DIR, such that the angle of turn relative to the last direction of movement is not greater than a right angle. In the result of such a step moving the predator beyond the edge of the arena, the value defining the last direction of movement (LDIR) is adjusted to reverse the last direction, and subroutine DIR is called. Subroutine SDIR takes a step of length L (one for all of this work) in the same direction as the last movement. In the event of such a step causing the predator to move beyond the edge of the arena, subroutine FDIR is called.

Subroutine ENC performs the operations common to all the search strategies when a location is searched. Firstly, the number of prey of each type present is determined; then, for each prey, a random number (between zero and one) is generated and, if this number is less than the input encounter success rate, the prey is considered to have been found. The number of prey found of each type is summed, and subtracted from the number present. If a map is to be printed, the locations of feeds and unsuccessful encounters are stored.

Subroutine FIX is used to fix the value of one of the searching parameters (encounter success rate or handling time for either prey) as a function of the input argument (X). This can be either the prey density or the number of prey eaten and, depending upon control options for each parameter, one of several models can be used. These models are outlined in the comment cards of the listing (Appendix Section A2.1) and include constant, linear, curvilinear, logarithmic, and switching relationships.

The remaining subprogrammes (SUMS,MAP,IRAND) are to be found in the listing (Appendix Section A2.1).

The control option for the search strategy used (IS) suggests the following nomenclature for the searching strategies:

- 1 random search
- 2 random walk
- 3 forward directed or on-going random walk
- 4a forward directed random walk of step length three
- 4b forward directed random walk of step length ten
- 4c aggregative walk with a step length of three in the normal searching mode
- 4d aggregative walk with a step length of ten in the normal searching mode
- 5 systematic local search in response to finding a prey, followed by the forward directed random walk.

On occasions in the following work, search strategies will be referred to by their control option reference number. For example (IS = 2) may be used to refer to the search strategy of the random walk.

6.3 OPTIMIZATION OF THE AGGREGATIVE WALK

Subroutine AGGEAT, described above, involves a normal search path of steps of length LLS alternating with turns using subroutine FDIR. When a prey is encountered, five time units are spent searching with a step length of one using subroutine DIR. In this section the step length of the normal searching phase (i.e. LLS) is varied to find the most suitable length for various arrangements of prey. The total time available is 1,000 time units, the handling time for each prey is 50 time units, and all encounters with prey are successful. Eight arrangements of prey are used to examine this response: a low density (of about 40) and a high density (of about 490) of prey arranged at random, using the negative binomial distribution with values for K of 1.0 and 0.05, and in clumps.

In this section and in the next on functional responses, a version of the simulation programme earlier than that described in the last section was used. This version, as mentioned, differs in the following particulars:

1. a larger arena of 100 x 100 is used,
2. subroutine CLUPUT distributes regularly arranged clumps of ten prey,
3. subroutine CLUEAT involves the systematic search of an area of 5 x 5 when a prey is found, rather than one of 3 x 3.

The predation results are given in Appendix Section A2.2 (Appendix Table A2.1) and the resultant figures given here are Figs. 6.1 & 6.2.

It can be seen from these results that, although a clear response is not obtained in some cases (e.g. low density aggregated prey), there is a tendency for the highest predation to occur when using a step length (LLS) of ten. An alternative peak at LLS = 3 is present for the high density aggregated and clumped prey.

Accordingly, in the following sections, the two values of LLS (3 and 10) will be used and the results from each will be compared.

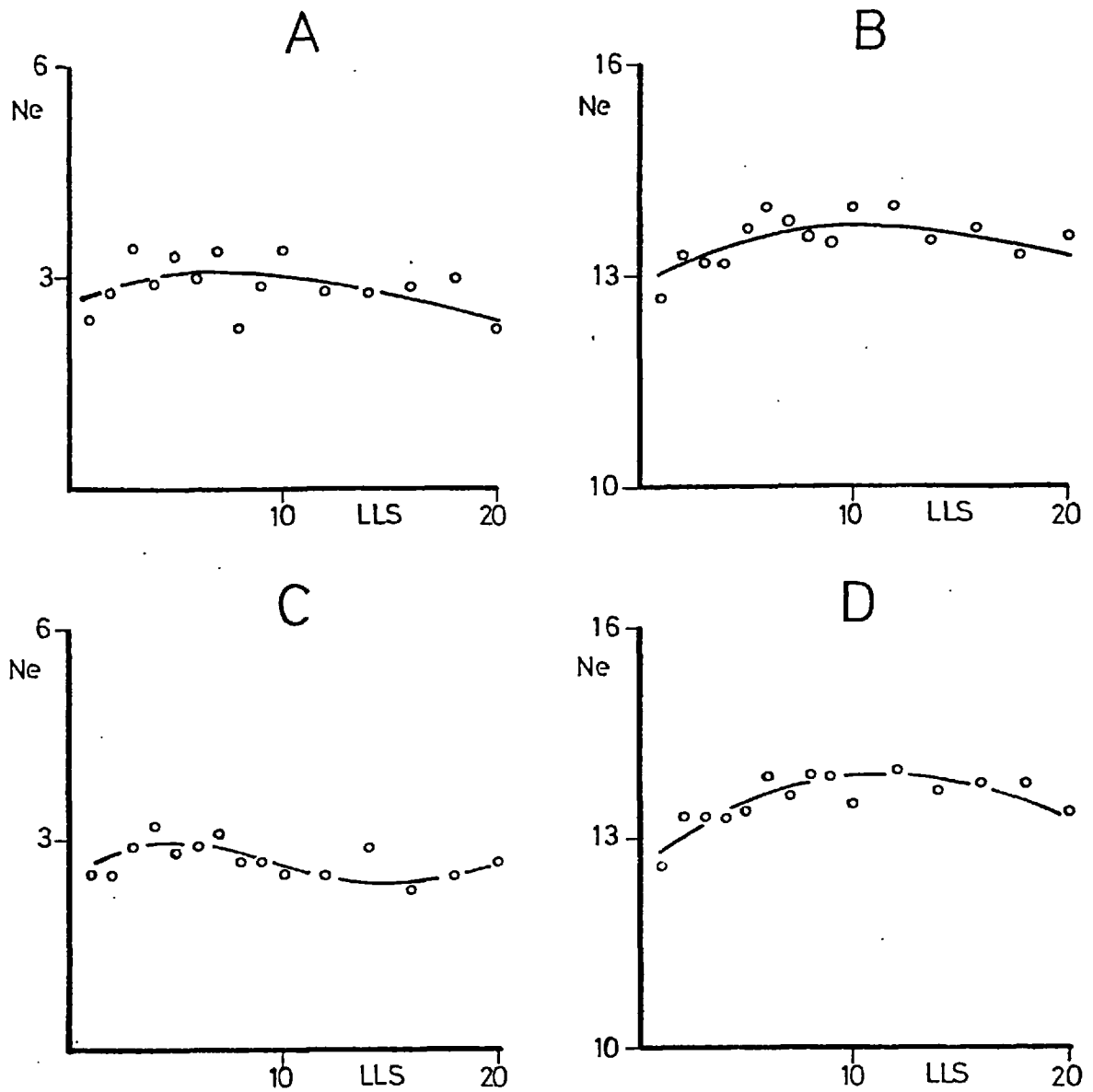


FIGURE 6.1 Optimization of subroutine AGGEAT: varying the step length of the normal searching phase (LLS), to find the optimum in terms of the number of prey eaten (Ne). Results from 20 replicates using:

- (A) - 40 prey arranged at random,
- (B) - 490 prey arranged at random,
- (C) - 39 prey arranged using the negative binomial distribution with an actual value for K of 1.5,
- (D) - 487 prey arranged using the negative binomial distribution with an actual value for K of 1.1.

Data from Appendix Table A2.1; the means only of Ne are used for clarity; the lines are fitted by eye.

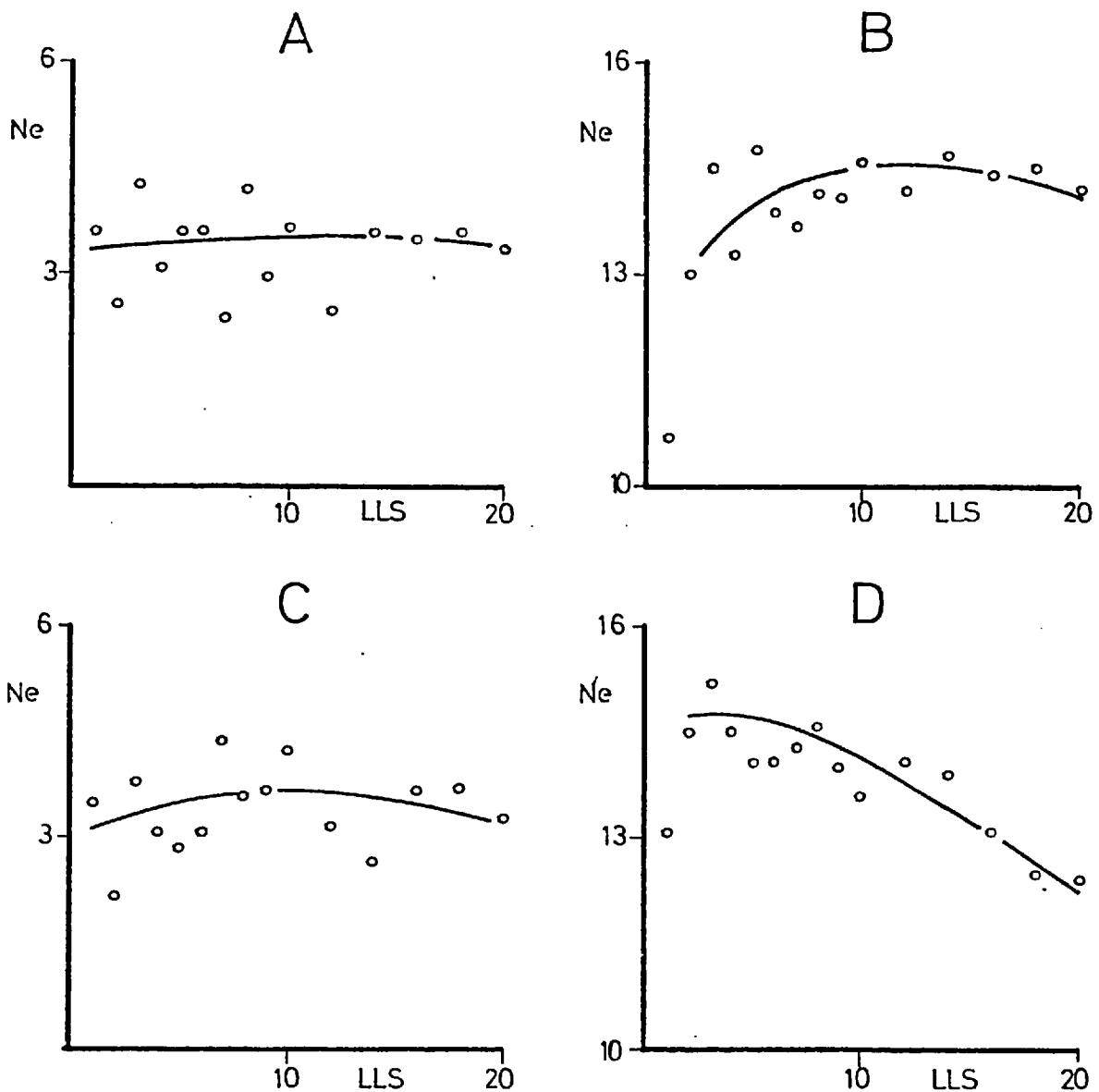


FIGURE 6.2 Optimization of subroutine AGGEAT: varying the step length of the normal searching phase (LLS), to find the optimum in terms of the number of prey eaten (Ne). Results from 20 replicates using:

- (A) - 44 prey arranged using the negative binomial distribution with an actual value for K of 0.054,
 - (B) - 463 prey arranged using the negative binomial distribution with an actual value for K of 0.053,
 - (C) - 40 prey arranged in regularly distributed clumps of ten,
 - (D) - 490 prey arranged in regularly distributed clumps of ten.
- Data from Appendix Table A2.1; the means only of Ne are used for clarity; the lines are fitted by eye.

6.4 SEARCH STRATEGIES AND PREY DISTRIBUTIONS

6.4.1 Simulations and Analysis

In this section the functional responses for each predator search strategy and each prey distribution will be generated and compared. As in the last section, the total time available is 1,000 time units, the handling time for each prey is 50 time units, the encounter success rate is 1.0, an arena of 100 x 100 is used, and subroutines CLUPUT and CLUEAT differ from those described in Section 6.2 (see Section 6.3).

Eight prey densities of up to 1,024 were used for each response, and thirty replicates were run for each. The predation results are given in Appendix Table A2.2.

The Random Predator Equation was fitted to each functional response using a modified version of the least squares best fit approach described in Section 2.2, in which the handling time is preset at the correct value of 50 time units. The resultant values of the search efficiency (a) and the mean square residual variance (R^2) of the fitted response are given in Table 6.1. However, it has been pointed out (Section 2.3) that the $\ln S \times N_e$ figures (logarithm of the proportion of prey surviving \times the number of prey eaten) should be examined when fitting the Random Predator Equation; accordingly, all these functional responses were examined in this way. Most showed normal straight line regressions well described by the abstracted search efficiency (e.g. Fig. 6.3 shows the responses obtained for four combinations of search strategy and prey distribution). Some, however, showed apparently non linear results and so, a further 30 replicates were run for these, and the results from all 60 were examined.

This showed (Appendix Table A2.2; Table 6.1) that some of these were, in fact, linear, but left four which clearly were not. Taking a further 30 replicates of these four, the results from 90 replicates were examined. The most markedly divergent of these resulted from the use of the forward directed random walk of step length ten ($IS = 4b$) to search for regularly arranged prey (Fig. 6.4). In particular, the $\ln S$ value at the prey density of 16 is very low i.e. predation is very high. The explanation for this is

due to the fact that the prey are regularly arranged 20 units apart. This means that, once the predator has found one prey, its chances of finding another are greatly increased. This is demonstrated in Fig. 6.5. It follows that, if the prey are arranged ten units apart (i.e. at a density of 81), this effect will also be present. Accordingly, 90 replicates at a prey density of 81 were generated, and these were found to also show this phenomenon (Fig. 6.4). It also follows that, using the same search strategy, but with a step length of three, prey at three unit intervals (i.e. at a prey density of 1,024) and at six unit intervals (i.e. at a prey density of 256) will also show this effect. This is, in fact, the case, and provides the second non linear response (Fig. 6.6). The third case results from using the same strategy (LLS = 10; IS = 4b) to search for clumped prey (Fig. 6.7); at a density of 160 (i.e. with the clump centres 20 units apart) the same phenomenon can be observed.

The fourth non linear result was obtained using the aggregative walk (LLS = 10; IS = 4d) to search, once again, for regularly arranged prey (Fig. 6.8). It can be seen that the Ne axis intercept (i.e. the maximum consumption rate = T/Th) is less than 20 (the expected rate: $T/Th = 1000/50 = 20$). Abstracting both the search efficiency (a) and the handling time (Th) using the least squares best fit technique, a handling time of 54.7 time units is obtained (Table 6.1). This suggests the explanation that, since the prey are widely spaced, each time a prey is found, five time units are wasted in the short step length mode, resulting in an effective handling time of 55 time units. If this is the case, then at high densities, where the prey are within five units of each other (i.e. at the densities of 529 and 1,024), the effective handling time will be reduced; this seems to be the case (Fig. 6.8), and a curved line, fitted by eye, shows that the data is reasonably described on this basis.

FIGURE 6.3 Functional response results: examples of the $\ln S \times N_e$ figures (logarithm of the proportion of prey surviving plotted against the number eaten). The figures show the results from using:

- (A) - random search (IS = 1),
- (B) - random walk (IS = 2),
- (C) - forward directed random walk (IS = 3),
- (D) - systematic local search in response to finding a prey (IS = 5),

to search for prey arranged at random.

Data from Appendix Table A2.2;

30 replicates run for each prey density;

the means only of N_e and $\ln S$ are used for clarity;

the mean of $\ln S$ is used, as opposed to the \ln of mean S ;

the fitted lines use the search efficiency of the Random Predator Equation obtained by the least squares best fit to the functional response with the handling time held constant at the correct value of 50 time units (see Table 6.1).

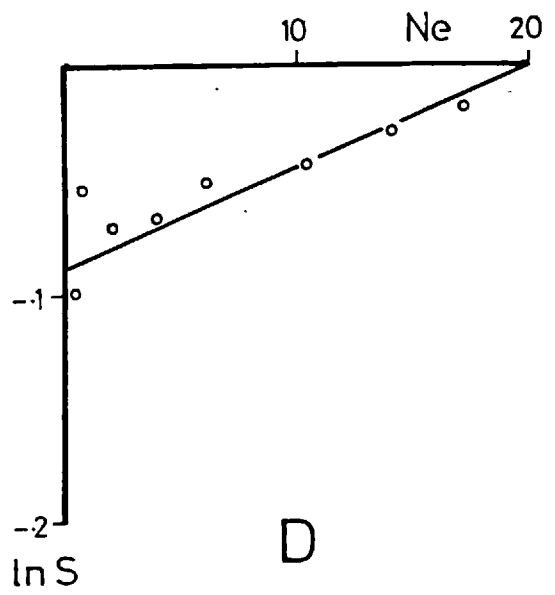
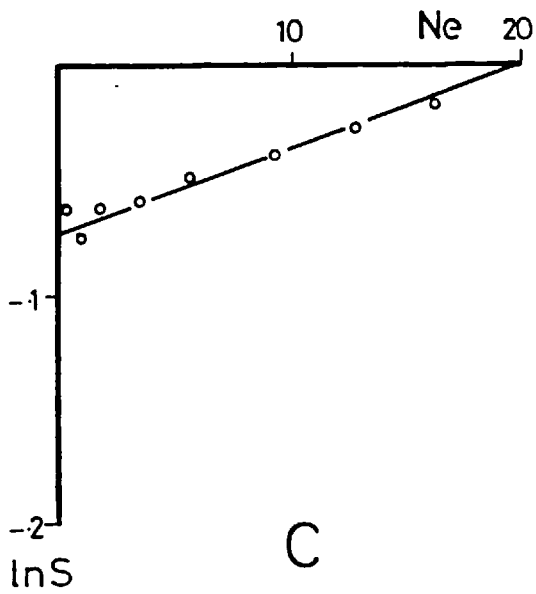
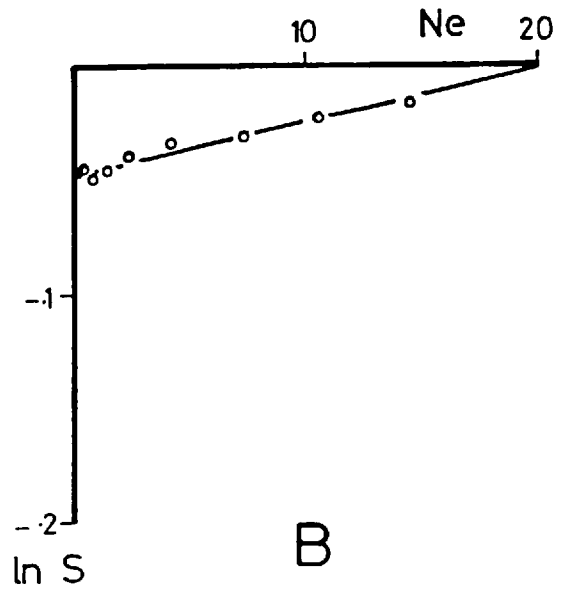
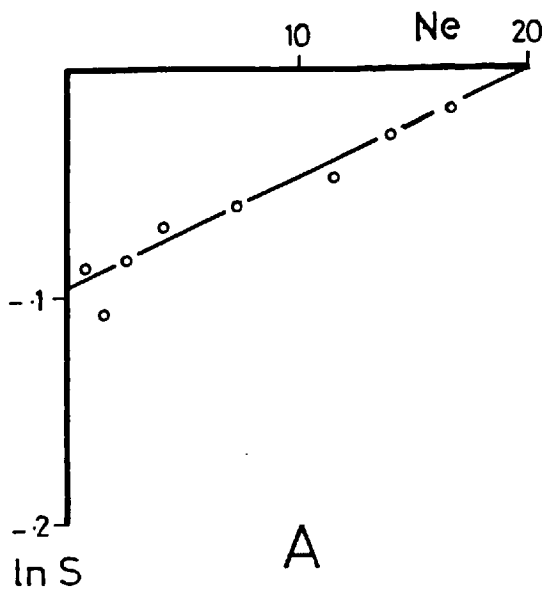
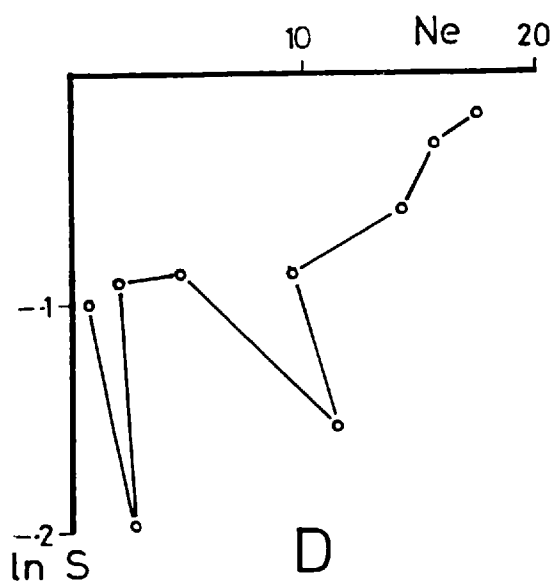
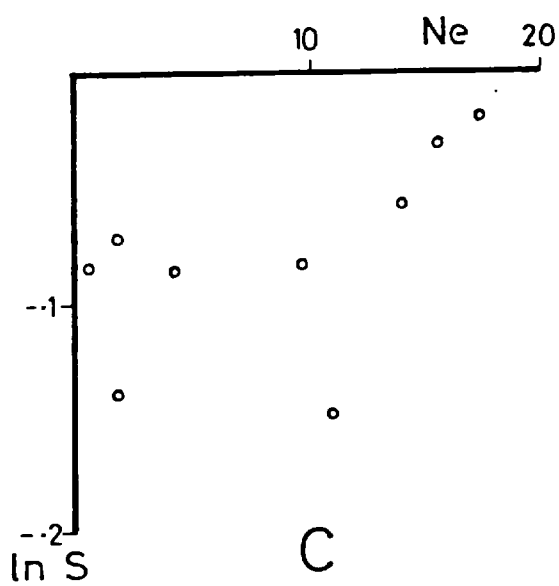
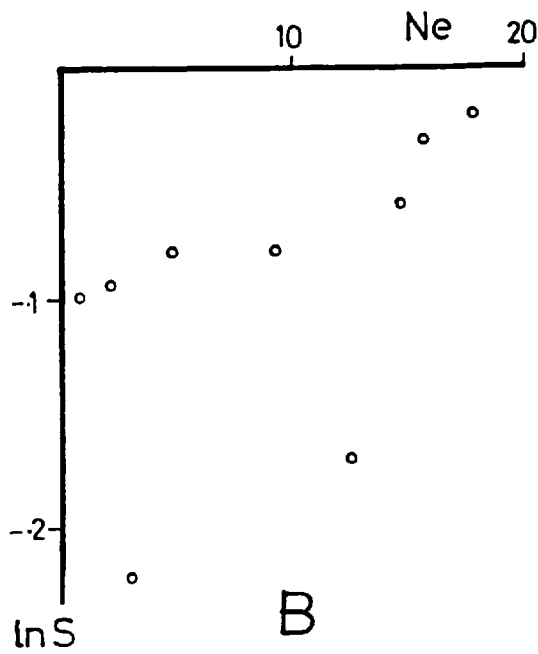
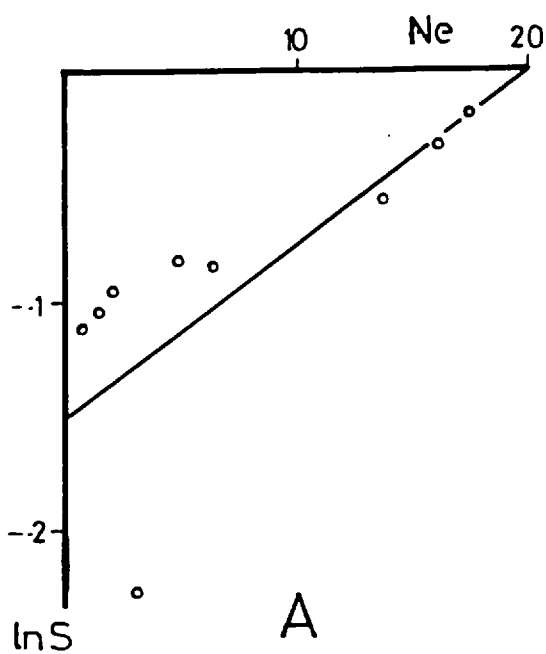


FIGURE 6.4 Functional response results: the $\ln S \times N_e$ plots for the functional response using the forward directed random walk of step length ten to search for regularly arranged prey; the markedly non linear nature of the relationship can be seen. The figures are:

- (A) - the first 30 replicates,
- (B) - the second 30 replicates,
- (C) - the third 30 replicates,
- (D) - the mean results of all 90 replicates.

In Figs. B, C, & D the extra point for $N = 81$ has been added - see text;
data from Appendix Table A2.2;
the means only of $\ln S$ and N_e are used for clarity;
the mean of $\ln S$ rather than the \ln of mean S is used;
the fitted line of Fig. A uses the search efficiency of the Random Predator Equation obtained by the least squares best fit to the functional response with the handling time at the correct time of 50 time units (see Table 6.1);
the best fit value of the search efficiency for all 90 replicates and the point for $N = 81$ is 1.735 locations searched per time unit.



SCALE:



Distance units

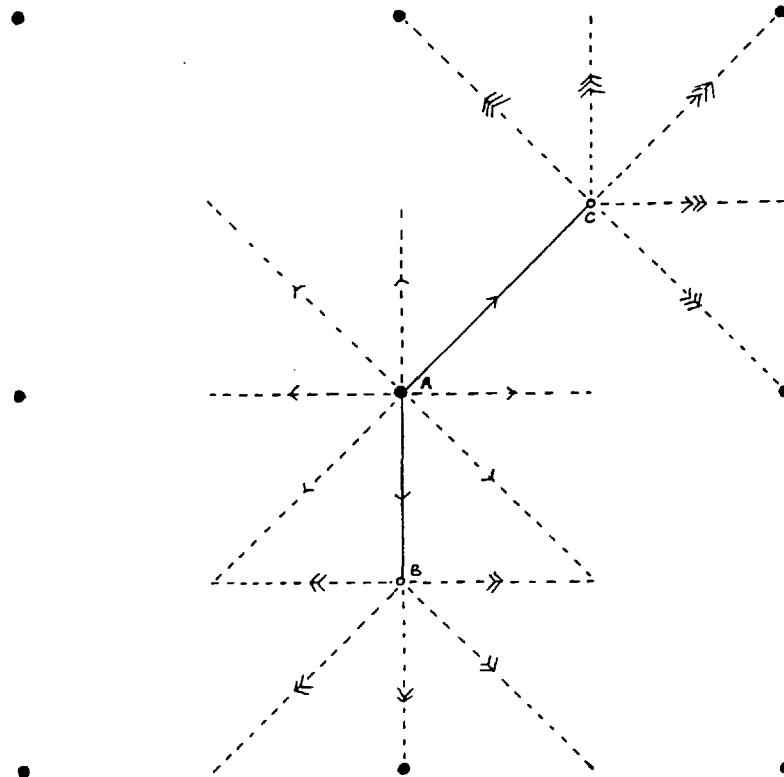


FIGURE 6.5 Diagram to show how prey (symbol •) arranged regularly at 20 unit intervals are heavily predated using the forward directed random walk of step length ten (IS = 4b). Thus, once a prey is encountered, for example, at position A, there are two types of move (single arrow) possible:

- 1) vertically or horizontally to, for example position B; any move from here (double arrow) leads to a 1 in 5 chance of finding a second prey at the end of the second step,
- 2) diagonally to, for example, position C; any move from here (treble arrow) results in a 3 in 5 chance of finding a prey at the end of the second step.

If both of these movements are made with equal frequency, then the probability of finding another prey in two steps (i.e. 20 time units) is 0.5. On the basis of random search, the probability would be $(20 \times 16)/10000 = 0.032$. Hence, it can be seen why this search strategy is so efficient.

FIGURE 6.6 Functional response results: the $\ln S \times N_e$ plots for the functional response using the forward directed random walk of step length three ($IS = 4a$) to search for regularly arranged prey. The non linear nature of the relationship can be seen. The figures are:

- (A) - the first 30 replicates,
- (B) - the second 30 replicates,
- (C) - the third 30 replicates,
- (D) - the mean results for all 90 replicates.

Data from Appendix Table A2.2;
the means only of $\ln S$ and N_e are used for clarity;
the fitted line of Fig. A uses the search efficiency ($a = 1.093$ locations/time unit) obtained by the least squares best fit to the functional response with the handling time at the correct value of 50 time units;
the best fit value of the search efficiency for all 90 replicates is 1.075 locations/time unit.

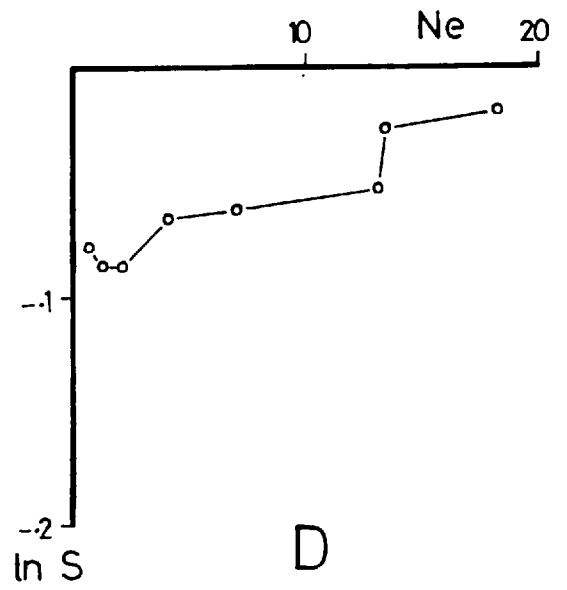
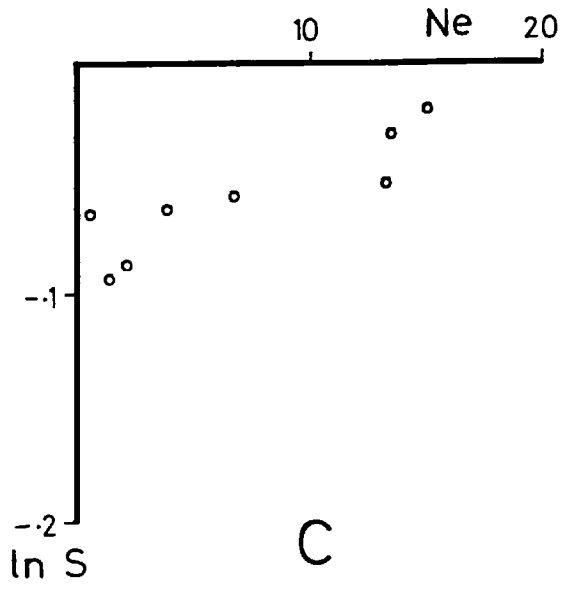
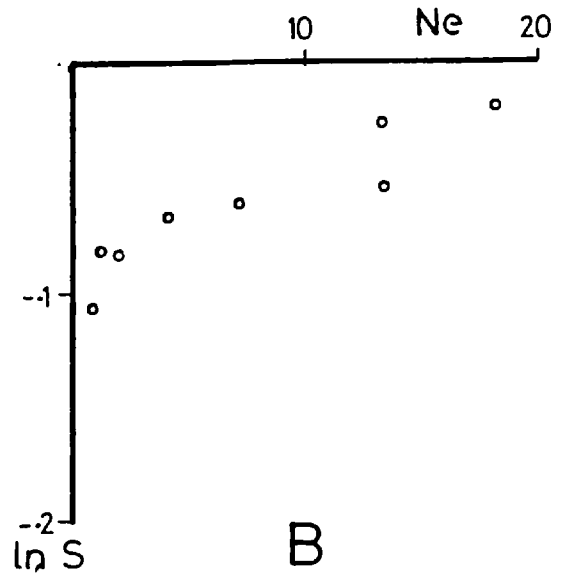
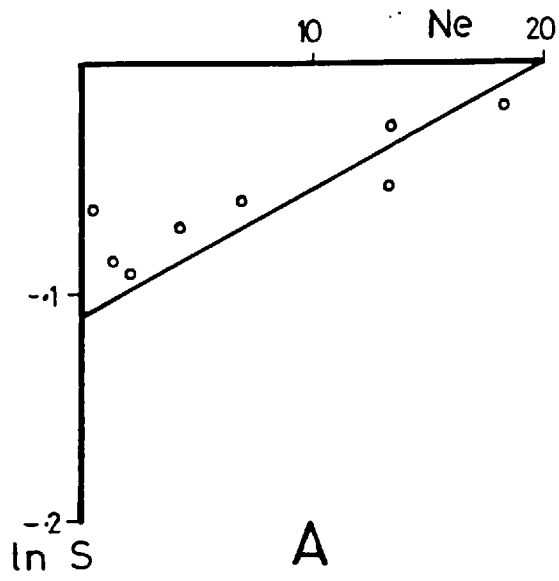


FIGURE 6.7 Functional response results: the $\ln S \times N_e$ plots for the functional response using the forward directed random walk of step length ten ($IS = 4b$) to search for regularly arranged clumps of ten prey. The non linear nature of the relationship can be seen. The figures are:

- (A) - the first 30 replicates,
- (B) - the second 30 replicates,
- (C) - the third 30 replicates,
- (D) - the mean results from all 90 replicates.

Data from Appendix Table A2.2;
the means only of $\ln S$ and N_e are used for clarity;
the mean of $\ln S$ is used;
the fitted line of Fig. A uses the search efficiency ($a = 1.037$ locations/time unit) obtained by the least squares best fit to the functional response with the handling time at the correct value of 50 time units.

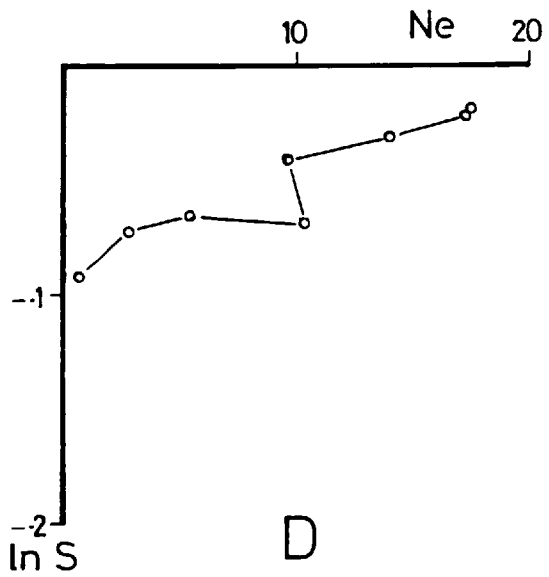
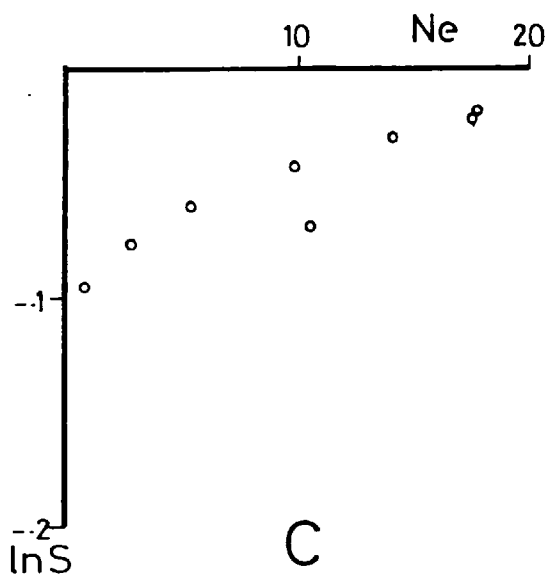
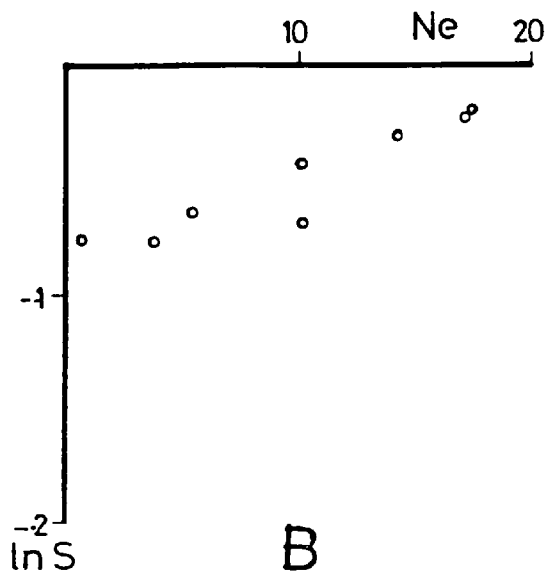
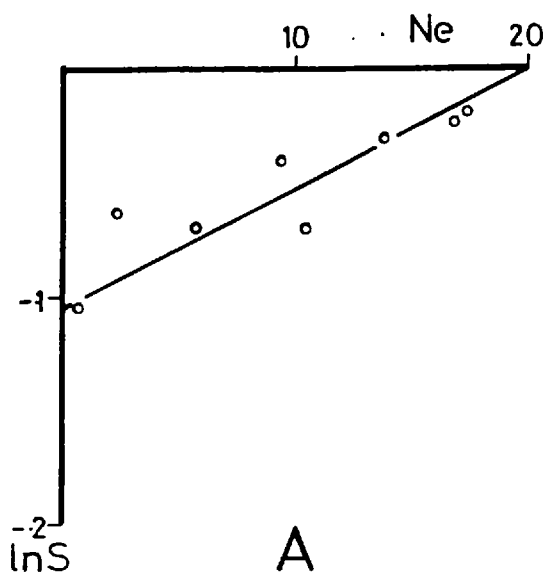
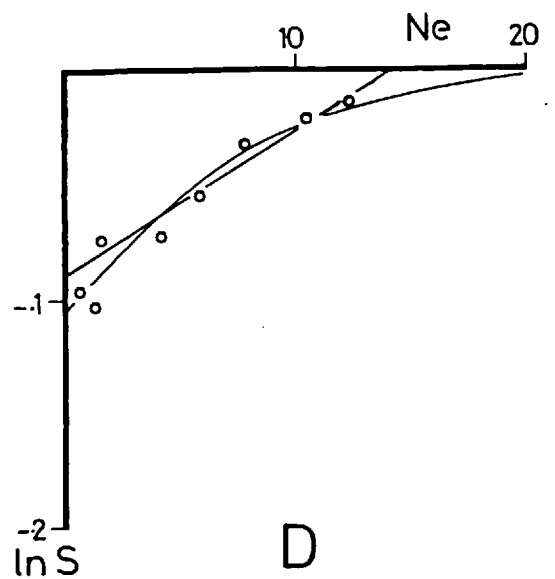
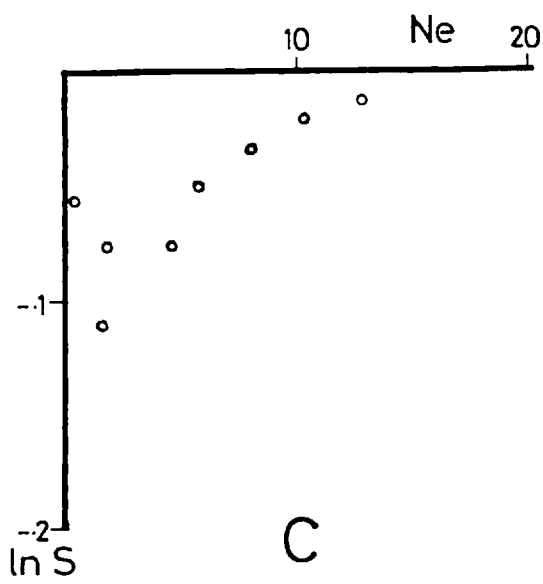
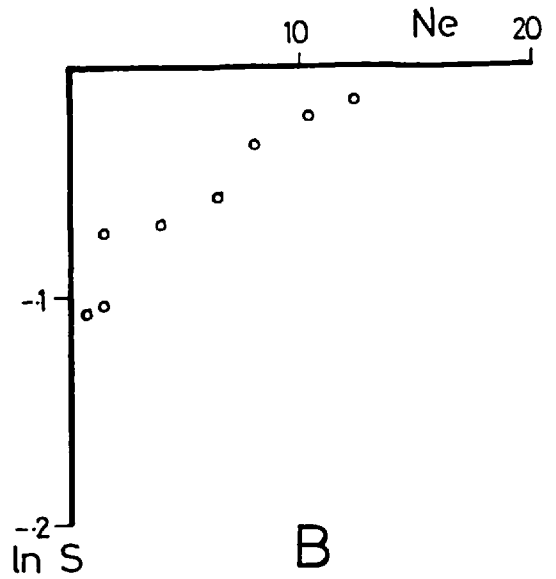
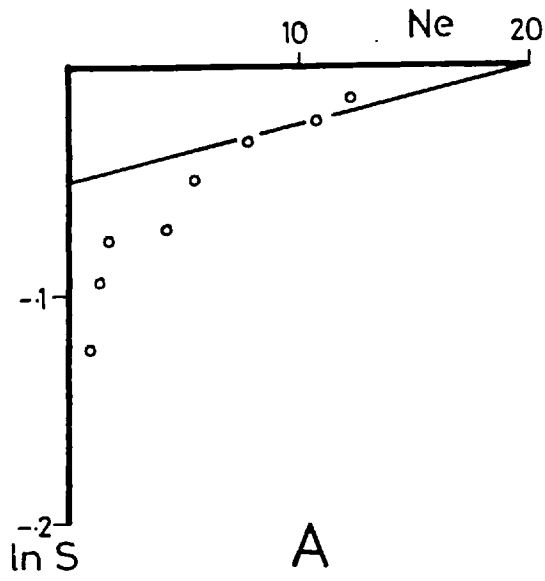


FIGURE 6.8 Functional response results: the $\ln S \times N_e$ plots for the functional response using the aggregative walk with a step length of ten for the normal phase ($IS = 4d$) to search for regularly arranged prey. It can be seen that the intercept on the N_e axis differs from the correct value ($T/Th = 20$). The figures are:

- (A) - first 30 replicates,
- (B) - second 30 replicates,
- (C) - third 30 replicates,
- (D) - the mean results from all 90 replicates.

Data from Appendix Table A2.2;
the means only of $\ln S$ and N_e are used for clarity;
the mean of $\ln S$ is used;
the fitted line of Fig. A uses the search efficiency ($a = 0.480$ locations/time unit) obtained by the least squares best fit to the functional response with the handling time at the correct value of 50 time units;
the straight line of Fig. D uses the parameters of the Random Predator Equation obtained by the least squares best fit to the functional response for both parameters ($a = 1.345$ locations/time unit; $Th = 54.73$ time units);
the curved line of Fig. D is fitted by eye to show that the true intercept on the N_e axis (T/Th) is still 20.



PREY : REGULAR		RANDOM		K = 0.05		CLUMPS		MEAN	
IS	a	R ²	a	R ²	a	R ²	a	R ²	
1	0.934	0.03	0.948	0.10	0.954	0.05	0.946	0.12	0.946
2	0.471	0.12	0.447	0.09	0.406	0.07	0.449	0.40 *1	0.443
3	0.748	0.02	0.720	0.10	0.668	0.12	0.767	0.81	0.726
4a	1.093	1.39 *3	0.906	0.03	0.778	0.22 *1	0.856	0.03	0.847 *5
4b	1.496	0.73 *3	0.954	0.03	1.032	1.30 *2	1.037	1.39 *3	0.993 *5
4c	0.757	0.06	0.874	0.13	0.950	0.11	1.190	0.55	0.943
4d	0.480	1.54 *4	0.880	0.07	1.128	0.09	1.134	0.52	1.047 *5
5	0.699	0.09	0.885	0.34	1.231	0.36	1.784	0.26	1.150

TABLE 6.1 Abstracted search efficiency (a) and mean square residual variance (R²) of the functional responses of Section 6.4 for all search strategies and prey arrangements. The search efficiencies were obtained by the least squares best fit to the functional response with the handling time (Th) held constant at the true value of 50 time units. The search strategies (IS) are those given at the end of Section 6.2. The results from thirty replicates were used unless otherwise stated, and these data are given in Appendix Table A2.2. The search efficiency (a) is given in units of locations searched per unit of time. Since only one parameter is abstracted from each set of data, there are insufficient degrees of freedom to permit an analysis of variance; hence the mean square residual variance is examined.

Notes:

- *1 60 replicates used
- *2 90 replicates used
- *3 non linear relationship
- *4 abstracting both a and Th by the least squares best fit to the functional response gives parameters of a = 1.345 locations/time unit and Th = 54.73 time units, which leads to a mean value for a of 1.222 locations/time unit
- *5 not including values of a from non linear relationships

6.4.2 Discussion

The search efficiencies for each of the functional responses are given in Table 6.1. In the following discussion these estimated search efficiencies will be given as locations of the arena searched per unit of time. Examining these, a number of points can be made:

- 1 Completely random search (IS = 1) results in a consistent search efficiency of 0.946, which is close to the true value of 1.0. This search efficiency is unaffected by the prey distribution.

- 2 Random walk (IS = 2) results in a low average search efficiency of 0.443. Again this is unaffected by the prey distribution. This strategy, similar to that used by Murdie (1971), is, by a large margin, the least efficient of the search strategies.

- 3 The forward directed random walk (IS = 3) leads to an average search efficiency of 0.726, independent of the prey distribution. This mean search efficiency, although greater than that resulting from the random walk, is still less efficient than the random search strategy.

- 4 The two forward directed random walks with long step lengths (4a & 4b) both gave artificially high values for the search efficiency for regular prey (as described in Section 6.4.1). Taking the mean search efficiency for the remaining three prey arrangements gives a value of 0.847 using the step length of three (IS = 4a), and 0.993 using the step length of ten (IS = 4b). Thus, it can be seen that the step length of ten is more efficient here, due to the relatively large component of systematic search. Neither strategy is significantly affected by the prey distribution.

- 5 Comparing the two aggregative walks (IS = 4c, 4d), it can be seen that the search efficiency increases as the prey aggregation increases. The strategy using the step length of ten (IS = 4d) gives an unsuitably low value for the search efficiency

when the prey are arranged regularly (see Section 6.4.1), and so, the efficiencies of these two search strategies are not directly comparable for this prey arrangement. The results when searching for prey arranged at random show nearly equal search efficiencies ($a = 0.874$ for 4c, $a = 0.880$ for 4d). When searching for the aggregated prey, the strategy using the step length of ten clearly shows a greater search efficiency ($a = 0.950$ for 4c, $a = 1.128$ for 4d), while, when searching for clumped prey, the strategy using a step length of three has a slight (perhaps insignificant) advantage ($a = 1.196$ for 4c, $a = 1.134$ for 4d). These results are in accordance with those from Section 6.3.

6 The strategy of systematic local search in response to finding a prey (IS = 5) also leads to increasing search efficiency as the prey aggregation increases. It can be seen that, for the aggregated and clumped distributions of prey, this is the most efficient of the strategies ($a = 1.231$ for aggregated prey, $a = 1.784$ for clumped prey), whilst comparing the mean search efficiencies shows that, overall, it is the most efficient search strategy (mean $a = 1.150$).

In conclusion, it has been found that regularly arranged prey tend to produce anomalies, and, therefore, will not be used in subsequent simulations. Regularly arranged clumps may also produce such anomalies and results should be examined for this; the random distribution of clumps would be a better approach, and this is used for the remainder of this work. Of all the strategies considered, only the forward directed random walk with the step length of ten (IS = 4b), the aggregative walk with the normal step length of ten (IS = 4d), and the systematic local search in response to finding a prey (IS = 5) are more efficient than totally random search. In the following sections particular attention will be paid to these three strategies.

6.5 SIGMOID AND DOME SHAPED FUNCTIONAL RESPONSES

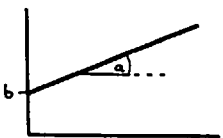
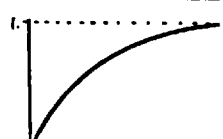
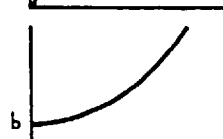


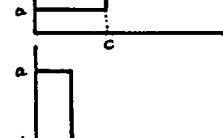
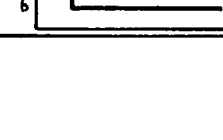


In Chapters 2 and 3 a number of models of sigmoid and dome shaped functional responses were discussed; in this section these and other possibilities will be examined by means of simulations. Subroutine FIX is used to define the handling time or encounter success rate (s) as functions of either the initial prey density or the number of prey eaten. Varying the encounter success rate provides a not unrealistic method of varying the search efficiency. Obviously, however, even the maximum encounter success rate will not increase the search efficiency beyond the limits imposed by the search strategy.

Various models of the parameters were considered and these are tabulated in Table 6.2. Each model has been given a reference number (S1 - 12, D1 - 3 as shown in Table 6.2), and they are considered in turn below:

Model S1: in this model the mean encounter success rate (\bar{s}) is a linear increasing function of the prey density. Since the encounter success rate can not exceed 1.0, this means that it rises linearly to 1.0, and then remains at 1.0 with increasing prey density. This results in a sigmoid functional response (Fig. 6.9A), and a $\ln S \times N_e$ figure showing the V shape characteristic of the sigmoid response (Fig. 6.9B). The figure of the calculated mean search efficiency plotted against the number of prey eaten (Fig. 6.9C) shows a relationship similar to the type II functional response but differing in that there is a positive intercept on the search efficiency axis.

Model S2: this model differs from S1 in that the instantaneous encounter success rate (s) is a linear function of the number of prey eaten. The results (Fig. 6.10) are, however, similar to those obtained using the model S1.

Model S3: the mean encounter success rate (\bar{s}) is a curvilinear function of the prey density, rising to a maximum value in a manner similar to the type II response. The model used is analogous to the Holling Disc Equation (Section 1.2.2). Again, the results (Fig. 6.11) are similar to those obtained using the model S1.

REF	J	MODEL	FIGURE OF THE MODEL	RESULT	PARAMETERS USED			FIG
					a	b	c	
S1	2	$\bar{s} = a N + b$		Sigmoid	0.02	0.2	-	6.9
S2	2	$s = a Ne + b$		Sigmoid	0.2	0.2	-	6.10
S3	5	$\bar{s} = a b N / (1 + a c N)$		Sigmoid	0.05	1.0	1.0	6.11
S4	5	$s = a b Ne / (1 + a c Ne)$		Unusable	-	-	-	-
S5	3	$\bar{s} = a \ln N + b$		Sigmoid	0.3	- 0.4	-	6.12
S6	3	$s = a \ln Ne + b$		Unusable	-	-	-	-
S7	6	$\bar{Th} = \exp(a \ln N + b) + c$		Unusable	-	-	-	-
S8	6	$Th = \exp(a \ln Ne + b) + c$		Type II	-	-	-	-
S9	4	$\bar{s} = a; \text{ IF } N > c, s = b$		Discontinuous	-	-	-	6.13
S10	4	$s = a; \text{ IF } Ne > c, s = b$		Approx. type II	-	-	-	-
S11	4	$\bar{Th} = a; \text{ IF } N > c, s = b$		Discontinuous	-	-	-	6.13
S12	4	$Th = a; \text{ IF } Ne > c, s = b$		Sigmoid if $a < 0$	- 40.	60.0	4.0	6.14

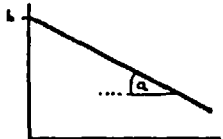
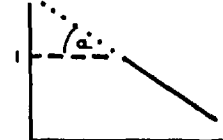
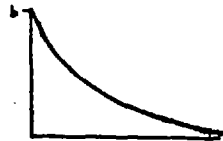
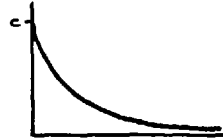
D1A	2	$\bar{s} = a N + b$		Dome shaped	- 0.0002	1.0	-	6.15
D1B	2	$\bar{s} = a N + b$		Dome shaped	- 0.0004	2.0	-	6.15
D2	3	$\bar{s} = a \ln N + b$		Dome shaped	- 0.11	1.0	-	6.16
D3	6	$\bar{s} = \exp(a \ln N + b) + c$		Type II	-	-	-	-

TABLE 6.2 Models used for the sigmoid and dome shaped functional responses. The parameter J is that used in subroutine FIX to determine the model used. The parameters a , b and c are those used in the simulations resulting in Figs. 6.9 - 6.16. The figures of the models show the parameter in question (s , instantaneous encounter success rate; \bar{s} , mean encounter success rate; T_h , instantaneous handling time; \bar{T}_h , mean handling time) as a function of the number of prey eaten (N_e) or the initial prey density (N), as defined by the model.

Model S4: the instantaneous encounter success rate (s) depends upon the number of prey eaten using the same description as for S3. However, since the value of s will remain at zero until the first prey is found, no prey will ever be found and the model is unusable.

Model S5: in this model the value of \bar{s} is an increasing logarithmic function of the prey density. Once again, the results (Fig. 6.12) are similar to those for S1.

Model S6: is the corresponding version of S5 in which s is defined by the number of prey eaten. Since the initial value of s can not be evaluated (as it involves taking the logarithm of zero) this model is also unusable.

Model S7: the mean handling time is defined by the relationship:

$$\bar{T}_h = \exp(a \ln N + b),$$

where \bar{T}_h is the mean handling time, N is the prey density and a & b are constants. The parameter a used is negative (Table 6.2); this results in an approximately type II functional response.

Model S8: is the instantaneous version of S7 (T_h as the corresponding function of N_e , the number of prey eaten), and as in the case of S6, is unusable due to the value of N_e being initially zero.

Model S9: here, \bar{s} will take one of two values depending upon the value of N . Fig. 6.13A shows that the resultant $\ln S \times N_e$ relationship can not be V shaped, and will lead to an approximately type II functional response.

Model S10: the instantaneous version of S9 (s defined by the value of N_e) leads to a smoothed version of the results obtained using S9 i.e. an approximately type II functional response is obtained.

Model S11: involves a choice of two values for the handling time, determined by the value of the prey density. Figures 6.13B & C show the two possible results. In Fig. 6.13B both handling times have positive values, and an approximately type II functional response would result. In Fig. 6.13C the initial handling time has a negative value, and it can be seen that the $\ln S \times N_e$ figure is approaching the V shape. If, in this latter case the change in the handling time were accompanied by an increase in search efficiency a V shape would result for the $\ln S \times N_e$ figure, as was the case for the two-regression model used in Chapter 3.

Model S12: is the instantaneous version of S11 (Th defined by the value of N_e) and results in a smoothed version of the same results (Fig. 6.14); hence, the functional response is slightly sigmoid and the $\ln S \times N_e$ relationship shows a somewhat doubtful V shape.

Thus, the models S1, S2, S3, S5 and S12 all produced sigmoid functional responses; the first four by varying the encounter success rate and the last by varying the handling time. The first four models all resulted in similar figures of the calculated search efficiency as a function of the number of prey eaten. Therefore, the HLB model used in Chapter 3 is suitable for the description of all these cases. Model S12, the only technique of varying the handling time which resulted in a sigmoid functional response (albeit a somewhat doubtful one), incorporated the effects of a negative handling time (cf. the two-regression model used in Chapter 3). Should the change in the handling time coincide with an increase in search efficiency, a more clearcut V shape of the $\ln S \times N_e$ relationship would result.

Three models considered likely to produce dome shaped functional responses were considered. In view of the conclusions of Section 2.4, all of these models describe the mean encounter rate as decreasing functions of the prey density.

Model D1: the mean encounter success rate (\bar{s}) is decreased linearly as a function of the prey density. Two versions were examined: in model D1A \bar{s} decreases continuously, while in model D1B it is initially constant, and then decreases more

rapidly than in model D1A. The mean search efficiency (\bar{a}) was calculated, and it can be seen (Fig. 6.15C) that the changes closely mirror those of \bar{s} . When the search efficiency is plotted as a function of the number of prey eaten (Fig. 6.15D), figures not dissimilar to those suggested in Section 2.4 (Fig. 2.7B & 2.8B) are obtained.

Model D2: involves the logarithmic decrease of \bar{s} as a function of prey density. The initially rapid decrease in the calculated value of \bar{a} (Fig. 6.16C) appears to have little effect, the final reductions at a low search efficiency and high prey density causing the slight dome shape.

Model D3: \bar{s} is defined by a decreasing function similar to the increasing function used for model S7, and this results in a type II response.

Thus, both the linear and logarithmic models of the decrease in search efficiency result in dome shaped functional responses, confirming that both may be suitable approaches (see Section 2.4).

FIGURE 6.9 Sigmoid functional response results obtained using the model S1 (see Table 6.2; the mean encounter success rate, $\bar{s} = a N + b$; $a = 0.02$, $b = 0.2$) to search for prey arranged at random. The figures are:

- (A) - the functional response: the number of prey eaten (N_e) plotted against the prey density (N). This is very close to the type II response.
- (B) - the logarithm of the proportion of prey surviving ($\ln S$) plotted against N_e . This shows very clearly the V shape characteristic of the sigmoid functional response.
- (C) - the calculated mean search efficiency (\bar{a}) (obtained by substituting the predation results and the known handling time into the Random Predator Equation and solving for \bar{a}) plotted against N_e . It can be seen that this is a curvilinear relationship, reminiscent of the type II functional response, but with an intercept on the \bar{a} axis defined by the parameter b of the model S1.

Fifty replicates were used for each prey density; data from Appendix Table A2.3; in Figs. A & B the means only of N_e and $\ln S$ are used for clarity, and these are used to calculate \bar{a} ; all the lines are fitted by eye.

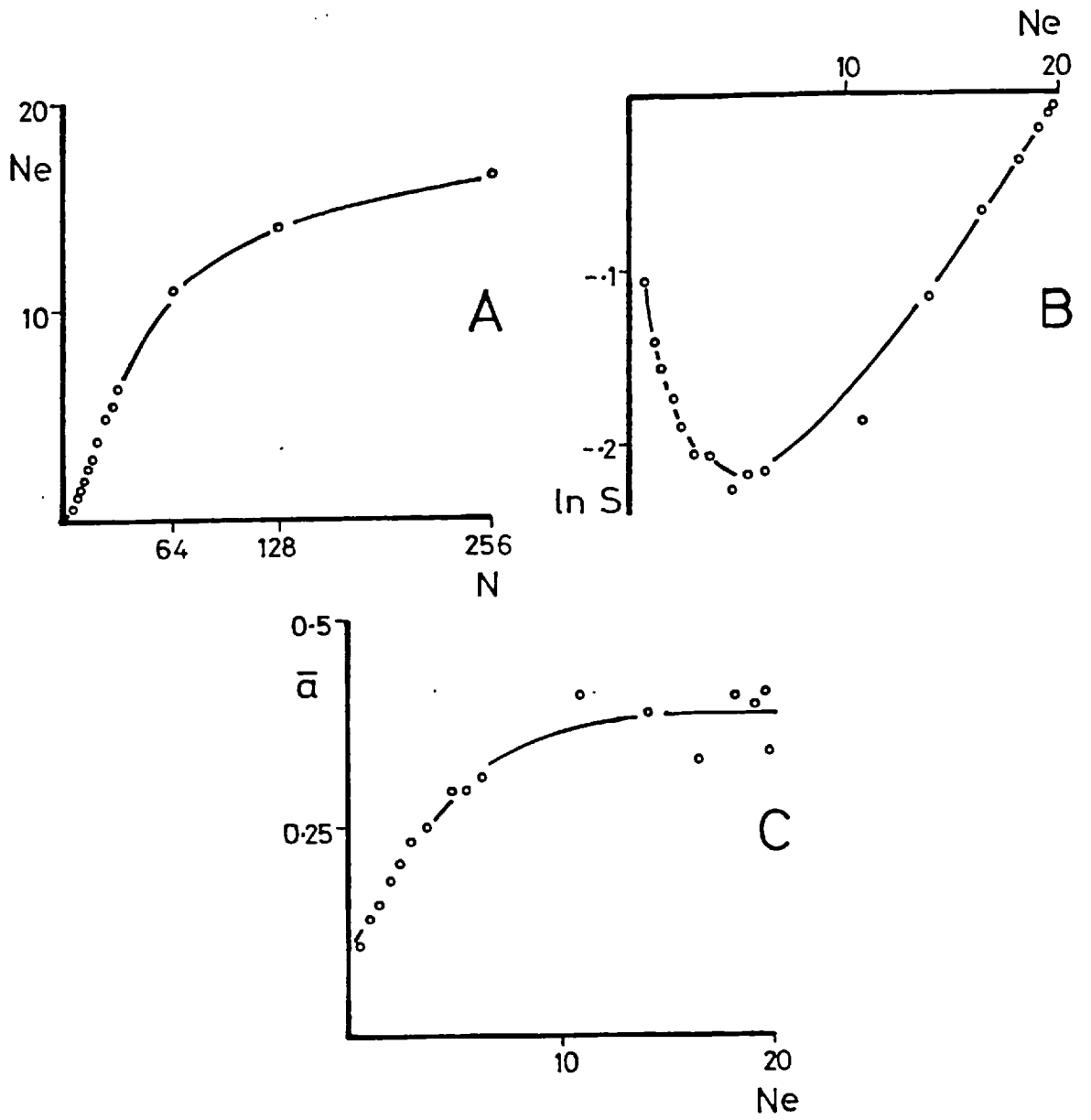


FIGURE 6.10

Sigmoid functional response results obtained using the model S2 (see Table 6.2; the instantaneous encounter success rate, $s = a Ne + b$; $a = 0.2$, $b = 0.2$) to search for random prey. The figures are:

- (A) - the functional response: the number of prey eaten (Ne) plotted against the prey density (N). This is very close to the type II response.
- (B) - the logarithm of the proportion of prey surviving ($\ln S$) plotted against Ne . This shows the V shape characteristic of the sigmoid functional response very clearly.
- (C) - the calculated mean search efficiency (\bar{a}) (obtained by substituting the predation results and the known handling time into the Random Predator Equation and solving for \bar{a}) plotted against Ne . It can be seen that this is a curvilinear relationship, reminiscent of the type II functional response, but with an intercept on the \bar{a} axis defined by the parameter b of the model S2.

Fifty replicates were used for each prey density; data from Appendix Table A2.3; in Figs. A & B the means only are used for Ne and $\ln S$ for clarity, and these are used to calculate \bar{a} ;
all the lines are fitted by eye.

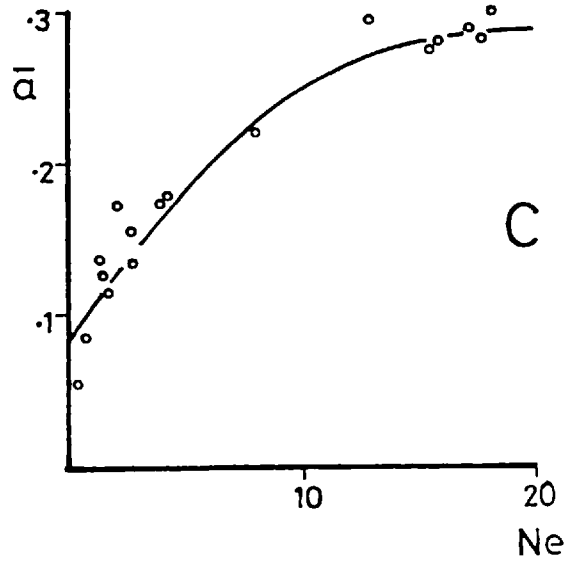
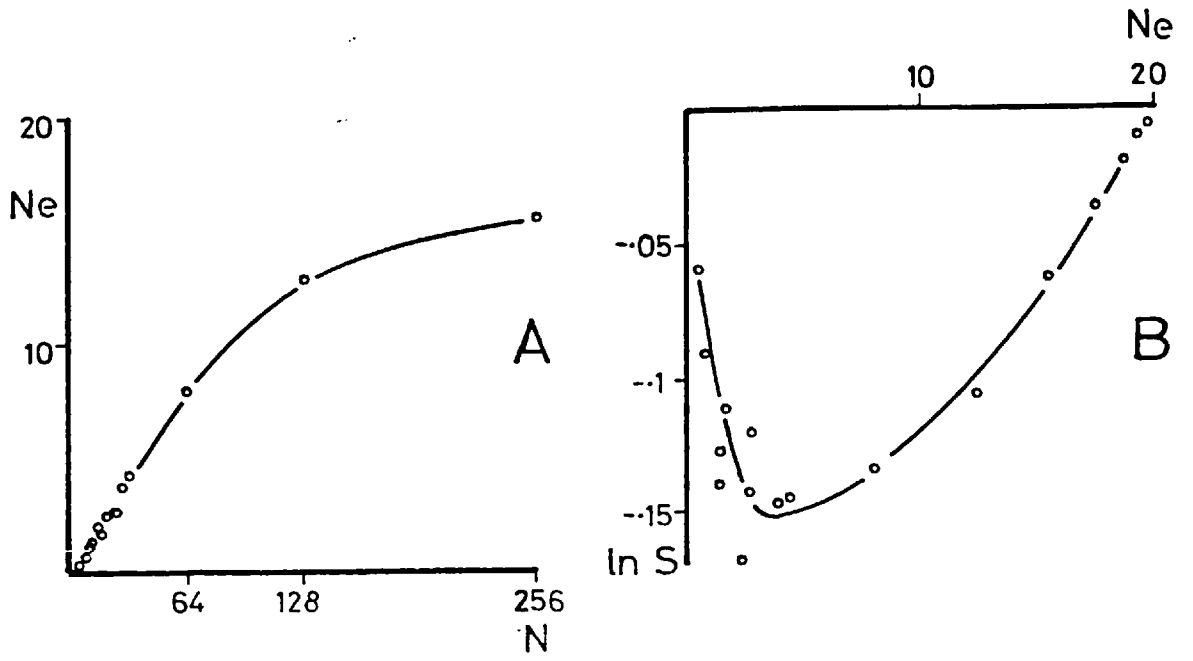


FIGURE 6.11 Sigmoid functional response results obtained using the model S_3 (see Table 6.2; the mean encounter success rate, $\bar{s} = a b N / (1 + a c N)$; $a = 0.05$, $b = 1.0$, $c = 1.0$) to search for random prey.

- (A) - the functional response: the number of prey eaten (N_e) plotted against the prey density (N). This is very close to the type II response.
- (B) - the logarithm of the proportion of prey surviving ($\ln S$) plotted against N_e . This clearly shows the V shape characteristic of the sigmoid functional response.
- (C) - the calculated mean search efficiency (\bar{a}) (obtained by substituting the predation results and the known handling time into the Random Predator Equation and solving for \bar{a}) plotted against N_e . It can be seen that this is a curvilinear relationship similar to the type II functional response, and that it passes through the origin.

Fifty replicates were used for each prey density; data from Appendix Table A2.3; in Figs A & B the means only of $\ln S$ and N_e are used for clarity, and these are used to find \bar{a} ; all the lines are fitted by eye.

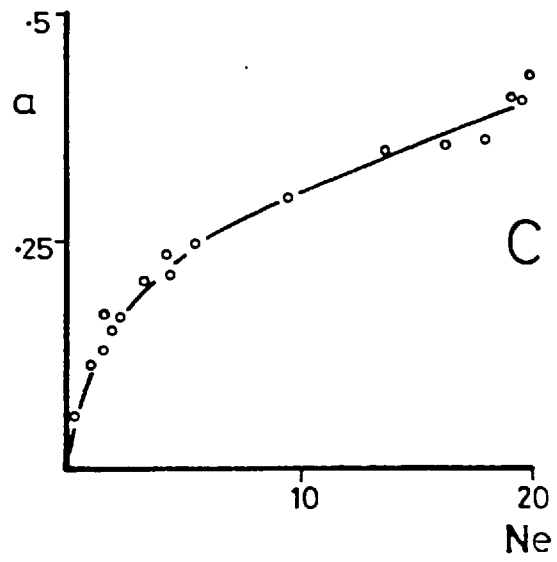
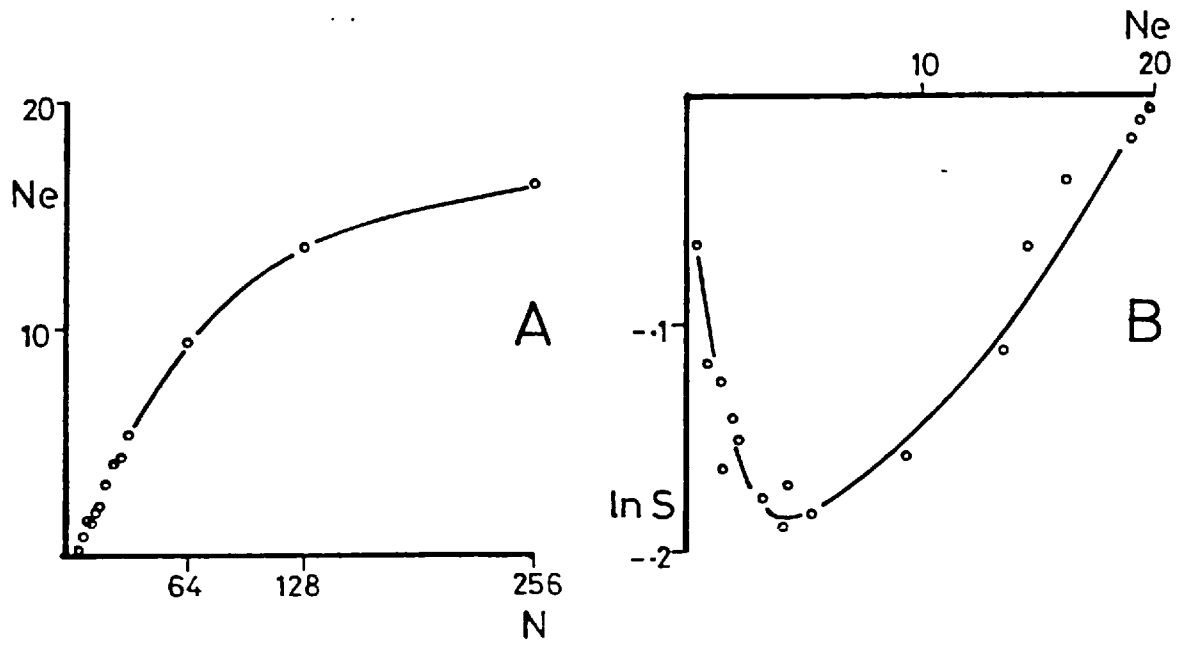


FIGURE 6.12 Sigmoid functional response results obtained using the model S5 (see Table 6.2; the mean encounter success rate, $\bar{s} = a \ln N + b$; $a = 0.3$, $b = -0.4$) to search for prey arranged at random.

- (A) - the functional response: the number of prey eaten (N_e) plotted against the prey density (N). This is very close to the type II response.
- (B) - the logarithm of the proportion of prey surviving ($\ln S$) plotted against N_e . This clearly shows the V shape characteristic of the sigmoid functional response.
- (C) - the calculated mean search efficiency (\bar{a}) (obtained by substituting the predation results and the known handling time into the Random Predator Equation and solving for \bar{a}) plotted against N_e . It can be seen that this is a curvilinear relationship similar to the type II functional response, and that it passes through the origin.

Fifty replicates were used for each prey density; data from Appendix Table A2.3; in Figs. A & B the means only of $\ln S$ and N_e are used for clarity, and these are used to calculate \bar{a} ; all the lines are fitted by eye.

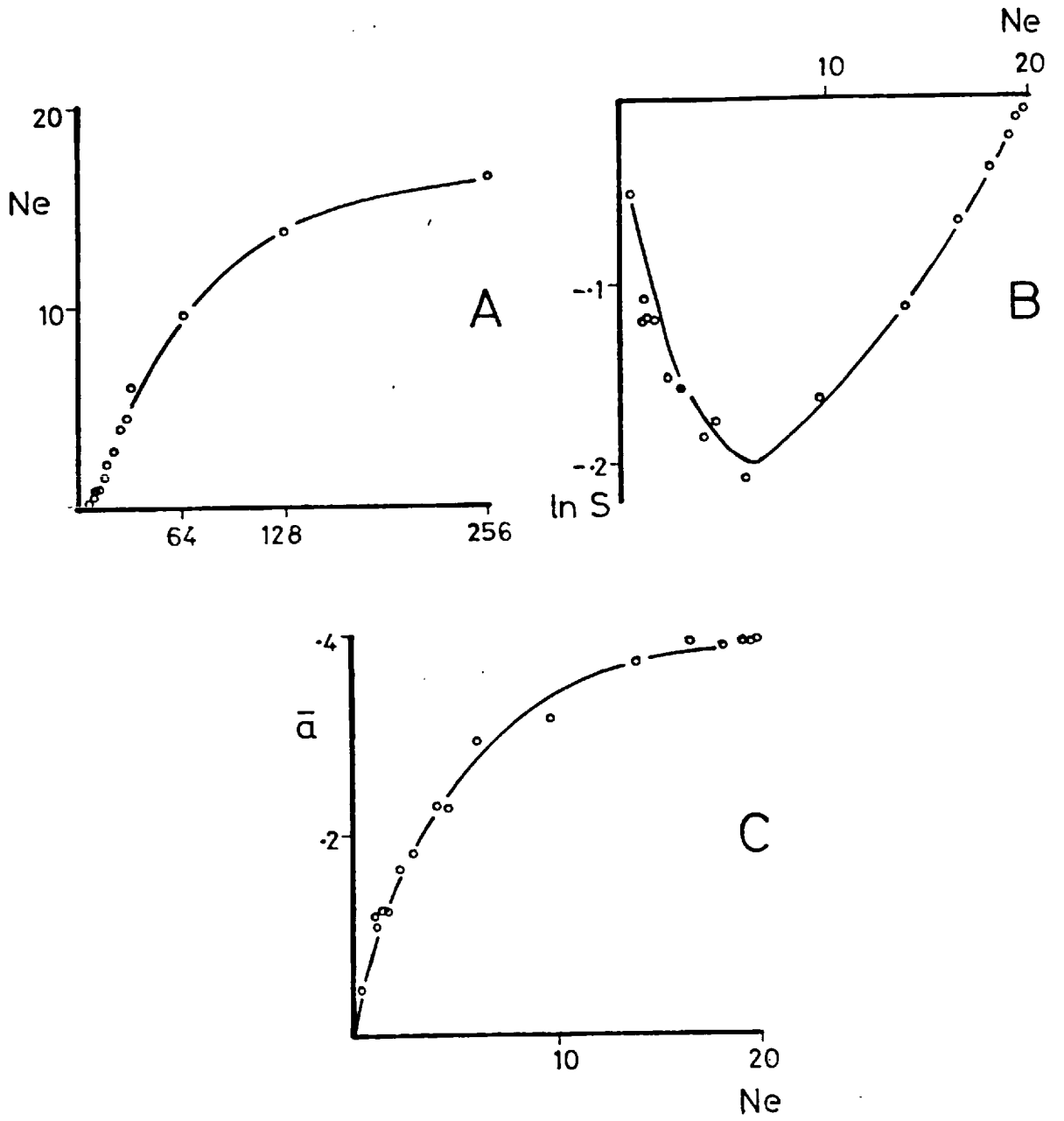
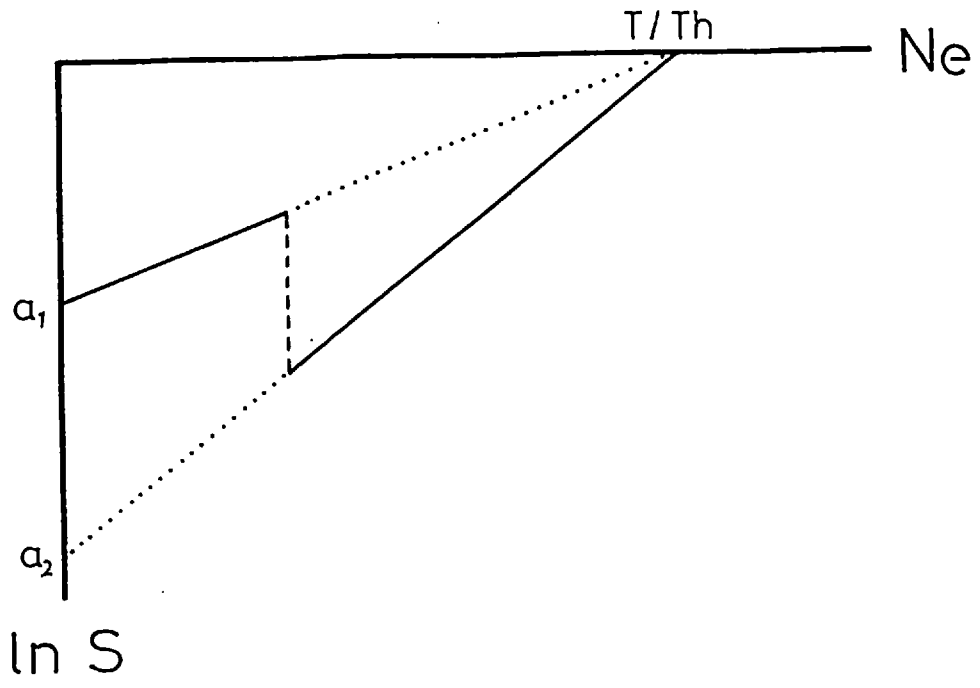
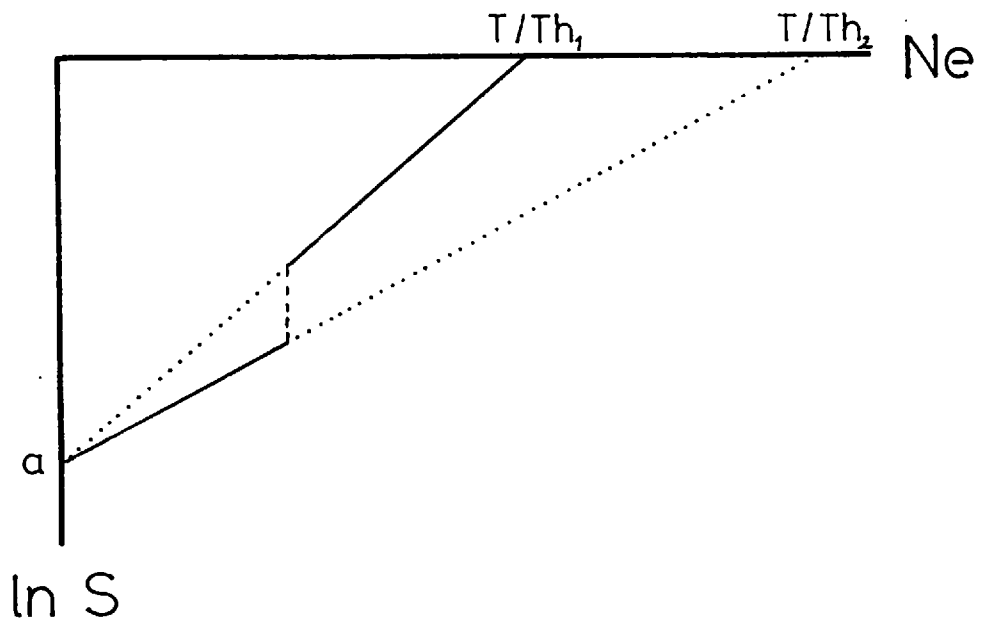


FIGURE 6.13 Hypothetical results for models S9 and S11.

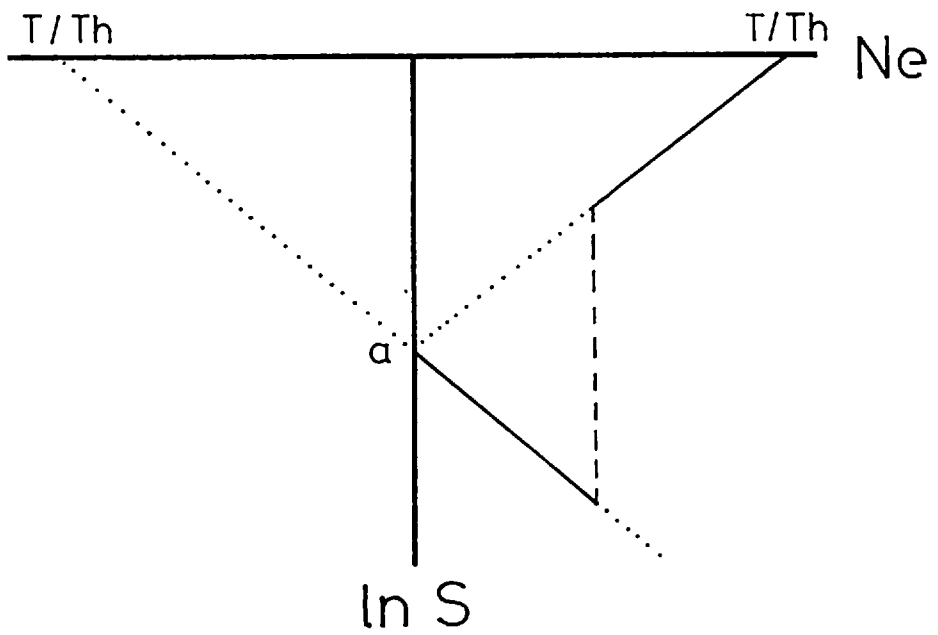
- (A) - the logarithm of the proportion of prey surviving ($\ln S$) plotted against the number of prey eaten (N_e) using hypothetical results from model S9. In this model the search efficiency (a) is defined by the initial prey density. Thus, at low densities the search efficiency is a_1 , and at high densities it is a_2 . This situation results in the figure shown, and the V shape characteristic of the sigmoid functional response cannot be obtained.
- (B) - $\ln S \times N_e$ for model S11. Here, the handling time (T_h) is defined by the prey density: at low densities the handling time is T_{h1} , and at high densities it is T_{h2} . In this figure both T_{h1} and T_{h2} are positive, and the result can be seen to preclude the possibility of a V shape arising.
- (C) - $\ln S \times N_e$ for model S11 (cf. Fig. B). In this figure T_h takes a negative value, and the $\ln S \times N_e$ relationship begins to approach the V shape. Note that if models S9 and S11 were combined, with suitable parameters, a V shape would be obtained.



A



B



C

FIGURE 6.14 Sigmoid functional response results obtained using the model S12 (see Table 6.2 ; the instantaneous value of the handling time T_h is - 40 for the first four prey, whereupon it changes to 60) to search for prey arranged at random. The figures are:

- (A) - the functional response: the number of prey eaten (N_e) plotted against the prey density (N). This is very close to the type II response.
- (B) - the logarithm of the proportion of prey surviving ($\ln S$) plotted against N_e . This shows a somewhat doubtful V shape, being basically a smoothed version of Fig. 6.13C.
- (C) - the calculated mean handling time ($\overline{T_h}$) (obtained by substituting the predation results together with an estimated search efficiency, from Fig. B, of 0.3, into the Random Predator Equation and solving for $\overline{T_h}$) plotted against N_e .

Fifty replicates were used for each prey density; data from Appendix Table A2.3; in Figs. A & B the means only of $\ln S$ and N_e are used for clarity, and these are used to calculate $\overline{T_h}$ for Fig. C; all the lines are fitted by eye.

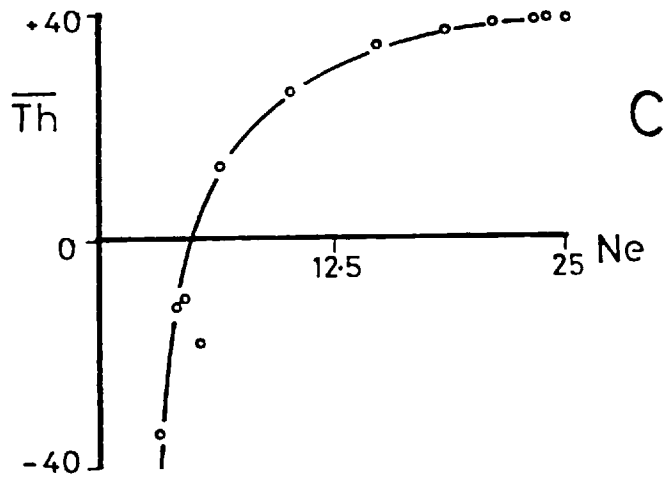
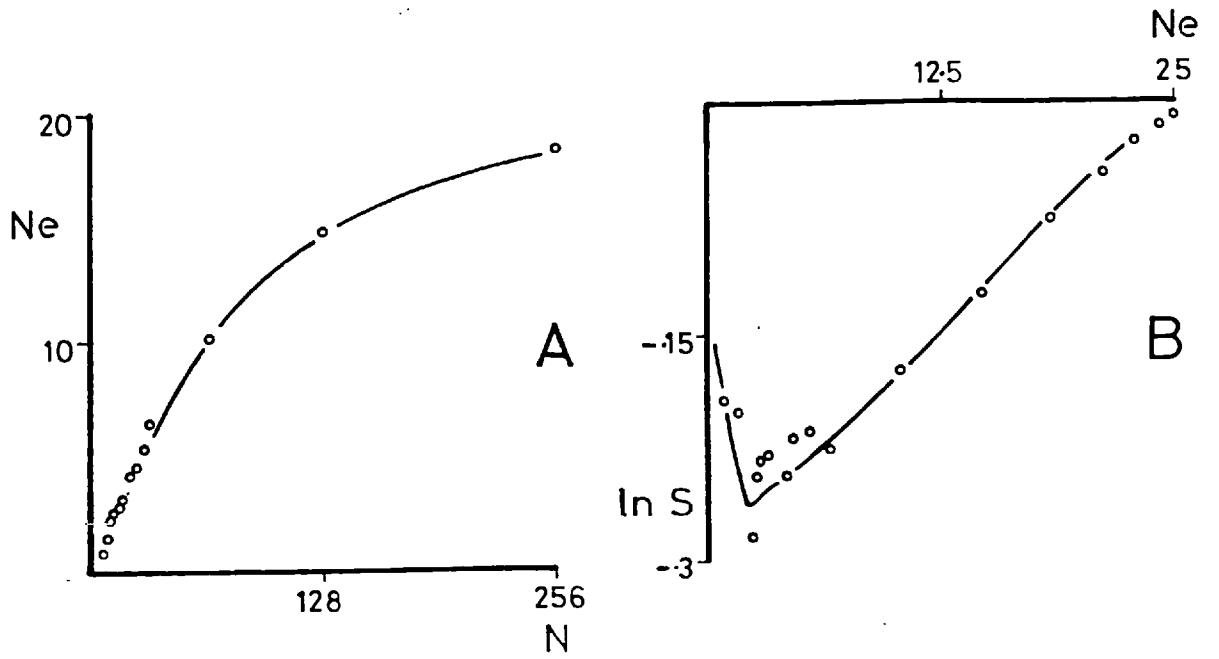


FIGURE 6.15 Dome shaped functional response results obtained using the models D1A (see Table 6.2; the mean encounter success rate, $\bar{s} = a N + b$; $a = - 0.0002$, $b = 1.0$) and D1B ($a = - 0.0004$, $b = 2.0$) to search for prey arranged at random. The figures are:

- (A) - the functional response: the number of prey eaten (N_e) plotted against the prey density (N). This shows a clear reduction in the numbers of prey eaten at the highest prey densities.
- (B) - the logarithm of the proportion of prey surviving ($\ln S$) plotted against N_e . The turn over at high values of N_e characteristic of the dome shaped functional response is apparent.
- (C) - the calculated mean search efficiency (\bar{a}) (obtained by substituting the predation results together with the known handling time into the Random Predator Equation and solving for \bar{a}) plotted against N .
- (D) - \bar{a} plotted against N_e .

The symbols used are \circ for model D1A, \times for model D1B and \bullet where both models are superimposed.

Fifty replicates were used for each prey density; data from Appendix Table A2.3;

in Figs. A & B the means only of $\ln S$ and N_e are used for clarity, and these are used to calculate the values of \bar{a} for Figs. C & D; all the lines are fitted by eye.

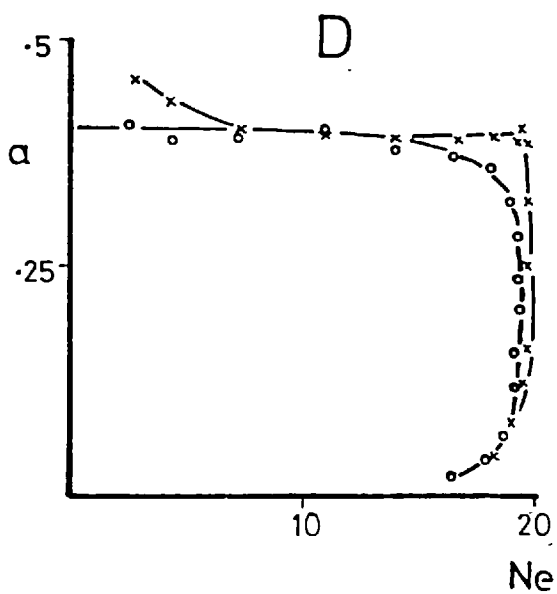
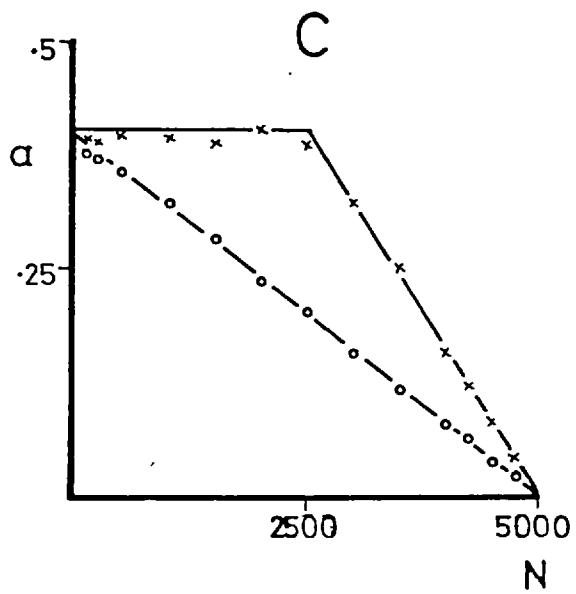
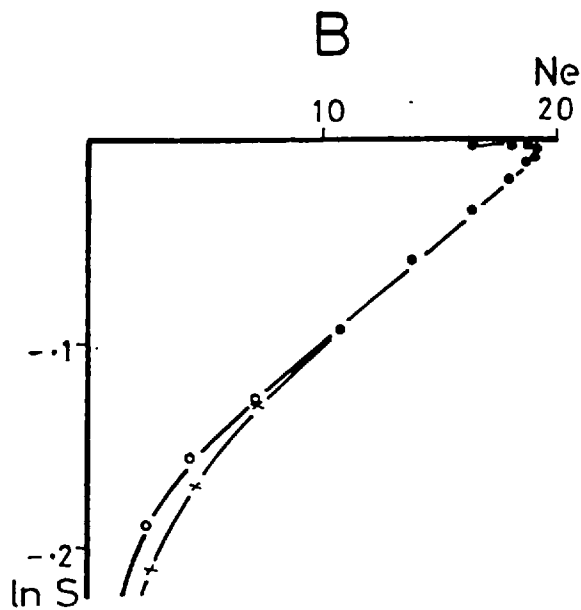
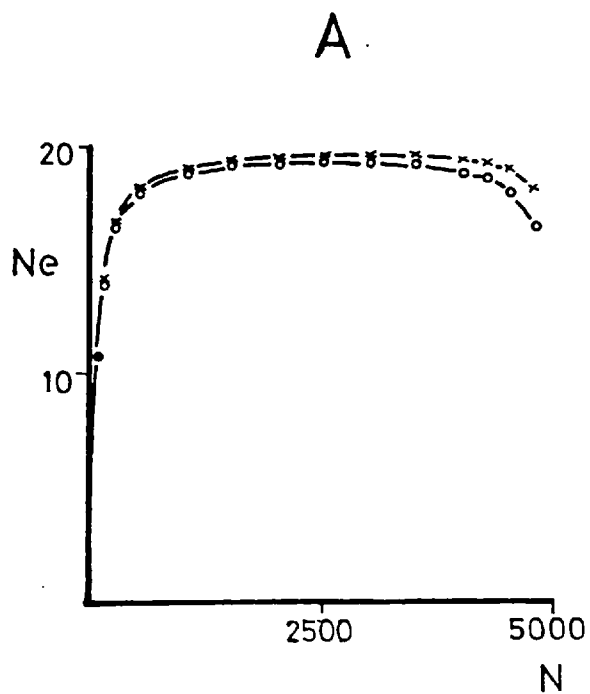
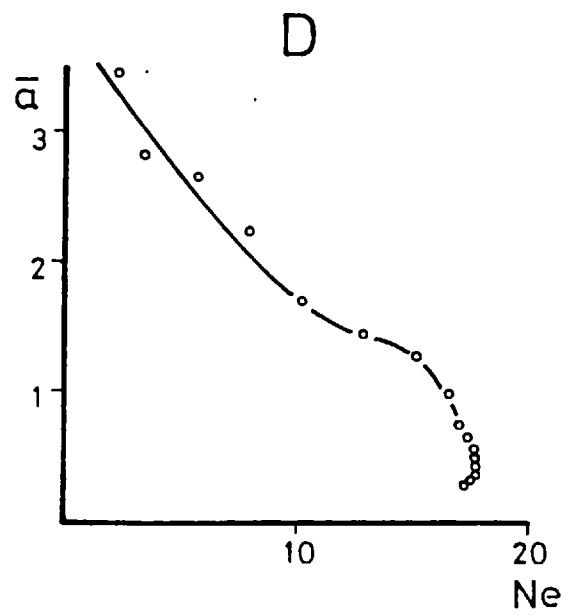
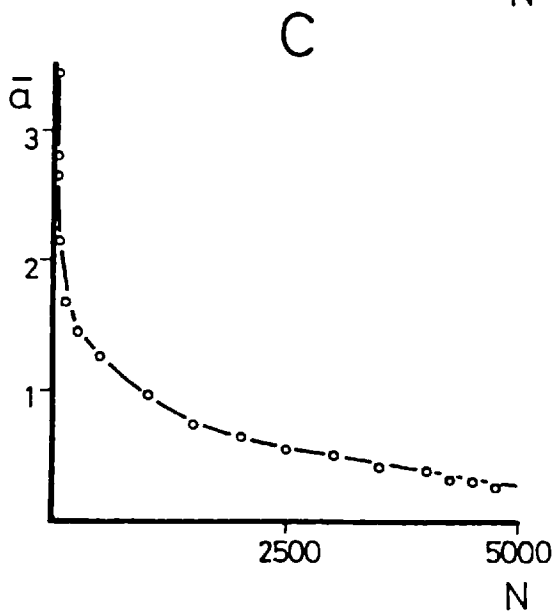
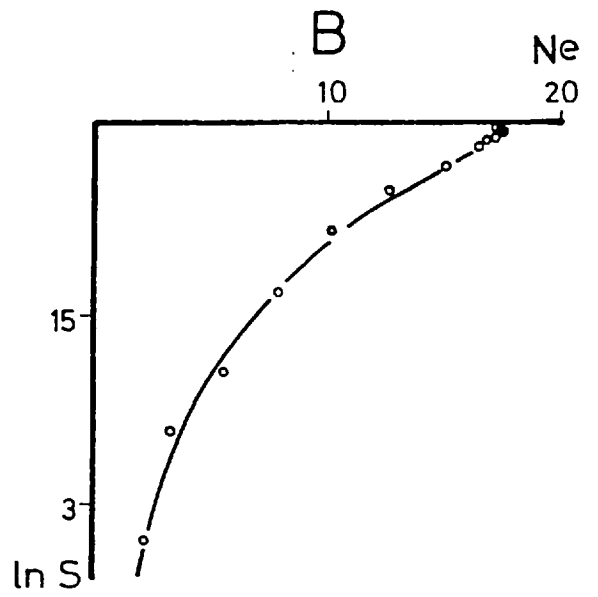
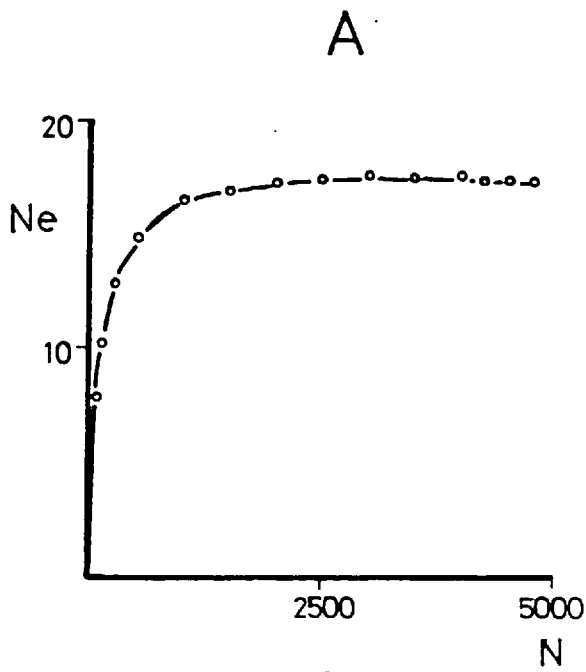


FIGURE 6.16 Dome shaped functional response results obtained using the model D2 (see Table 6.2; the mean encounter success rate, $\bar{s} = a \ln N + b$; $a = -0.11$, $b = 1.0$) to search for prey arranged at random. The figures are:

- (A) - the functional response: the number of prey eaten (N_e) plotted against the prey density (N). This shows a slight reduction in the numbers of prey eaten at the highest prey densities.
- (B) - the logarithm of the proportion of prey surviving ($\ln S$) plotted against N_e . The turn over at high values of N_e characteristic of the dome shaped functional response is just apparent.
- (C) - the calculated mean search efficiency (\bar{a}) (obtained by substituting the predation results together with the known handling time into the Random Predator Equation and solving for \bar{a}) plotted against N .
- (D) - \bar{a} plotted against N_e .

Fifty replicates were used for each prey density; data from Appendix Table A2.3; in Figs. A & B the means only of $\ln S$ and N_e are used for clarity, and these are used to calculate the values of \bar{a} for Figs. C & D; all the lines are fitted by eye.



6.6 AGGREGATIVE RESPONSES

6.6.1 Simulation and Analysis

In order to obtain aggregative responses, a 'giving up time' was used. This 'giving up time' (Hassell & May, 1974; Murdoch & Oaten, 1975) is the time which passes after the last prey is found, before the predator gives up and leaves a unit of habitat. Effectively this means that once the reward rate falls below some threshold value, the predator leaves the area. In this section a constant giving up time of 250 time units is used. In the next section (6.7), three different values of the giving up time will be used, and the results compared.

In this section all eight search strategies (IS = 1, 2, 3, 4a, 4b, 4c, 4d, and 5) used for Section 6.4 (on functional responses) will be used again. Since the use of regularly arranged prey was found to yield unrealistic results (Section 6.4), this method was not used in this section; instead a distribution using the negative binomial ($K = 2.0$) was used. It will be seen, however, that this distribution produces results not dissimilar to those obtained using the random distribution of prey. The other two prey distribution methods (negative binomial, $K = 0.05$ and clumped) are similar to those used in Section 6.4, except that, in using the negative binomial distribution, arena units of 2×2 are used, and for the clumped distribution, clumps of eight prey are distributed at random (see Section 6.2).

The results for this section are given in Appendix Table A2.4. Four methods of presenting these results have been used:

- 1) the logarithm of the number of prey eaten as a function of the logarithm of the initial prey density,
- 2) the number of prey surviving as a function of the initial prey density,
- 3) the aggregative response (note logarithmic scales): the logarithm of the time spent searching as a function of the logarithm of the initial prey density,
- 4) the overall reward rate (i.e. the quotient of the number of prey eaten and the time spent searching - N_e/T_s) as a function of the initial prey density.

Three examples of the first three methods are given as Figs. 6.17 - 19. These are for the search strategies of random search (IS = 1), aggregative walk (LLS = 10; IS = 4d), and systematic local search in response to a prey (IS = 5); the other search strategies produced similar figures and so these are omitted. Due to the large scales involved, the figures incorporating the number of prey eaten and the time spent searching have been plotted on logarithmic scales. The great similarity of the results for the prey distributed at random and using the negative binomial (K = 2.0) has led to one line being used to join these points.

The figures of the number of prey eaten and the time spent searching are similar. The quantitative differences between the various prey distributions are more marked in the figure of the time spent searching, but there are also qualitative differences between these two methods of presentation. This latter effect is clearly shown in Fig. 6.18 (IS = 4d) and Fig. 6.19 (IS = 5). Here, at low initial prey densities, more clumped prey are eaten than prey of the other distributions, but least time is spent searching for them i.e. once a clump is found, more prey will be found, but with these distributions there is a greater chance of the predator giving up.

The figures of the number of prey surviving are, at least at high initial prey densities, more informative than the figures of the number of prey eaten and the time spent searching. When the reward rates were considered (Appendix Table A2.4 - part 9), it was found possible to pool the results from several search strategies, as is shown in Fig. 6.20. These figures are perhaps the most informative method of presentation used.

On the basis of these results, a descriptive model of the number of prey eaten suggests itself. If the figures for the number of prey surviving as a function of initial prey density are examined (Figs. 6.17 - 19 B), it can be seen that the number surviving rises to a constant value in a manner similar to the type II functional response. Accordingly a model based on a type II functional response seems suitable. Thus, an equation of the form of the Random Predator Equation,

$$N_s = N(1 - \exp(-c(t - b N_s))), \quad . . . 6.1$$

can be used to describe this situation, where N_s is the number of prey surviving, N is the initial prey density and c , t , and b are constants analagous to the search efficiency, total time and handling time of the Random Predator Equation. Hence, the number of prey eaten can be described:

$$\begin{aligned} N_e &= N - N_s = N \exp(-c(t - b N_s)) \\ &= N \exp(-c(t - b(N - N_e))) \end{aligned} \quad . . . 6.2$$

where N_e is the number of prey eaten. Alternatively the Disc Equation could be the basis of a model:

$$\begin{aligned} N_s &= c b t / (1 - c b N_s) \\ N_e &= N - c b t / (1 - c b (N - N_e)). \end{aligned}$$

The model based upon the Random Predator Equation (Eqn. 6.1) will be used in this work due to the readiness with which the parameters can be abstracted using programme BESTFIT (Appendix Section A1.3).

These three parameters can be interpreted as follows: t/b defines the maximum value of N_s (i.e. it is the ratio which is important, one of these constants can be arbitrarily defined - for this work t), while c defines the curvature, or the rate at which this maximum is arrived at, and is a measure of the survivability of the prey or inefficiency of the predator. Therefore, at high initial prey densities, the ratio t/b defines the number of survivors, while at low initial prey densities this is largely defined by the parameter c .

For each of the aggregative responses, the parameters b and c were abstracted using programme BESTFIT (Appendix Section A1.3), and these are tabulated in Table 6.3. Using these abstracted parameters, the number of prey surviving is plotted in the figures (Figs. 6.17 - 19 B), and it can be seen that a good fit is obtained, except at low densities of prey arranged using the negative binomial distribution ($K = 0.05$) where the parameter c is underestimated. This should, therefore, be borne in mind when the abstracted parameters are compared.

FIGURE 6.17 Aggregative response results obtained using the strategy of random search ($IS = 1$) to search for

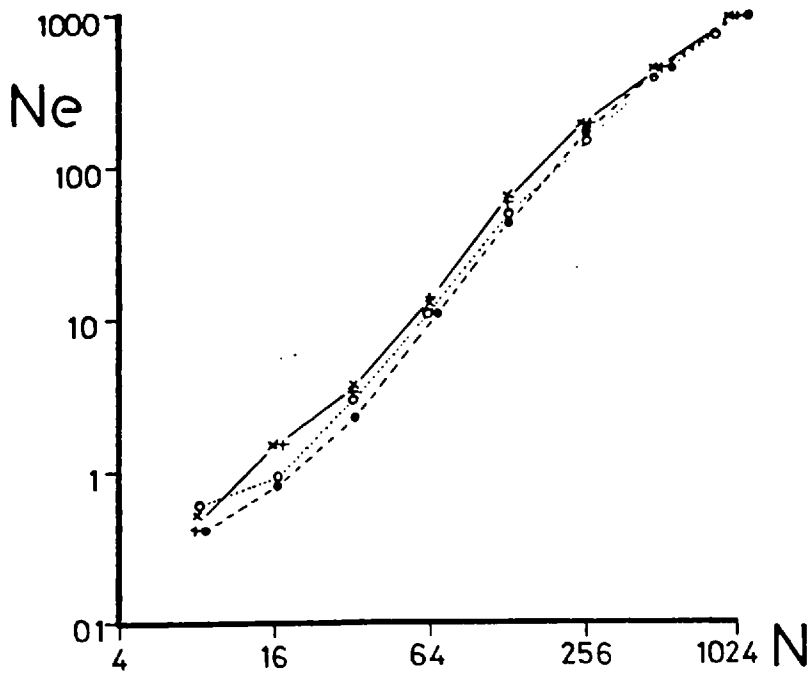
- 1) prey arranged at random (symbol \times),
- 2) prey arranged using the negative binomial distribution with $K = 2.0$ (symbol $+$); this and the last distribution are pooled and the points joined up with a single solid line,
- 3) prey arranged using the negative binomial distribution with $K = 0.05$ (symbol \circ ; dotted line),
- 4) prey arranged in clumps of eight distributed at random (symbol \bullet ; broken line).

(A) - the number eaten (N_e) plotted against the initial prey density (N). Logarithmic scales are used for clarity. The points are connected to show their relationships.

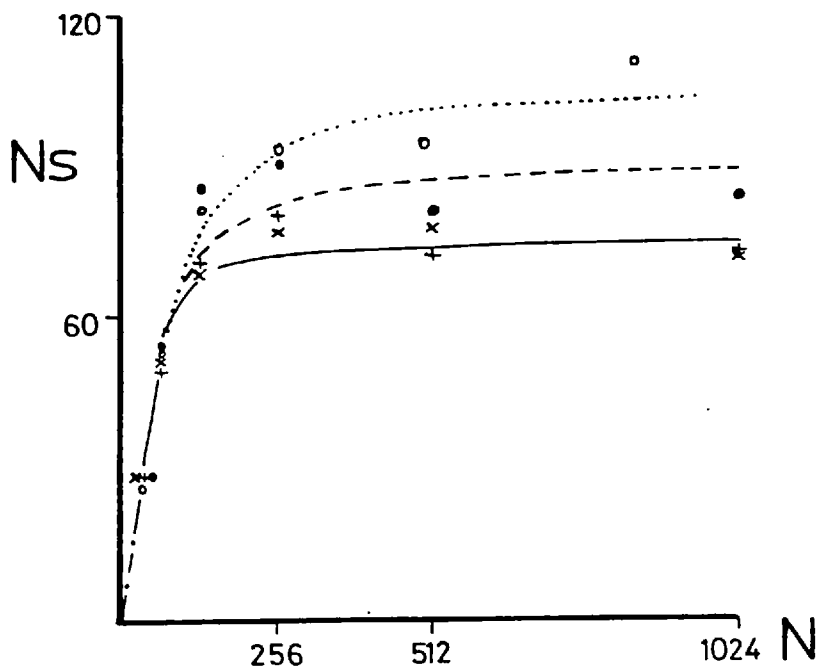
(B) - the number of prey surviving (N_s) plotted against N . Linear scales are used. The fitted lines use the parameters given in Table 6.3 in Eqn. 6.1.

(C) - the aggregative response: the time spent searching (T_s) plotted against N . As for Fig. A, logarithmic scales are used for clarity. The points are connected to show their relationships.

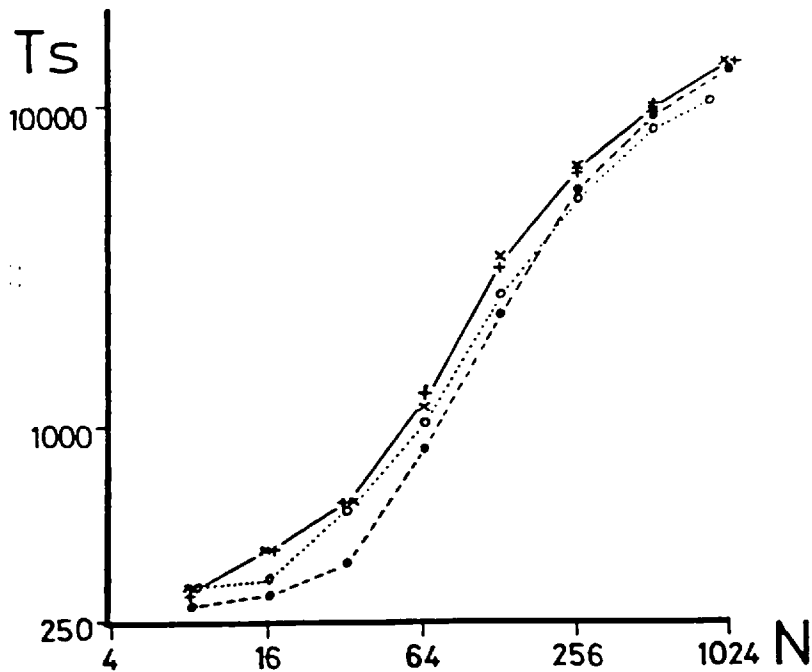
Fifty replicates were used; the means only are used in the figures for clarity; data from Appendix Table A2.4.



A



B



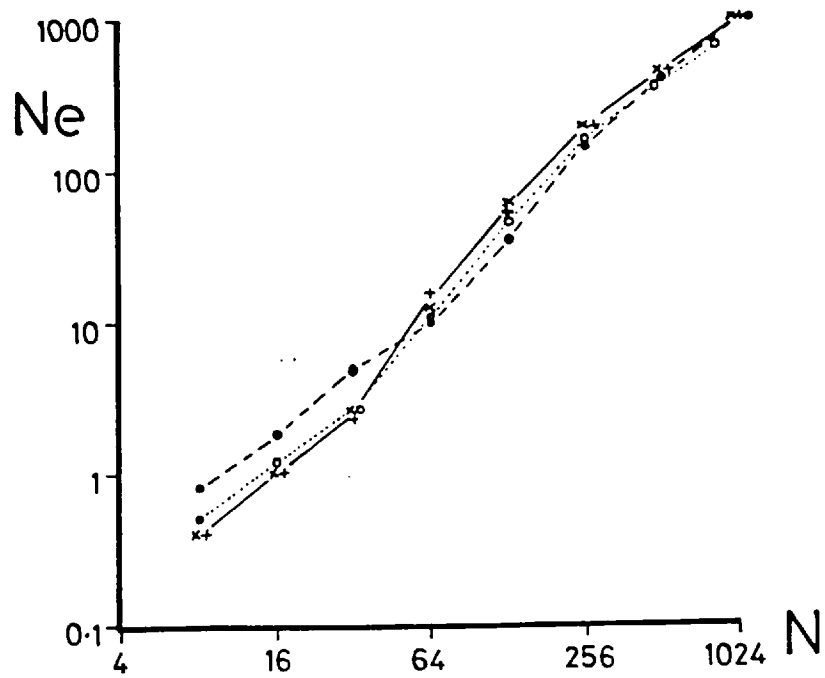
C

FIGURE 6.18 Aggregative response results obtained using the aggregative walk with the normal step length of ten (IS = 4d) to search for:

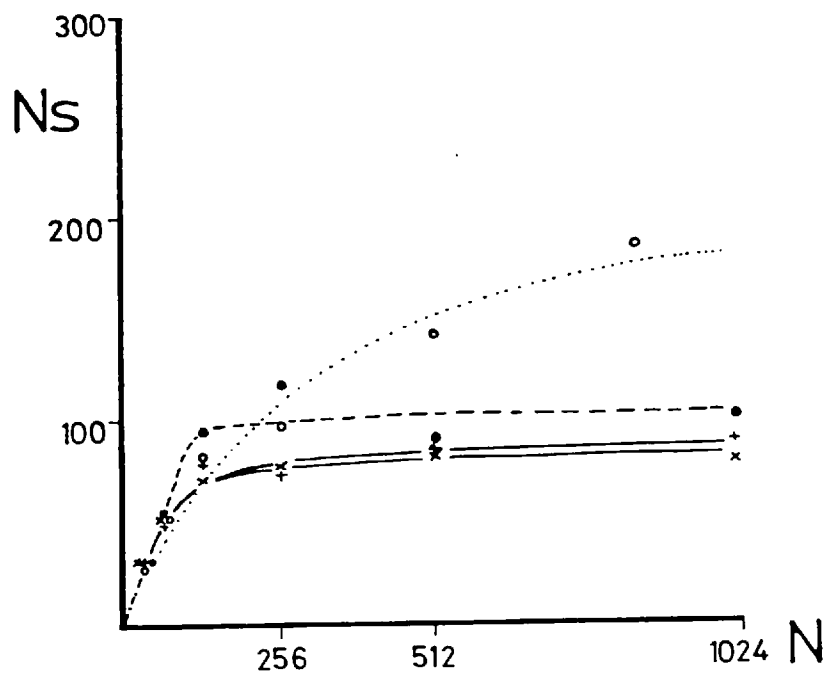
- 1) prey arranged at random (symbol \times),
- 2) prey arranged using the negative binomial distribution with $K = 2.0$ (symbol $+$); this and the last distribution are pooled and the points joined with a single line,
- 3) prey arranged using the negative binomial distribution with $K = 0.05$ (symbol \circ ; dotted line),
- 4) prey arranged in clumps of eight distributed at random (symbol \bullet ; broken line).

- (A) - the number eaten (N_e) plotted against the initial prey density (N). Logarithmic scales are used for clarity. The points are connected to show their relationships.
- (B) - the number of prey surviving (N_s) plotted against N . Linear scales are used. The fitted lines use the parameters given in Table 6.3 in Eqn. 6.1.
- (C) - the aggregative response: the time spent searching (T_s) plotted against N . As for Fig. A, logarithmic scales are used for clarity and the points are connected to show their relationships.

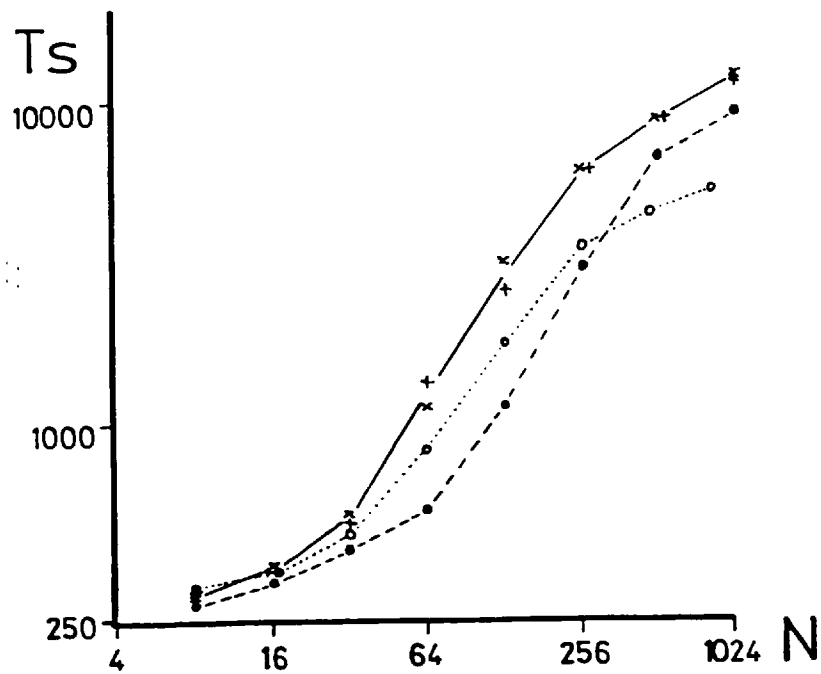
Fifty replicates were used; the means only are used in the figures for clarity; data from Appendix Table A2.4.



A



B



C

FIGURE 6.19 Aggregative response results obtained using the search strategy incorporating systematic local search in response to finding a prey ($IS = 5$) to search for:

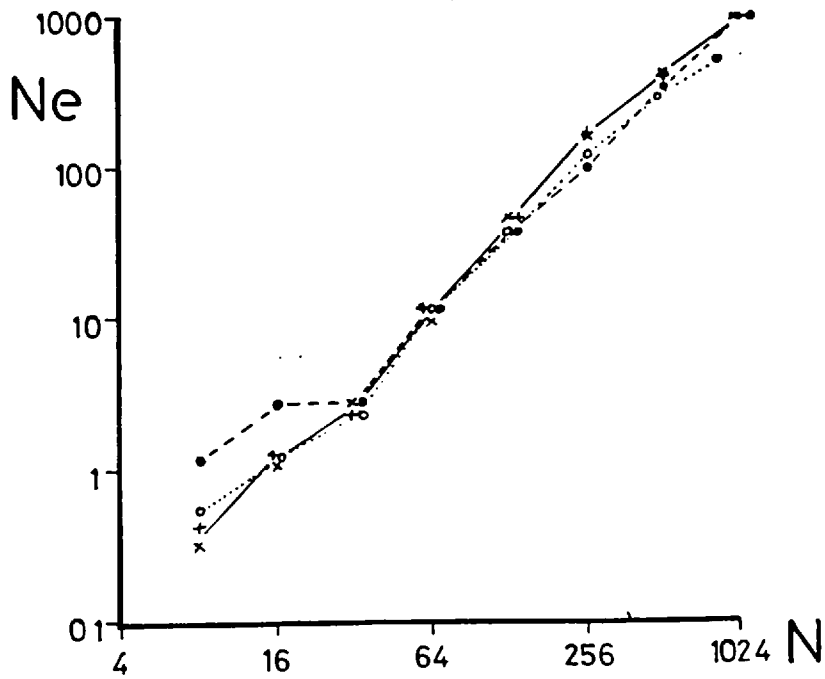
- 1) prey arranged at random (symbol \times),
- 2) prey arranged using the negative binomial distribution with $K = 2.0$ (symbol $+$); this and the last distribution are pooled and the points joined with a single, solid line,
- 3) prey arranged using the negative binomial distribution with $K = 0.05$ (symbol \circ ; dotted line),
- 4) prey arranged in clumps of eight distributed at random (symbol \bullet ; broken line).

(A) - the number eaten (N_e) plotted against the initial prey density (N). Logarithmic scales are used for clarity. The points are connected to show their relationships.

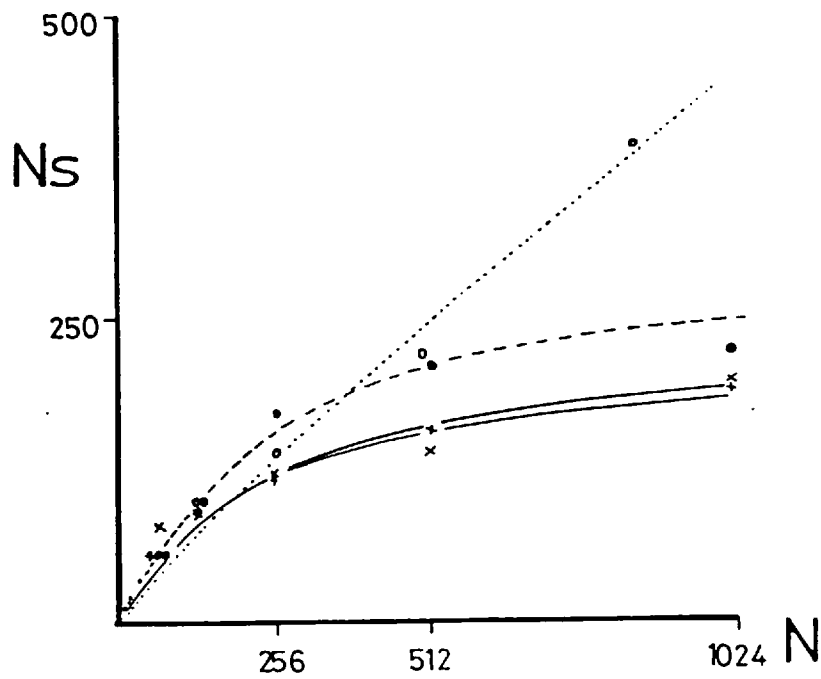
(B) - the number of prey surviving (N_s) plotted against N . Linear scales are used. The fitted lines use the parameters given in Table 6.3 in Eqn. 6.1.

(C) - the aggregative response: the time spent searching (T_s) plotted against N . As for Fig. A, logarithmic scales are used for clarity and the points are connected to show their relationships.

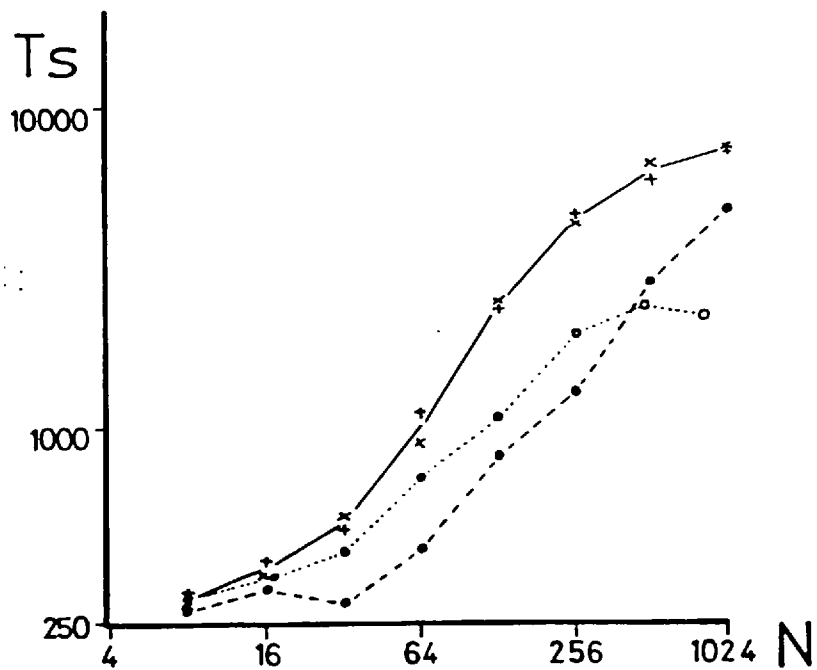
Fifty replicates were used; the means only are used in the figures for clarity; data from Appendix Table A2.4.



A



B

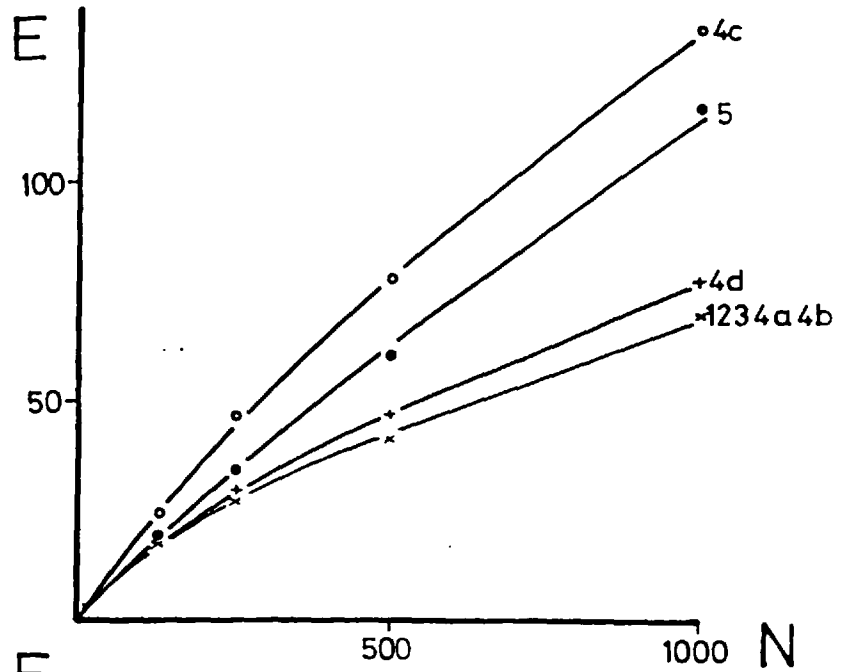


C

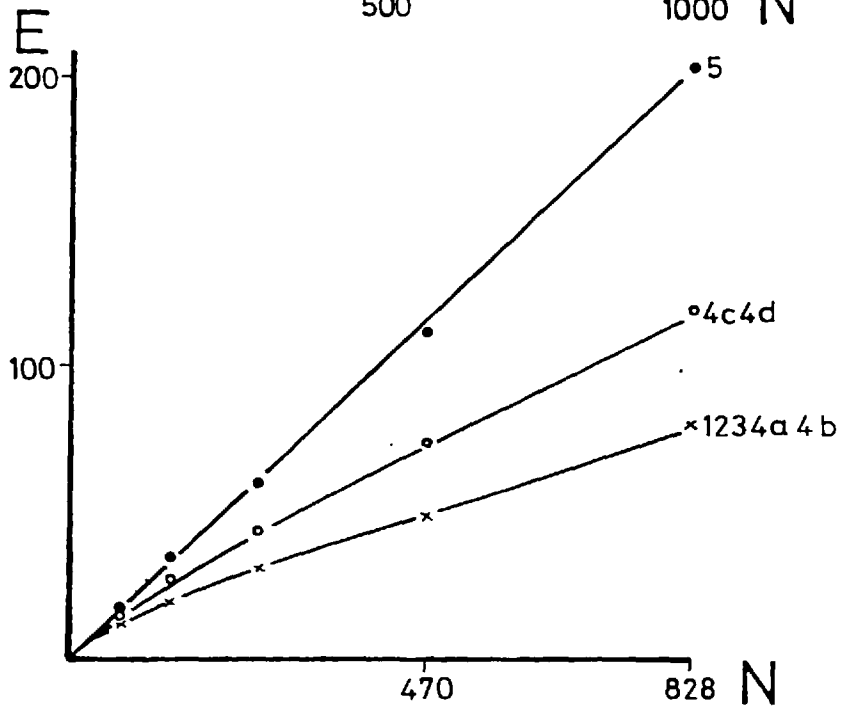
FIGURE 6.20 Aggregative response results obtained using all the search strategies (IS = 1, 2, 3, 4a, 4b, 4c, 4d, 5 as outlined at the end of Section 6.2). A measure of the overall efficiency ($E = Ne/Ts$) is plotted against the initial prey density (N). The figures are:

- (A) - pooled results of the prey arranged at random and using the negative binomial distribution with $K = 2.0$.
- (B) - prey arranged using the negative binomial distribution with $K = 0.05$.
- (C) - prey arranged in clumps of eight distributed at random.

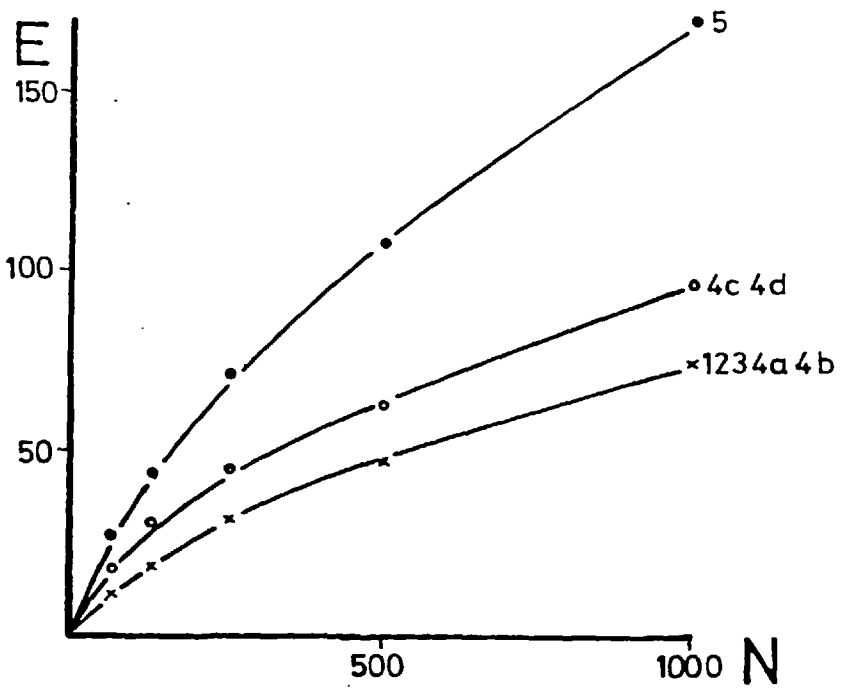
Data from Appendix Table A2.4 - part 9; where the values of E are considered sufficiently similar, these are pooled from various search strategies as shown.



A



B



C

SEARCH STRATEGY	PREY DISTRIBUTION	ABSTRACTED PARAMETERS		F VALUE	RANKINGS			
		c	b		1	2	3	4
1	Random	.007975	13.156	458.6	1	4	1	8
	K = 2.0	.007975	13.138	270.8	1	3	1	8
	K = .05	.003655	9.281	740.8	4	1	1	8
	Clumps	.004827	11.021	189.9	3	2	4	8
2	Random	.001659	1.621	1967.5	4	3	7	1
	K = 2.0	.001729	1.685	1809.6	3	4	7	1
	K = .05	.002056	0.084	52665.6	2	1	2	1
	Clumps	.002587	1.156	5931.0	1	2	7	1
3	Random	.001852	5.243	473.5	2	3	6	3
	K = 2.0	.001804	5.414	470.3	3	4	6	3
	K = .05	.001037	0.568	439.5	4	1	5	2
	Clumps	.003511	4.219	1844.4	1	2	6	3
4a	Random	.003626	10.769	1524.3	2	4	3	6
	K = 2.0	.003325	9.999	837.0	3	3	5	4
	K = .05	.000863	1.708	259.8	4	1	7	4
	Clumps	.008234	7.476	194.8	1	2	3	4
4b	Random	.002911	9.492	623.0	3	3	5	4
	K = 2.0	.003871	10.190	717.1	2	4	4	5
	K = .05	.001433	3.780	181.0	4	1	3	6
	Clumps	.018910	8.345	258.5	1	2	2	6
4c	Random	.002997	9.630	1452.4	3	3	4	5
	K = 2.0	.004375	10.316	867.5	1	4	2	6
	K = .05	.000984	2,347	261.5	4	1	6	5
	Clumps	.004021	7.545	944.9	2	2	5	5
4d	Random	.004715	11.977	1562.1	2	4	2	7
	K = 2.0	.004073	11.244	316.3	3	3	3	7
	K = .05	.001214	4.533	221.6	4	1	4	7
	Clumps	.024312	9.715	137.4	1	2	1	7
5	Random	.001326	4.360	138.9	3	3	8	2
	K = 2.0	.001522	4.840	429.8	2	4	8	2
	K = .05	.000845	0.715	418.3	4	1	8	3
	Clumps	.001982	3.466	326.1	1	2	8	2

TABLE 6.3 The parameters c and b of Eqn. 6.1 fitted to the aggregative responses of Section 6.6. The search strategies are as outlined at the end of Section 6.2. The F values are all highly significant (df = 1,7 or 1,8, $P < 0.001$). The rankings are (1) the parameter c for each search strategy, (2) $1/b$ for each search strategy, (3) c for each prey distribution and (4) $1/b$ for each prey distribution - i.e. the lower the ranking, the more prey are eaten.

6.6.2 Discussion

The estimated parameters of Eqn. 6.1 are given in Table 6.3, where they have been ranked in order of prey survivability. Hence it can be seen that:

- 1) In all cases, at high initial prey densities, most prey survive from the distribution using the negative binomial with $K = 0.05$.
- 2) In most cases, at low initial prey densities, more prey survive from the clumped distribution than from the others. (Note: the parameter c for the prey arrangements using the negative binomial ($K = 0.05$) is underestimated, and prey survivability for these distributions is probably greater than indicated.)
- 3) From the predator's viewpoint, for a high initial prey density, the strategy of completely random search leads to more prey being found of every distribution. The second most successful search strategy is, in most cases, the aggregative walk with a step length of ten ($IS = 4d$), while the other aggregative walk ($LLS = 3$; $IS = 4c$) and the forward directed random walk with a step length of ten ($IS = 4b$) are the next most successful.
- 4) When searching for prey with a low initial density, the most successful strategy is the systematic local search in response to finding a prey ($IS = 5$), while completely random search ($IS = 1$) and the aggregated walk ($LLS = 10$; $IS = 4d$) are the least successful.

Thus, from the viewpoint of the prey, on average, the largest number will survive a single aggregative response if they are arranged in as aggregated a manner as possible. One interesting feature of all the figures is the crossover of the responses to aggregated ($K = 0.05$) and clumped prey. Thus, at the highest prey densities more of the latter are eaten than of the former. This is because at high prey densities the clumped prey are not as highly aggregated as the prey distributed using the negative binomial ($K = 0.05$). To demonstrate this point, the frequencies of prey density classes for the highest density (828) of the aggregated prey ($K = 0.05$) are shown as Fig. 6.21. It can be seen that

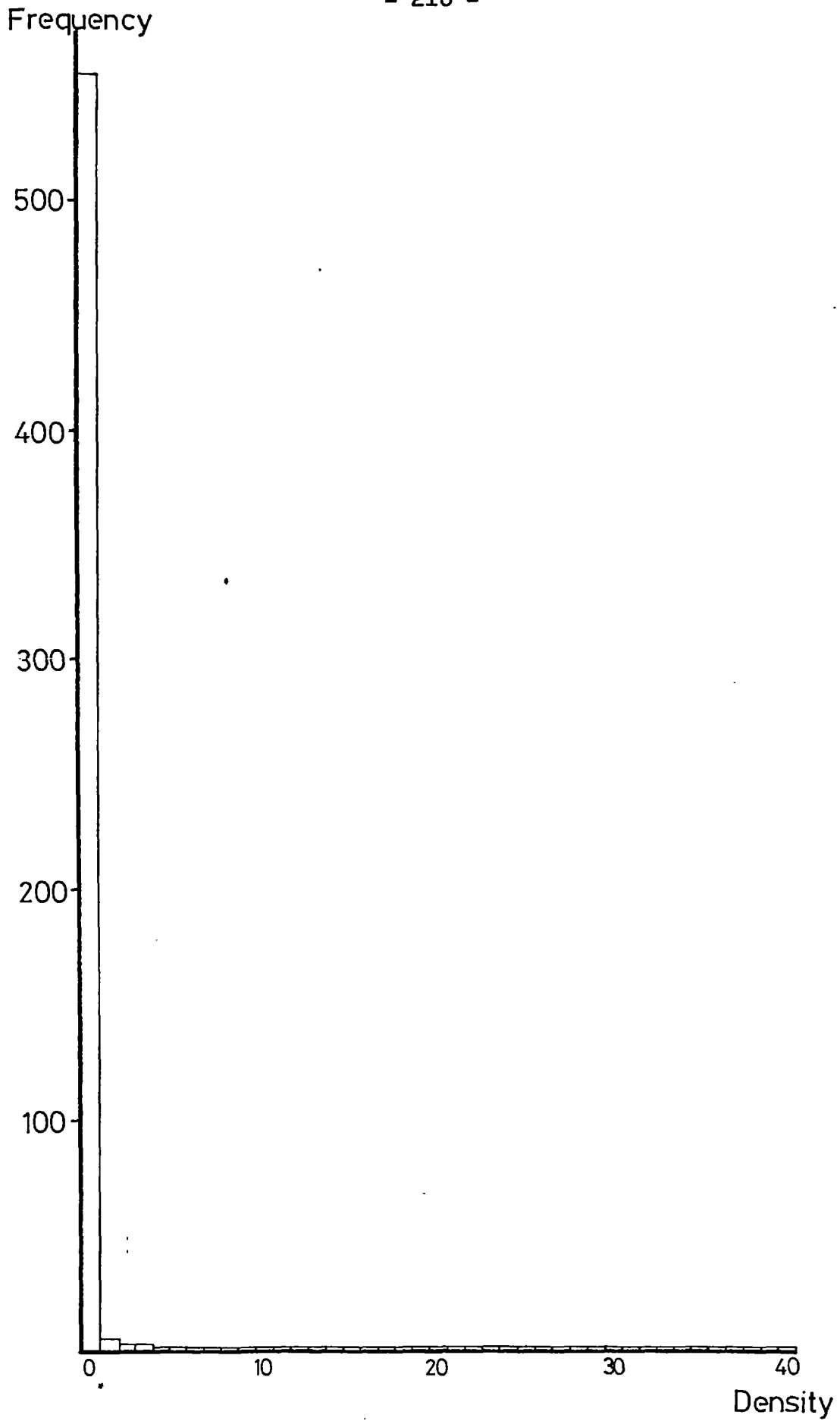


FIGURE 6.21 Frequency distribution of aggregated prey ($K = 0.05$) at a total density of 828 amongst 625 units.

some very dense patches are present, and the distribution is effectively more aggregated than the randomly distributed clumps of eight prey. Therefore, in an environment subdivided into units in which a predator uses a giving up time, the best distribution strategy for the prey is to be as highly aggregated as possible within each unit.

From the predator's viewpoint, however, the number of prey eaten is likely to be less important than the rate at which the prey are found. A gross estimate of this 'efficiency' can be obtained as the quotient of the number of prey eaten and the time spent searching. Accordingly the overall predation rates are given in Appendix Table A2.4 - part 9. From these Fig. 6.20 was constructed and some rather different results can be seen:

- 1) ' With the exception of strategies 4c, 4d, and 5, there is not a great deal of difference between the various search strategies.
- 2) Strategy 4c is clearly the most efficient when searching for prey arranged at random ($ID = 2$) and in a slightly aggregated manner ($ID = 3, K = 2.0$). Strategy 5 is slightly less efficient, while 4d is only a little more efficient than the remaining strategies.
- 3) In searching for the highly aggregated ($ID = 3, K = 0.05$) and clumped ($ID = 4$) prey, there is not much difference between strategies 4c and 4d. Strategy 5 is clearly the most efficient for finding prey of these distributions - in the case of the clumped prey this is also evident at low initial prey densities.

Comparing the effects of the different prey distributions, the first two ($ID = 2$ and $ID = 3, K = 2.0$) clearly lead to similar results. The efficiency with which the remaining two distributions are found differs depending upon the initial prey density. Thus, at low initial prey densities, clumped prey are more rapidly found, while at high initial prey densities, aggregated ($K = 0.05$) prey are found with greater efficiency. Thus the crossover of the responses to these two prey arrangements is confirmed when the efficiencies are examined.

Therefore, within one unit of habitat, the more aggregated the prey are, the more will survive, but the greater will be the search efficiency of the predator. The interaction of these two phenomenon will largely determine the most suitable distribution of the prey.

Clearly the most successful search strategies are not the most efficient; this latter assessment is probably of more relevance. Thus, considering the relative efficiencies of the search strategies, the three which lead to intensive local search when a prey is found are the most suitable for a predator trying to maximize energy input.

6.7 EFFECTS OF THE GIVING UP TIME

6.7.1 Simulation and Analysis

In this section the effects of using different values of the giving up time are examined. Aggregative responses were generated using three values of the giving up time (50, 100, 200), with two search strategies (random search, IS = 1; aggregative walk, LLS = 10, IS = 4d) and two prey distributions (random, ID = 2; clumped, ID = 5). The results of 50 replicates for a range of prey densities are given in Appendix Table A2.5. It can be seen that, apart from the initial giving up time, the time spent searching shows a close correlation with the number of prey eaten; hence, these results are shown as the number of prey eaten and the number surviving as functions of the initial prey density.

As was noted in the last section, the number of prey surviving can be described by a type II functional response equation (e.g. Eqn. 6.1). The parameters obtained by using programme BESTFIT (Appendix Section A1.3) to fit Eqn. 6.1 to the data are given in Table 6.4. It was pointed out in the last section that the rate of prey capture or overall efficiency is of more relevance than the number of prey captured, and so the overall efficiencies have been calculated (Appendix Table A2.5) and the figures of the efficiency as a function of the initial prey density are given (Fig. 6.25).

FIGURE 6.22 Aggregative response results obtained using three different giving up times:

- 1) 50 time units (symbol \times ; solid line),
- 2) 100 time units (symbol \circ ; broken line),
- 3) 200 time units (symbol \bullet ; dotted line).

The number of prey eaten (N_e) is shown as a function of the initial prey density (N), when using:

- (A) - random search ($IS = 1$) to search for prey arranged at random ($ID = 2$),
- (B) - random search ($IS = 1$) to search for clumped prey ($ID = 4$),
- (C) - the aggregative walk ($LLS = 10$; $IS = 4d$) to search for prey arranged at random ($ID = 2$),
- (D) - the aggregative walk ($LLS = 10$; $IS = 4d$) to search for clumped prey ($ID = 4$).

Fifty replicates were used for each prey density; the means only are used in the figures for clarity; data from Appendix Table A2.5; fitted lines use the parameters of Table 6.4 in Eqn. 6.2.

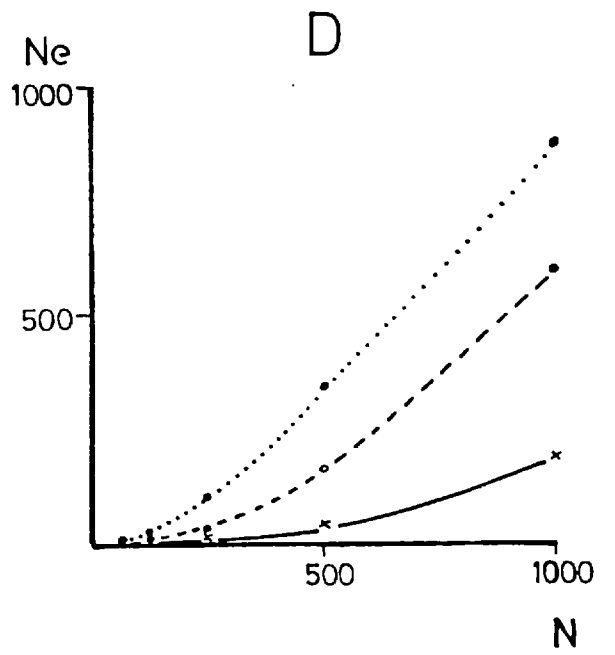
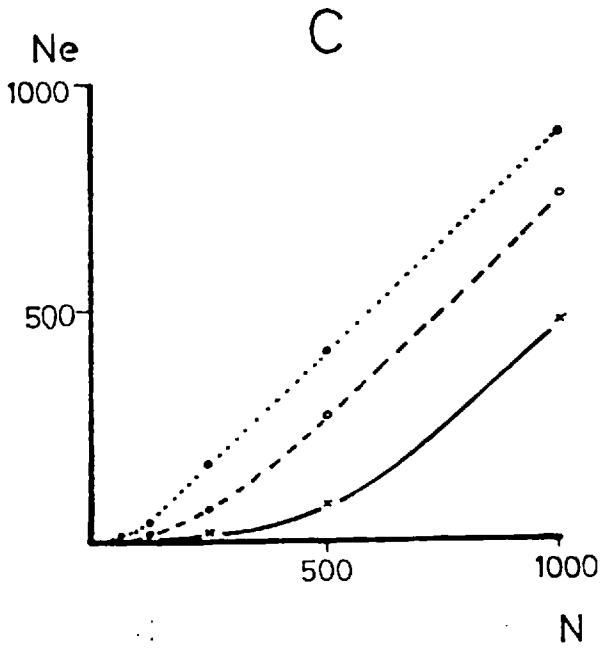
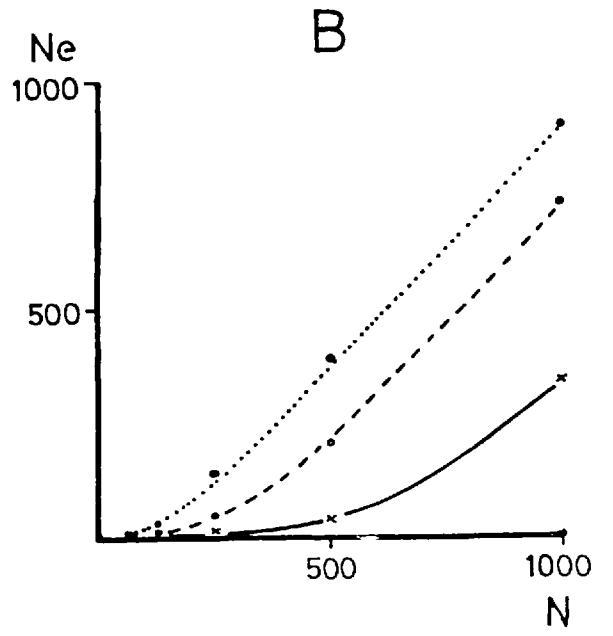
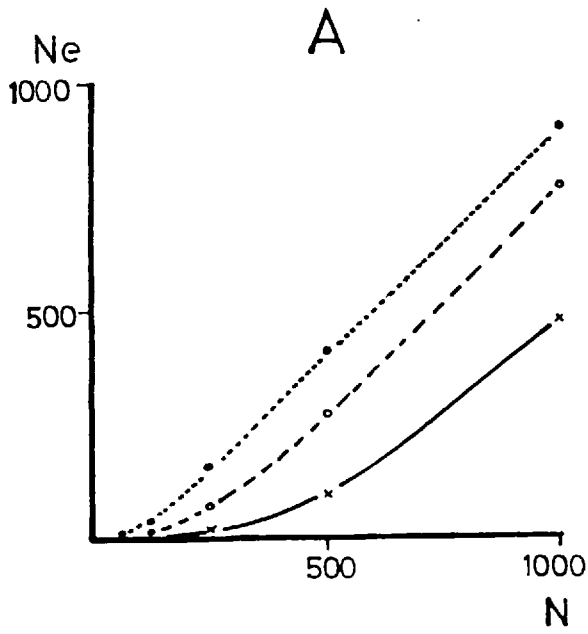


FIGURE 6.23 Aggregative response results obtained using three different giving up times:

- 1) 50 time units (symbol \times ; solid line),
- 2) 100 time units (symbol \circ ; broken line),
- 3) 200 time units (symbol \bullet ; dotted line).

The number of prey surviving (N_s) is shown as a function of the initial prey density (N), when using:

- (A) - random search ($IS = 1$) to search for prey arranged at random ($ID = 2$),
- (B) - random search ($IS = 1$) to search for clumped prey ($ID = 4$),
- (C) - the aggregative walk ($LLS = 10$; $IS = 4d$) to search for prey arranged at random ($ID = 2$),
- (D) - the aggregative walk ($LLS = 10$; $IS = 4d$) to search for clumped prey ($ID = 4$).

Fifty replicates were used for each prey density; the means only are used in the figures for clarity; data from Appendix Table A2.5; fitted lines use the parameters of Table 6.4 in Eqn. 6.2.

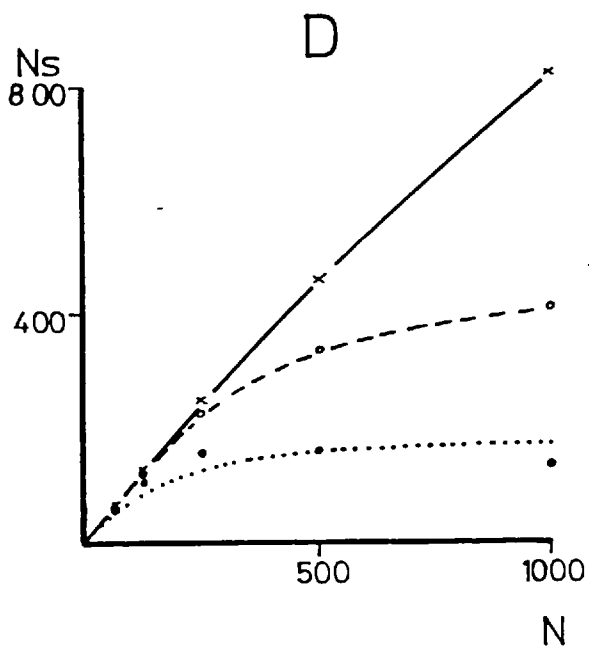
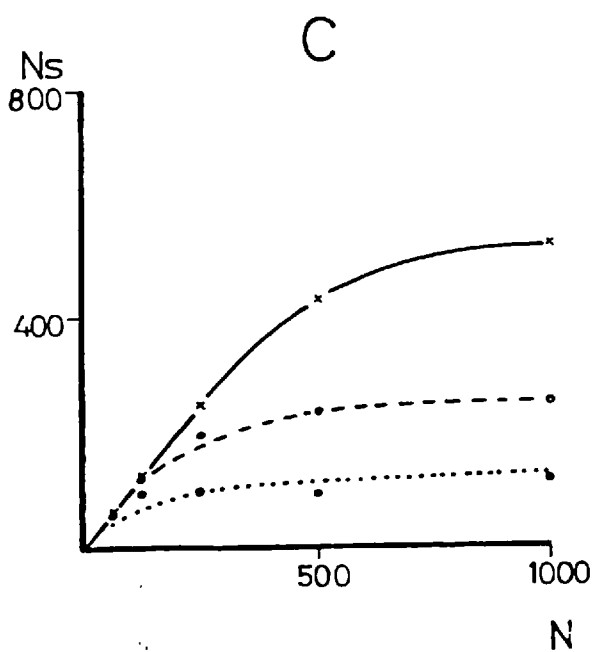
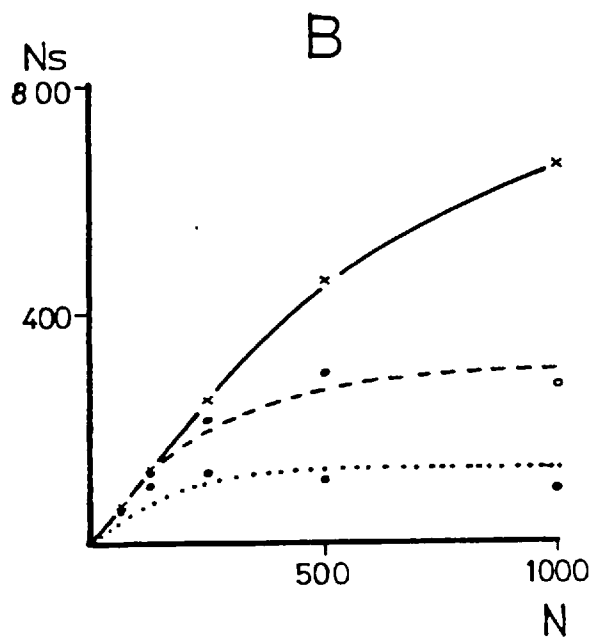
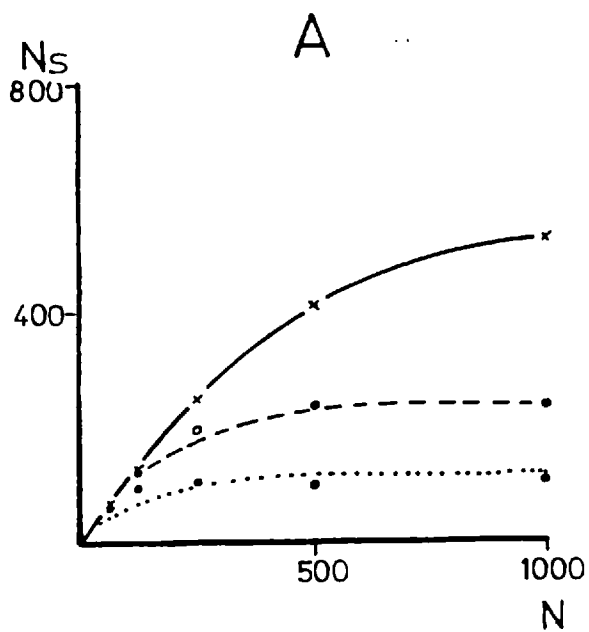


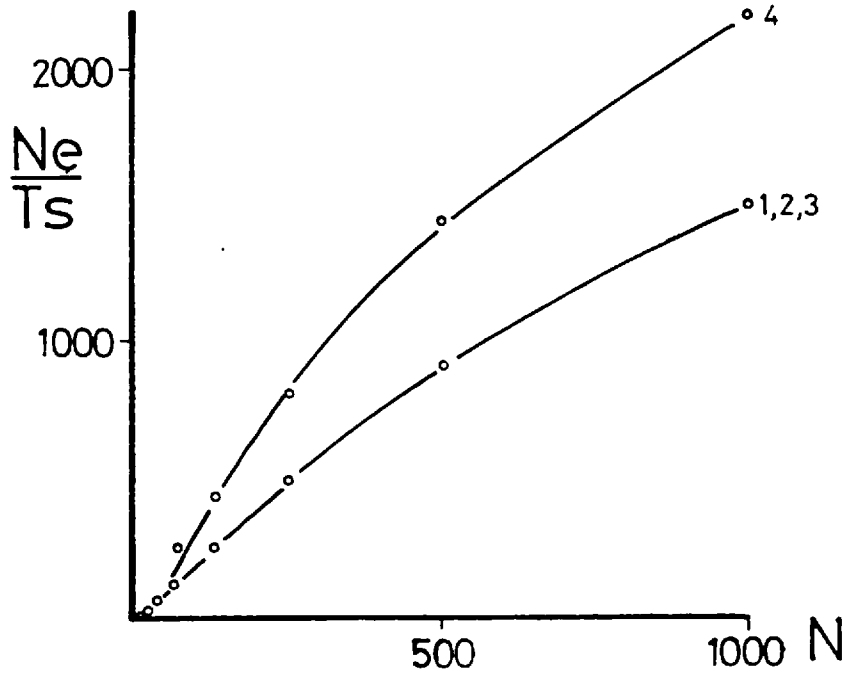
FIGURE 6.24 Aggregative response efficiency results obtained using the giving up times of:

- (A) - 50 time units,
- (B) - 100 time unit,
- (C) - 200 time units.

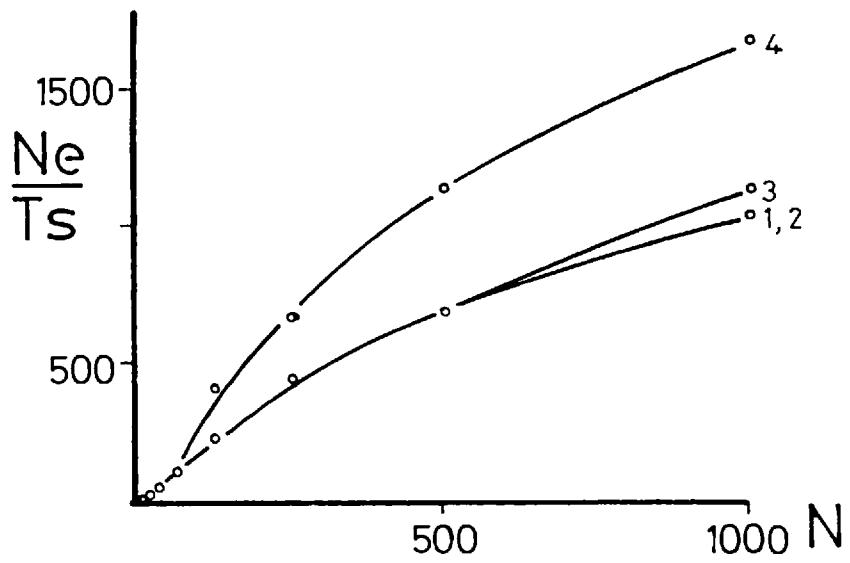
The figures show the measure of overall search efficiency ($E = N_e/T_s$; N_e = number of prey eaten, T_s = time spent searching) plotted against the initial prey density (N). The various combinations of search strategies and prey distributions are:

- 1) random search ($IS = 1$) and prey distributed at random ($ID = 2$),
- 2) random search ($IS = 1$) and clumped prey ($ID = 4$),
- 3) aggregative walk ($LLS = 10$; $IS = 4d$) and prey distributed at random ($ID = 2$),
- 4) aggregative walk ($LLS = 10$; $IS = 4d$) and clumped prey ($ID = 4$).

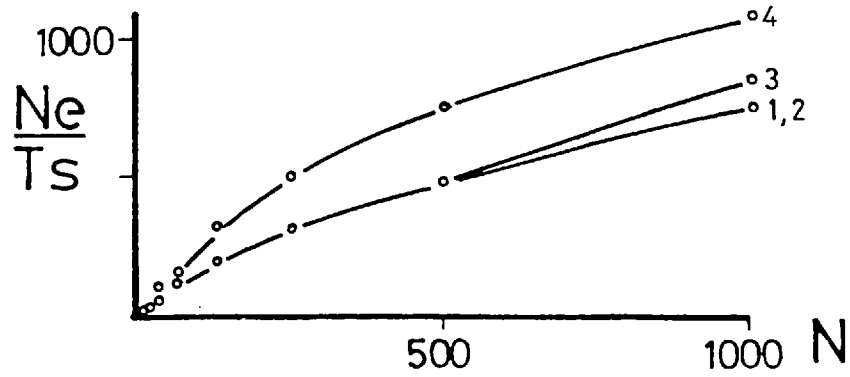
Fifty replicates were used for each prey density; the means of N_e and T_s were used to calculate the efficiency; data from Appendix Table A2.5; the results from some combinations of search strategy and prey distribution are pooled, as shown; the lines are fitted by eye.



A



B



C

GIVING UP TIME	IS ID	ABSTRACTED PARAMETERS		F VALUE	
		c	b		
50	1	2	.00529	1.633	$>10^6$
		4	.00572	1.234	$>10^5$
	4d	2	.00732	1.697	36317
		4	.00359	0.640	$>10^5$
100	1	2	.00590	4.022	5641
		4	.00753	3.345	563
	4d	2	.00590	3.751	34859
		4	.00391	2.119	95622
200	1	2	.00829	9.824	537
		4	.02456	9.304	270
	4d	2	.00531	9.250	248
		4	.00883	6.452	168

TABLE 6.4 Abstracted parameters (c & b) of Eqn. 6.1 for the aggregative responses of Section 6.7, obtained by the least squares best fit to the $N_s \times N$ relationship. The search strategies used are random search (IS = 1), and the aggregative walk with a long step length of ten (IS = 4d). The prey are arranged either at random (IS = 2), or in randomly distributed clumps of eight (IS = 4). All F values are highly significant (df = 1,7, $P < 0.001$).

6.7.2 Discussion

Examining the figures of the predation results (Fig. 6.22) a number of points can be made:

- 1) At the lowest value of the giving up time (50 time units); the figure of the number of prey eaten (and hence, due to their similarity, the aggregative response) has an initially marked exponential phase, which changes to a linear relationship with increasing prey density.
- 2) As the giving up time increases, this exponential phase becomes less marked.
- 3) If an upper time limit were to be imposed, the low giving up time would result in the figure of the number eaten (and hence, the aggregative response) being sigmoid in shape. As the value of the giving up time increased, this relationship would approach that of the type II functional response.
- 4) Therefore, it can be seen that the ratio of the giving up time to the maximum time available defines the shape of the aggregative response - a point made by Hassell & May (1974) who went on to point out the stabilizing effects of such aggregative responses.
- 5) For both predator search strategies, more of the prey distributed at random are found than of those distributed in clumps.
- 6) Comparing the success of the two strategies, it can be seen that, when searching for prey arranged at random, there is little difference between the two search strategies. When searching for clumped prey, however, the strategy of random search ($IS = 1$) is clearly more successful. Once again (cf. Section 6.6.2), this is probably due to the aggregative walk being more likely to 'strand' the predator in fully exploited areas, and cause it to give up.
- 7) The differences noted in point 6 above are all more pronounced with the lowest giving up time.

Turning now to the figures of the success rate or efficiency as a function of the initial prey density (Fig. 6.24), as in the last section on aggregative responses, a rather different picture emerges:

- 1) Clearly, increasing the giving up time decreases the predator's efficiency.
- 2) Random search ($IS = 1$) is equally efficient with either prey distribution, and less efficient than the aggregative walk ($IS = 4d$). When searching for the prey arranged at random, the aggregative walk is only slightly more efficient than random search, but when searching for clumped prey, it is a great deal more efficient.
- 3) Again, these differences are more pronounced with the low giving up time.

Thus, it can be seen that the giving up time has a marked effect upon the aggregative response, perhaps more so than the prey distribution and predator search strategy. As in the last section it was found that the success and efficiency of search strategies do not go together, the least successful tending to be the most efficient.

6.8 THE EFFECTS OF ALTERNATIVE PREY UPON AGGREGATIVE RESPONSES

6.8.1 Simulation and Analysis

Since many predators are polyphagous, the density of a particular prey type (type A) may be of less importance in determining the number of that type eaten in an aggregative response, than the density and arrangement of an alternative prey type (type B) occupying the same habitat. Accordingly, in this section, the effects of various densities and arrangements of the alternative prey (type B) will be examined.

Firstly, the strategy of random search ($IS = 1$) was used to obtain aggregative responses to the four combinations of two arrangements (random & clumped) of each of the two prey types; these responses being obtained at three densities (16, 64, and 128) of prey type B. The results from 50 replicates are given in Appendix Table A2.6 - parts 1 - 3. Secondly, the aggregative walk ($IS = 4d$) was used for the four combinations of prey arrangements, with a density of 64 for prey type B. Appendix Table A2.6 - part 4 contains the results from 50 replicates under these conditions.

The results for the four combinations of prey arrangements, when random search was used, are sufficiently similar to justify pooling the results, and so in Fig. 6.25 the means of all four combinations are used. The results obtained using the aggregative walk are shown in Fig. 6.26. The logarithmic scales used in two of these figures were necessary to show the differences between the four combinations.

The model based upon the Random Predator Equation (Eqn. 6.1) was fitted to the data of the number of prey surviving for each aggregative response (see Section 6.6.1). The resultant parameters are given in Table 6.5.

FIGURE 6.25 The effects of three densities of an alternative prey (type B) upon the aggregative response to prey type A. The densities of prey type B are:

- 1) 16 (symbol ×),
- 2) 64 (symbol ◦),
- 3) 128 (symbol •).

The figures are:

- (A) - the number of prey type A eaten (N_e) plotted against the initial density of prey type A (N), using logarithmic scales for both,
- (B) - the number of prey type B eaten (N_e') plotted against $\ln N$,
- (C) - the aggregative response: the logarithm of the time spent searching ($\ln T_s$) plotted against $\ln N$,
- (D) - the overall predator efficiency (Efficiency = $(N_e + N_e')/T_s$) plotted against $\ln N$.

Fifty replicates were used for each combination of prey densities; the logarithmic scales are used for clarity; the logarithm of the mean values of N_e and T_s are used; the means only are used in the figures for clarity; data from Appendix Table A2.6; the lines are fitted by eye.

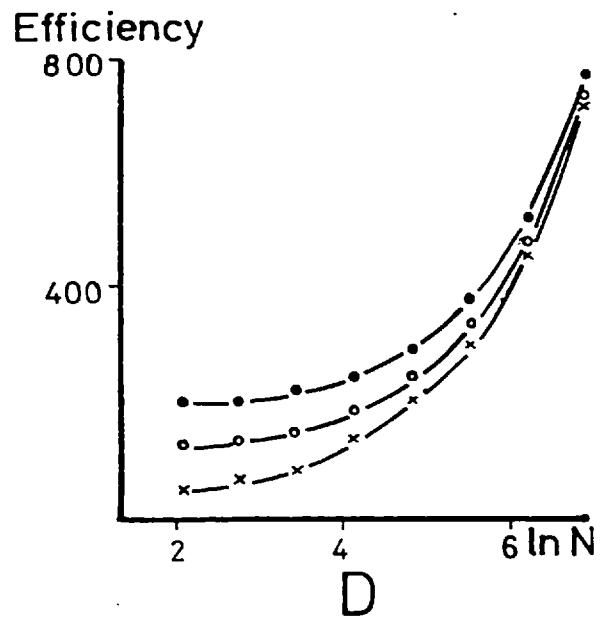
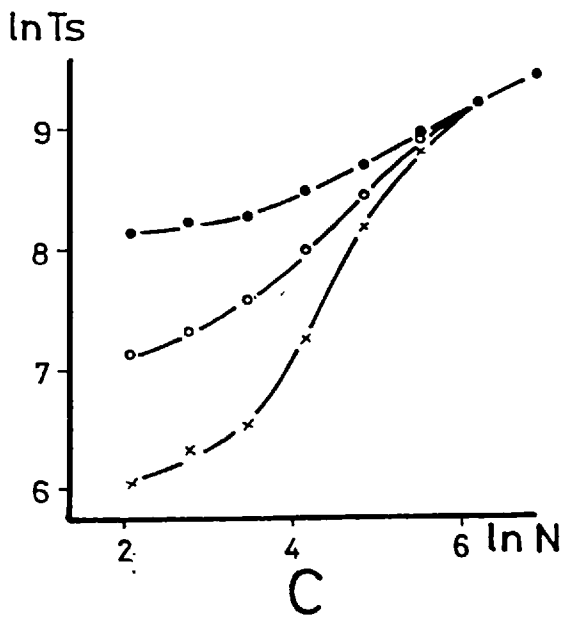
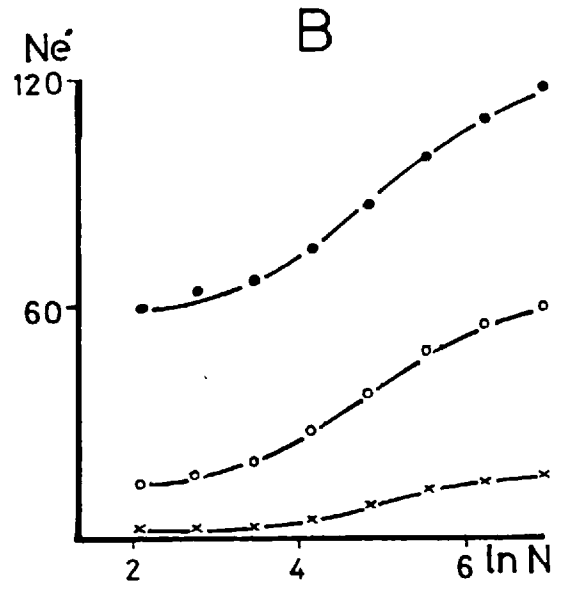
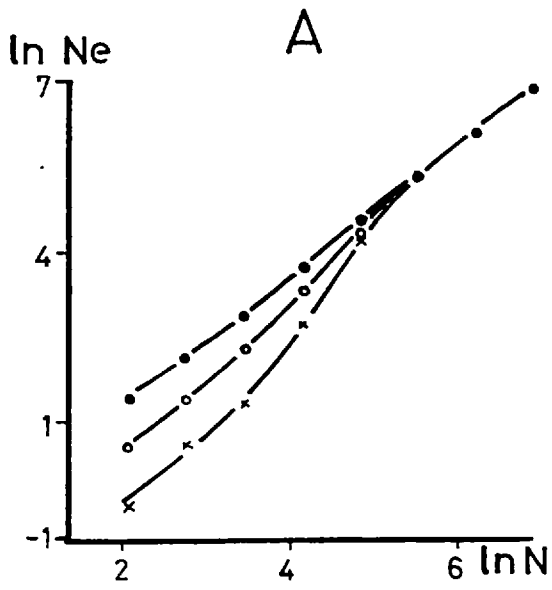


FIGURE 6.26

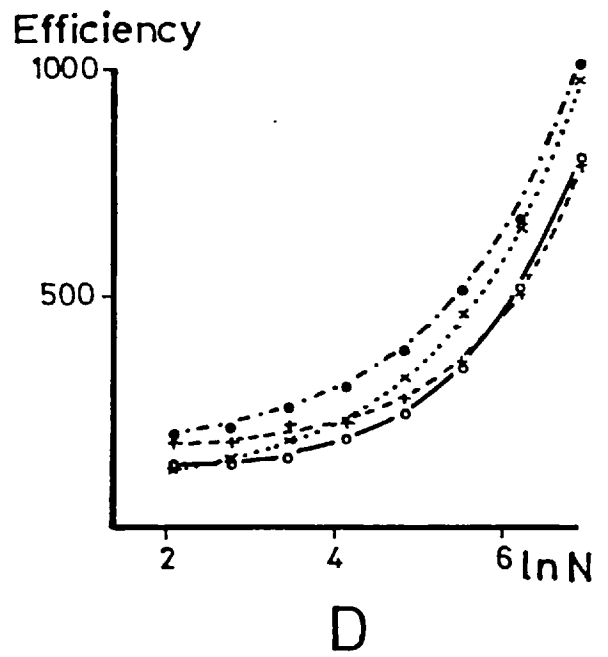
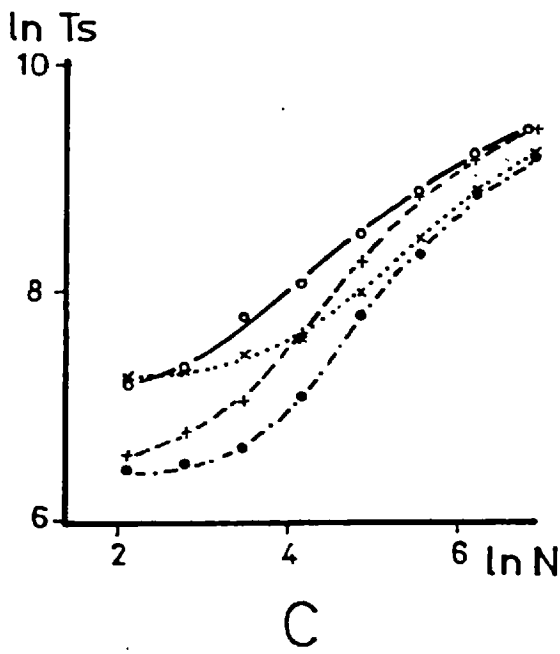
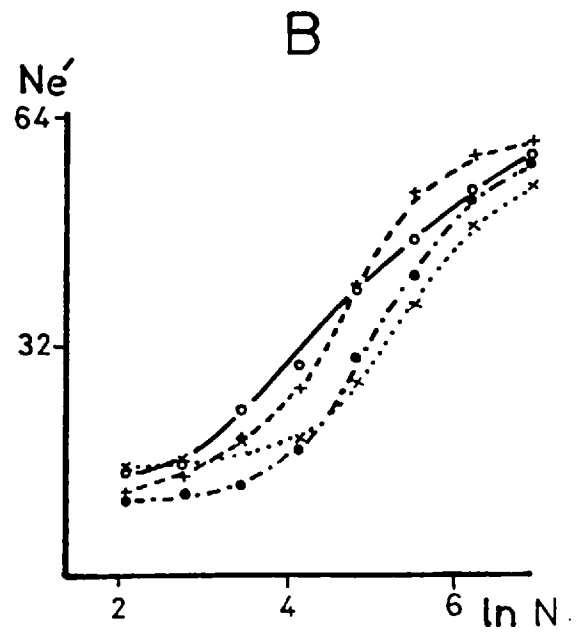
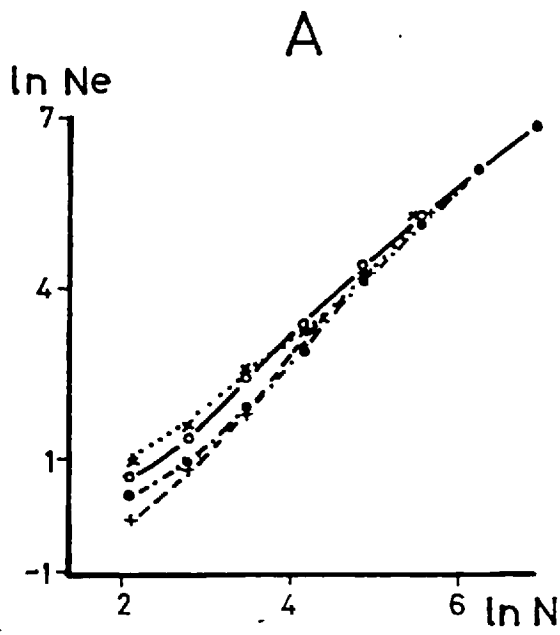
The effects of the arrangements of two types of prey (A and B) upon the aggregative response when the aggregative walk is used. Prey type B is present at a density of 64. The prey arrangements are:

- 1) type A at random; type B at random (symbol \circ ; solid line),
- 2) type A at random; type B clumped (symbol $+$; broken line),
- 3) type A clumped; type B at random (symbol \times ; dotted line),
- 4) type A clumped; type B clumped (symbol \bullet ; line of dots and dashes).

The figures are:

- (A) - the logarithm of the number of prey type A eaten ($\ln N_e$) plotted against the logarithm of the initial density of prey type A ($\ln N$),
- (B) - the number of prey type B eaten (N_e') plotted against $\ln N$,
- (C) - the aggregative response: the logarithm of the time spent searching ($\ln T_s$) plotted against $\ln N$,
- (D) - the overall predator efficiency (Efficiency = $(N_e + N_e')/T_s$) plotted against $\ln N$.

Fifty replicates were used for each combination of prey densities; the logarithmic scales are used for clarity; the logarithm of the mean values of N_e and T_s are used; the means only are used in the figures for clarity; data from Appendix Table A2.6; the lines are fitted by eye.



SEARCH STRATEGY	N'	PREY DISTRIBUTION		ABSTRACTED PARAMETERS		F VALUE
		IDa	IDb	c	b	
random search	16	random	random	.00367	13.4	849
		random	clumps	.00397	13.5	1695
		clumps	random	.00397	11.7	1662
		clumps	clumps	.00617	12.9	720
		pooled results		.00426	12.8	1560
	64	random	random	.00160	14.7	7145
		random	clumps	.00176	14.0	1689
		clumps	random	.00155	12.3	2489
		clumps	clumps	.00261	12.8	1062
		pooled results		.00182	13.4	1230
	128	random	random	.000645	13.2	916
		random	clumps	.000842	14.4	376
		clumps	random	.000793	13.1	7652
		clumps	clumps	.001402	10.1	24708
		pooled results		.000830	13.4	1418
aggregative walk (LLS = 10)	64	random	random	.00145	12.8	3976
		random	clumps	.00287	13.1	3439
		clumps	random	.00171	10.9	1300
		clumps	clumps	.00253	10.0	793

TABLE 6.5 Abstracted parameters (c & b) of Eqn. 6.1 for the aggregative responses of Section 6.8, obtained by the least squares best fit to the $N_s \times N$ relationship (Section 6.6). All the F values are highly significant (df for single aggregative responses = 1,6, $P < 0.001$; df for pooled results = 1,30, $P < 0.001$).

6.8.2 Discussion

A number of interesting points can be seen from these simulation results. Considering firstly, the effects of the density of prey type B on the results when random search ($IS = 1$) is used (Fig. 6.25), the following points may be made:

- 1) Perhaps the most obvious point is that, as the density of prey type A increases, the differences caused by the different densities of prey type B decrease. This is particularly clear in the figures of $\ln N_e \times \ln N$ (Fig. 6.25A) and $\ln T_s \times \ln N$ (Fig. 6.25C). Hence, from Table 6.5, it can be seen that the values of the parameter b of Eqn. 6.1, which defines predation at high prey densities, are similar for all densities of prey type B. This convergence occurs because, at low densities of prey type A, the changes in the density of type B cause an appreciable change in the total density, and hence in the time spent searching; on the other hand, at high densities of type A, the different densities of type B cause little change in the total density, and negligible change in the period spent searching.
- 2) At the lower densities of type A (i.e. less than 128), the increase in the density of type B leads to an appreciable increase in the time spent searching (Fig. 6.25C) and hence, to a lesser extent, in the number of prey type A found (Fig. 6.25A). Therefore, in Table 6.5, it can be seen that the values of the parameter c of Eqn. 6.1, which largely defines prey survival at low prey densities, decrease as the density of prey type B increases.
- 3) The converse of point 2 is also true: as the density of prey type A increases, the number of type B eaten increases (Fig. 6.25B).
- 4) The efficiency of the predator (i.e. the total number of prey eaten divided by the time spent searching = $(N_e + N_e')/T_s$) increases as the density of either prey type increases (Fig. 6.25D). The differences caused by the different densities of prey type B are still apparent at the high densities of type A. This is due to the inclusion of the number of type B eaten in the efficiency term.

Turning now to the effects of the alternative prey when the aggregative walk ($IS = 4d$) is used (Fig. 6.26), several points can be made.

At high densities of prey type A, the number of type A eaten seems to be unaffected by the prey arrangements used (Fig. 6.26A). The values of the parameter b of Eqn. 6.1, as given in Table 6.5, suggest, however, that less are eaten when type A is clumped.

Depending upon the prey density, consumption by the predator varies with the prey arrangements used. Accordingly, at low densities of A, the combinations can be ranked by the numbers of prey type A eaten:

$$A_4/B_2 > A_2/B_2 > A_4/B_4 > A_2/B_4 ,$$

where the numerals refer to ID the control option for the prey arrangement ($ID = 2 = \text{random}$; $ID = 4 = \text{clumped}$), for example A_4/B_2 implies that type A is arranged in clumps, while type B is arranged at random. At intermediate densities of prey type A, this ranking changes to

$$A_2/B_2 > A_4/B_2 > A_2/B_4 > A_4/B_4 ,$$

as can be seen in Fig. 6.26A. These latter rankings are confirmed by the parameters of Table 6.5, where it can be seen that the ranking at intermediate densities of type A also applies at high densities. The efficiencies (Fig. 6.26D) can also be ranked. Thus, at low densities of type A:

$$A_4/B_2 \approx A_2/B_2 > A_2/B_4 \approx A_4/B_4 ,$$

while at high densities this changes to:

$$A_2/B_2 \approx A_2/B_4 > A_4/B_2 \approx A_4/B_4 .$$

The changeover point is at approximately a density of 64 type A i.e. where the two prey types are present in equal densities. Similar effects can be seen for the searching time (Fig. 6.26C) and the number of type B eaten (Fig. 6.26B).

Clearly the most frequent prey type has the dominant effect upon the overall results. Thus, at low densities of type A, the combination A₄/B₂ is predominantly arranged at random, while at high densities it is predominantly arranged in clumps. The converse is true of the combination A₂/B₄, and this provides the explanation of the transformation of the rankings noted above.

Therefore, particularly in view of the results of Fig. 6.26B, one can conclude that if species B must share a unit of habitat with species A, there are three possible situations which may arise:

- 1) Type A is present at a low density and arranged at random. Therefore, less of type B will be eaten in one aggregative response, if it also is arranged at random.
- 2) Alternatively, if type A is present at a high density and arranged at random, less of type b will be eaten in one aggregative response, if it is arranged in clumps.
- 3) The third situation arises if type A is arranged in clumps. In this case, less of type B will be eaten in one aggregative response if it too is arranged in clumps.

Although certain conclusions may thus be drawn on the best distribution strategies of prey, it should be borne in mind that this also maximizes the predator's efficiency (compare Figs. 6.26 B and D), and so considering the effects of one aggregative response may be unrealistic.

6.9 DISCUSSION AND CONCLUSIONS

In this chapter, a number of aspects of predator-prey interactions have been examined. Most of these have used only one prey type, but in the last section the effects of alternative prey were introduced. In Sections 6.3, 6.4, and 6.5 functional responses were examined, while Sections 6.6, 6.7, and 6.8 dealt with aggregative responses.

All the search strategies used were found to produce normal, type II functional responses (Section 6.4). Comparing the various strategies, it was of interest to note the relatively high search efficiency resulting from completely random search. Only the strategies which incorporated substantial systematic elements (IS = 4b, 4d, 5) were more successful. The strategies which included a response to finding a prey were the most successful when searching for aggregated and clumped prey. It has been demonstrated (see Table 6.1) that the functional responses of all combinations of predator search strategy and prey distribution are well described by the Random Predator Equation. Thus, although the Random Predator Equation was intended to apply only to random search (Rogers, 1972), it also provides a good description and assessment of the parameters for other searching methods (Massell, Lawton & Beddington, 1976).

In Chapter 4 it was found that there was little change in the functional response as prey aggregation increased, except in the case of the 'clumped' distribution (regularly distributed clumps of ten), where the anthocorids were more successful. It is, therefore, interesting to note a similar phenomenon in these simulations. In Table 6.1 it can be seen that search strategies 1, 2, 3, 4a, and 4b which do not involve behavioural changes in response to finding a prey, show little change in efficiency with increasing prey aggregation. Strategies 4c, 4d, and 5, however, which involve changes in the search path in response to finding a prey, show only an appreciable increase in search efficiency when highly aggregated prey distributions are used.

Several methods of varying the encounter success rate were found to result in sigmoid, type III functional responses. When the mean search efficiency was calculated by substitution

in the Random Predator Equation, it was found to form a curvilinear relationship with the number of prey eaten (Section 6.5). This provides support for the model of the sigmoid response (Hassell, pers. comm.) used in Chapter 3. Several functions incorporating a decreasing encounter success rate in response to prey density resulted in dome shaped functional responses.

The aggregative response simulations (Section 6.6) showed that maximizing the number of prey found in one aggregative response and maximizing a predator's overall efficiency are incompatible. Thus, the strategy of completely random search ($IS = 1$) leads to most prey being found, but it is the least efficient. It was found that the greatest number of prey survived, and the predator's efficiency was greatest, when the most aggregated distribution of prey was used. Similarly, in Section 6.7. it was found that reducing the giving up time reduces the number of prey eaten, and increases the predator's efficiency.

The effects of alternative prey upon functional responses may, more readily, be examined by means of deterministic models. The effects upon aggregative responses, however, are more complex, and simulations such as those of Section 6.8 provide a suitable means of examining these. Thus, in Section 6.8, the simulations suggested the consequences of different densities of alternative prey and the effects of the combination of two arrangements of the two prey types. The conclusions about habitat sharing inter-species (Section 6.8.2) can also be applied to habitat sharing intra-species. Thus, similar conclusions may be drawn as to the best strategy of dispersal for additions to a population.

It has been shown that the results of these simulations can readily be interpreted, and often could be derived by deductive means. The usefulness of such a simulation model often lies in the focussing of attention upon aspects of behaviour and their consequences, rather than the quantitative results. However, any conclusions derived here rest upon a firmer basis than if they had been arrived at by purely deductive means.

CHAPTER 7

CONCLUDING REMARKS

Although there are discussion and conclusion sections at the end of each chapter of this work, there are a number of points which, because of their overall importance and wider applicability, ought to be re-emphasized here.

It was shown in Chapter 2 that the currently standard method of parameter abstraction for the Random Predator Equation (Rogers, 1972) is unsatisfactory. Two alternative approaches were considered. The first, finding the best fit linear relationship (of $\ln S \times Ne$) allowing for both variables being subject to error, was also considered to have drawbacks. The second, a least squares best fit to the functional response, was considered to be more suitable. This second approach can also be adopted using a least χ^2 or a maximum likelihood criterion as to the best fit. It is acknowledged, however, that this least squares approach does reduce the effects of the predation results at low prey densities, and hence, will result in the estimate of the handling time being more accurate. On the other hand, the $\ln S \times Ne$ transformation reduces the effects of the predation results at high prey densities, and this may lead to a better estimate of the search efficiency. Accordingly, it is recommended that, for abstracting the parameters of the Random Predator Equation, a least squares (a least χ^2 , or a maximum likelihood) approach should be used, and, for this purpose, a computer programme such as BESTFIT (Appendix Section A1.3) would be suitable. Should subsequent examination of the $\ln S \times Ne$ figure reveal inconsistencies at low prey densities, further consideration should be given to the problem, and, perhaps, a combination of methods used.

The following approach for obtaining varying parameter models of the functional response has been developed in this work:

- 1) obtain functional response results,
- 2) make continuous observations (either on the functional response experiments or on separate experiments) and record, in particular, the handling time for successive prey eaten,
- 3) find the mean (or overall) handling times for successive prey eaten, and describe them with a suitable relationship as a function of either the number of prey eaten or the initial prey density,
- 4) substitute this overall relationship into the Random Predator Equation and calculate values of the mean search efficiency for the functional response results,
- 5) these values can now be used to define the mean search efficiency with a suitable relationship, again as a function of either the number of prey eaten or the initial prey density,
- 6) substitute the relationships describing the handling time and search efficiency into the Random Predator Equation to obtain the final functional response equation.

Using this approach, two dome shaped functional response models (Section 2.4.3) and a satiation model (Section 3.3.5) were developed.

When examining the two prey interactions of Chapters 3 and 5, the analytical procedure provided a theme which could be described as a recipe for detecting preference. The component stages can be outlined as follows:

- 1) obtain the functional responses to the individual prey types and describe them with suitable functional response models (preferably the Random Predator Equation),
- 2) combine these two functional responses to predict predation when both prey types are present,
- 3) examine predation over a range of combinations of densities of the two prey types and compare this with the predicted predation,
- 4) any deviations from the predicted predation may be considered as 'deliberate' preference, as opposed to the 'automatic' preference defined by the different searching parameters (see Section 3.4).

The introduction of the terms 'automatic' and 'deliberate' preference in Section 3.4 provides a, perhaps oversimplified, descriptive basis for this approach. Thus 'automatic' preference implies that prey are eaten in the same ratio as that at which they are encountered, whilst 'deliberate' preference occurs when the ratio of the prey types eaten differs from the ratio at which they are encountered. In this approach, it is assumed that the encounter rates can be predicted from the individual functional responses (i.e. the search efficiencies and handling times remain constant). Should one of the searching parameters change in the two prey situation, the encounter rates will differ from those predicted, and apparent 'deliberate' preference will result. Therefore, although the two terms are useful in this context, it should not be assumed that 'automatic' preference is always defined by the predictions based upon the individual functional responses. Ideally, continuous observations should be made to determine the encounter rates. This could usefully have been done for the work of Chapter 3.

It should be noted that this approach is most suitable when the individual functional responses are described by the Random Predator Equation, where the parameters are constant. When varying parameter models of the functional response become necessary (e.g. Chapter 3) it should be determined whether these changes in the searching parameters will affect the parameters for the other prey type. Thus, in Chapter 3, it was found that an increase in the search efficiency for type I prey led to an increase in the search efficiency for type II prey. The choice of a suitable functional response model should reflect whether the parameters for the other prey will be affected.

In Chapter 3 it was shown that, when two prey types form an homogenous mixture, the mixed predation can be predicted from the individual functional responses. In Chapter 5, however, by providing similar prey in different parts of an arena habitat, it was shown that the predation by the anthocorids was not predicted by this approach, but that habitat selection occurred, which became more apparent with the passage of time. Accordingly, when applied to a larger more heterogenous system, this approach may well be less suitable. The two prey form of the Random Predator may, however, be used descriptively by abstracting parameters

from the mixed predation data (Lawton, Beddington & Bonser, 1974), to provide a description of the predation in such an interaction.

It is hoped that this work has provided a firmer framework for the understanding of the predator-single-prey interaction, and will help to form a foundation for the study of the interactions of polyphagous predators and their prey.

SUMMARY

- 1 The literature of the field is reviewed, particular attention being paid to the functional response models, preference, and the effects of prey aggregation (Chapter 1).

- 2 The abstraction of the parameters of the Random Predator Equation is considered. The currently standard technique (regression analysis of $\ln S \times Ne$) is considered unacceptable. Alternative approaches are examined and a least squares best fit to the functional response is recommended (Section 2.2).

- 3 The implications of sigmoid and dome shaped functional responses are described, illustrating the usefulness of the $\ln S \times Ne$ figure (Section 2.3).

- 4 Models for varying the behaviour of the predator in response to prey density and/or the number of prey eaten are introduced and examined (Section 2.4).

- 5 Two models of the dome shaped functional response are derived (Section 2.4.3).

- 6 The functional responses of Coccinella septempunctata to two size classes of an aphid prey, Brevicoryne brassicae, in a simple, small arena are examined. Predation when both prey classes are present is examined and is found to be well described by predictions based on the functional responses to the individual prey classes (Chapter 3).

- 7 A model which describes the effects of satiation is derived and fitted to the functional response of C. septempunctata to adult (type II) B. brassicae (Section 3.3.5).

- 8 The terms 'automatic' and 'deliberate' preference are introduced to describe preference resulting from different encounter rates and the deliberate selection or rejection of prey (Section 3.4).

- 9 Functional responses of Anthocoris nemorum to ovae of Pieris brassicae are examined in a simple arena. Four different arrangements of the prey, of increasing aggregation are used. The responses to the different arrangements, at three different time intervals, are analysed and compared. Only the most aggregated distribution produces results differing significantly from the others. Recording predation at the three time intervals confirms the casual observation that long periods of predator inactivity occur (Chapter 4).
- 10 Using a more complex arena, the effects of the distribution and arrangement of the ovae on plants are examined. The functional responses to individual ovae on the edges of the leaves and to clumps of ovae on the centre of the leaves are examined, as well as the predation when both prey distributions are offered. Predictions based on the functional responses to the individual prey arrangements give a poor description of the observed predation when both arrangements are used. Continuous observations reveal that the anthocorids, by the end of the 20 hour experimental period, search to a greater extent in the areas of highest prey density (Chapter 5).
- 11 A computer simulation programme is developed to imitate predator searching behaviour. The programme is able to mimic and extend some of the observed behaviour (Chapter 6).
- 12 The important points of this work are re-emphasized in the concluding remarks (Chapter 7).

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APPENDIX 1

LISTINGS AND DESCRIPTIONS OF COMPUTER PROGRAMMES

A1.1 INTRODUCTION

During the course of this work, a number of computer programmes were developed. The simulation programme described in Chapter 6 is listed as Appendix Section A2.1; the remaining programmes which may be of use in this field are given here. Each of the following functions and programmes is briefly described and listed:

A1.2 XNEWT functions - a series of functions which use Newton's approximation to solve various functional response equations,

A1.3 programme BESTFIT - a programme which, using one of the XNEWT functions, finds the set of parameters which provide the best fit to an input set of data,

A1.4 programme PUT - the programme used in Chapter 4 to arrange prey in a square arena using the negative binomial distribution,

A1.5 Programme PREDICT - a programme which is used to predict predation in a two prey situation, using the parameters of the Random Predator Equation for the individual prey functional responses.

Al.2 XNEWT Functions

The functions listed below use Newton's approximation (see e.g. Marriot,1970) to calculate the number of prey eaten for a given prey density using various functional response equations. Summarizing the use of Newton's approximation in this process, the basic functional response equation:

$$N_e = f(a, T_h, T, N, N_e),$$

is transformed to:

$$C = 0 = N_e' - f(a, T_h, T, N, N_e'),$$

where N_e' is an estimate of the true value of N_e . C is now differentiated with respect to N_e' :

$$dC/dN_e' = f'(a, T_h, T, N, N_e'),$$

and a new estimate of N_e (N_e'') is given by:

$$N_e'' = N_e' - C/(dC/dN_e').$$

using the new estimate the process is repeated until sufficient accuracy is obtained. The functions are:

Section	Function	Model used	Section	Equation
Al.2.1	XNEWTR	Random Predator Equation	2.2	2.1
Al.2.2	XNEWTO	'over-predation' model	3.3.5	3.8
Al.2.3	XNEWTW	dome shaped (Williams)	2.4.3.1	2.8
Al.2.4	XNEWTY	dome shaped (Yao)	2.4.3.2	2.11
Al.2.5	XNEWTH	HLB model	3.3.2	3.4
Al.2.6	XNEWTC	Satiation model	3.3.5	3.11

Al.2.1 Function XNEWTR

```

1      FUNCTION XNEWTR (XN,A,B,T,IRUN)
      C
      C      FUNCTION XNEWTR USES NEWTONS APPROXIMATION TO CALCULATE THE NUMBER
      C      OF PREY EATEN USING THE ROGERS RANDOM PREDATOR EQUATION:
      C      NE = N(1 - EXP(- A(T - TH.NE)))
      C
      C      INPUT PARAMETERS ARE:
      C
      C      1.  XN - PREY DENSITY (N) OF THE MODEL
      C      2.  A - SEARCH EFFICIENCY (A) OF MODEL
      C      3.  B - HANDLING TIME (TH) OF THE MODEL
      C      4.  T - TOTAL TIME (T) OF THE MODEL
      C      5.  IRUN - CONTROL OPTION TO PRINT OUT THE MODEL.
      C
2      IF (IRUN.NE.0) GOTO3002
3      IRUN=1
4      WRITE(6,2000)
5      2000 FORMAT(/.* RANDOM PREDATOR EQUATION FITTED FOR A + TH*)
6      3002 CONTINUE
7      EST=XN*(1.-EXP(-A*T))
8      EATMAX=T/B
9      IF (EST.GE.EATMAX) EST=EATMAX*9./10.
10     DO 3000 J=1,10
11     BR=EXP(-A*(T-B*EST))
12     CEE=EST-XN*XN*BR
13     SLOPE=1.+XN*A*B*BR
14     3000 EST=EST-CEE/SLOPE
15     XNEWTR=EST
16     RETURN
17     END

```

Al.2.2 Function XNEWTO

```

1      FUNCTION XNEWTO (A,B,C,T,X,ENE,IRUN)
      C
      C      FUNCTION XNEWTO
      C
      C      THIS FUNCTION USES A NEWTONS APPROXIMATION TO SOLVE THE OVER-
      C      PREDATION MODEL SUGGESTED BY COCK (PHD THESIS - SECTION 3.3.5):
      C      NE=N(1-EXP(-A.NE(T-TH.NE)/(NE-C)))
      C
      C      INPUT PARAMETERS ARE :
      C
      C      1.  A - SEARCH EFFICIENCY (A) OF MODEL
      C      2.  B - HANDLING TIME (TH) OF MODEL
      C      3.  C - PARAMETER (C) OF MODEL
      C      4.  T - TOTAL TIME (T) OF MODEL
      C      5.  X - PREY PRESENT (N) OF MODEL
      C      6.  ENE - ESTIMATE OF NUMBER OF PREY EATEN
      C      7.  IRUN - CONTROL OPTION TO PRINT OUT MODEL USED
      C
2      EST=ENE
3      3000 BR=EXP(-A*EST*(T-B*EST)/(EST-C))
4      D=(A*B*EST*EST-2.*A*C*B*EST+A*C*T)/((EST-C)*(EST-C))
5      SLOPE=1.+X*BR*D
6      CEE=EST-X*(1.-BR)
7      E=EST-CEE/SLOPE
8      D=ABS((E-EST)/E)
9      EST=E
10     IF (D.GT.0.0001) GOTO3000
11     XNEWTO=E
12     IF (IRUN.EQ.0) GOTO3001
13     RETURN
14     3001 WRITE(6,2000)
15     2000 FORMAT(/.* THIS PROGRAM FINDS THE BEST VALUES FOR A,TH + C FOR THE
16     COCK MODEL OF OVER-PREDATION AT LOW PREY DENSITIES*)
17     RETURN
18     END

```

Al.2.3 Function XNEWTW

```
1      FUNCTION XNEWTW (XM,D,XN,C,T,DENS,ENE)
      C
      C      FUNCTION XNEWTW
      C
      C      THIS FUNCTION USES A NEWTONS APPROXIMATION TO SOLVE THE PREDATION
      C      MODEL BASED ON THE DATA OF WILLIAMS (PERS. COMM.) :
      C      NE=N(1-EXP(-TM.N*D) (T-EXP(XN.LN(NE)+C)NE)))
      C
      C      INPUT PARAMETERS ARE :
      C
      C      1. - XM - PARAMETER (M) OF MODEL
      C      2. D - PARAMETER (D) OF MODEL
      C      3. XN - PARAMETER (XN) OF MODEL
      C      4. C - PARAMETER (C) OF MODEL
      C      5. T - TOTAL TIME (T) OF MODEL
      C      6. DENS - PREY DENSITY (N) OF MODEL
      C      7. ENE - ESTIMATE OF NUMBER EATEN
      C
2      EST=ENE
3      3000 BR=EXP((-XM*DENS-D)*(T-EXP(XN*ALOG(EST)+C)*EST))
4      F=EXP(XN*ALOG(EST)+C)*(DENS*XM+D)*(1.+XN)
5      SLOPE=1.+DENS*BR*F
6      CEE=EST-DENS*(1.-BR)
7      DELTA=CEE/SLOPE
8      E=EST-DELTA
9      DIFF=ABS((E-EST)/E)
10     EST=E
11     IF(DIFF.GT.0.00001)GOTO3000
12     XNEWTW=E
13     RETURN
14     END
```

Al.2.4 Function XNEWTY

```
1      FUNCTION XNEWTY (XM,D,XN,C,T,DENS,ENE)
      C
      C      FUNCTION XNEWTY
      C
      C      THIS FUNCTION USES A NEWTONS APPROXIMATION TO SOLVE THE PREDATION
      C      MODEL BASED ON THE DATA OF YAO (PERS. COMM.) :
      C      NE=N(1-EXP(-EXP(M.LN(N)+D) (T-(XN.NE+C)NE)))
      C
      C      INPUT PARAMETERS ARE :
      C
      C      1. - XM - PARAMETER (M) OF MODEL
      C      2. D - PARAMETER (D) OF MODEL
      C      3. XN - PARAMETER (XN) OF MODEL
      C      4. C - PARAMETER (C) OF MODEL
      C      5. T - TOTAL TIME (T) OF MODEL
      C      6. DENS - PREY DENSITY (N) OF MODEL
      C      7. ENE - ESTIMATE OF NUMBER EATEN
      C
2      EST=ENE
3      3000 BR=EXP(-EXP(XM*ALOG(DENS)+D)*(T-EST*(XN*EST+C)))
4      F=EXP(XM*ALOG(DENS)+D)*(2.*XN*EST+C)
5      SLOPE=1.+DENS*BR*F
6      CEE=EST-DENS*(1.-BR)
7      DELTA=CEE/SLOPE
8      E=EST-DELTA
9      DIFF=ABS((E-EST)/E)
10     EST=E
11     IF(DIFF.GT.0.00001)GOTO3000
12     XNEWTY=E
13     RETURN
14     END
```

Al.2.5 Function XNEWTH

```

1      FUNCTION XNEWTH (B,C,TH,T,X,ENE)
      C
      C      FUNCTION XNEWTH
      C
      C      THIS FUNCTION USES A NEWTONS APPROXIMATION TO SOLVE THE PREDATION
      C      MODEL SUGGESTED BY HASSELL (PERS. COMM) :
      C      NE=N(1-EXP(-B.N(T-TH.NE)/(1+C.N)))
      C
      C      INPUT PARAMETERS ARE :
      C
      C      1. B - PARAMETER (B) OF MODEL
      C      2. C - PARAMETER (C) OF MODEL
      C      3. TH - HANDLING TIME (TH) OF MODEL
      C      4. T - TOTAL TIME (T) OF MODEL
      C      5. X - PREY DENSITY (N) OF MODEL
      C      6. ENE ESTIMATE OF NUMBER OF PREY EATEN
      C
2      EST=ENE
3      3000 BR=EXP(-B*X*(T-TH*EST)/(1+C*X))
4          F=B*X*TH/(1+C*X)
5          SLOPE=1.+X*BR*F
6          CEE=EST-X*(1.-BR)
7          E=EST-CEE/SLOPE
8          D=ABS((E-EST)/E)
9          EST=E
10         IF(D.GT.0.00001)GOTO3000
11         XNEWTH=E
12         RETURN
13         END

```

Al.2.6 Function XNEWTC

```

1      FUNCTION XNEWTC (A,B,C,D,G,T,X,EST,IRUN)
      C
      C      THIS FUNCTION USES NEWTONS APPROXIMATION TO SOLVE THE SATIATION
      C      MODEL SUGGESTED BY COCK (PHD THESIS - SECTION 3.3.5)
      C      NE = N(1 - EXP(- ABAR(T - THBAR.NE)))
      C      WHERE ABAR = EXP(C.LN(NE) + D) + G
      C      AND THBAR = A.NE/(1 + A.B.NE)
      C
      C      INPUT PARAMETERS ARE:
      C
      C      A,B,C,D,G - PARAMETERS OF THE MODEL
      C      T - TOTAL TIME (T)
      C      X - PREY DENSITY (N)
      C      EST - ESTIMATE OF THE NUMBER OF PREY EATEN (NE)
      C      IRUN - CONTROL OPTION TO PRINT OUT THE MODEL USED.
      C
2      IF(IRUN.NE.0)GOTO3000
3      WRITE(6,2000)
4      IRUN=1
5      3000 CONTINUE
6          DO 3001 J=1,10
7              ABART=EXP(C*A*LOG(EST)+D)
8              DIV=1.+A*B*EST
9              BR=EXP(-(ABART+G)*(T-A*EST*EST/DIV))
10             CEE=EST-X*X*BR
11             DA=-ABART*T*C/EST
12             DB=ABART*EST*A*(C-2.)
13             DC=(ABART*(DB-A*A*B*EST*EST))/(DIV*DIV)
14             DD=(2.*A*EST+G*DIV-A*A*B*G*EST*EST)/(DIV*DIV)
15             SLOPE=1.+X*BR*(DA+DC+DD)
16             3001 EST=EST-CEE/SLOPE
17             XNEWTC=EST
18             2000 FORMAT(/,* COCK SATIATION MODEL USED :*,/
19                 1* NE = N(1-EXP(-ABAR(T-THBAR.NE)))*,/,
20                 2* ABAR = EXP(C.LN(NE)+D)+G*,/,
21                 3* THBAR = A.NE/(1+A.B.NE)*)
19         RETURN
20         END

```


Al.3 Programme BESTFIT

Programme BESTFIT was designed to find the parameters which cause the Random Predator Equation (Rogers, 1972) to give the best fit to an input set of data. It can, however, readily be adapted to fit other equations to data by changing the function used. Programme BESTFIT calls subroutine EVAL which uses function XNEWTR (see Section Al.2.1) to calculate values of the number of prey eaten (N_e) for each value of the prey density (N), and for each set of the parameters (a & T_h). The initial parameter limits are input; ten values over the range of these limits are used for each parameter, giving 100 combinations. Using each combination of parameters, N_e is calculated for every value of N and the square of the difference from the observed value of N_e is calculated. Once this has been done, the squares of the differences are summed, and the combination of parameters which resulted in the smallest sum of squares is used as the basis for the new set of parameter limits (i.e. this best estimate $\pm 1/10$ of the previous range of limits). When ten successive reductions of the limits have been made, the parameters giving the best fit are taken as the best estimate.

Input for the programme is as listed in the comment cards (listing page 1). NPROB is used as described in Davies (1971): each problem has a number not equal to zero, after the last set of data a NPROB value of zero causes the programme to terminate execution. For the Random Predator Equation, C is the total time available (T). The data can be input in one of two forms: if TYPE is input as 1.0, a series of values of N is input, followed by a corresponding series of values of N_e ; if TYPE is input as 2.0, the series of values of N is followed by the number of replicates for each value of N , which is followed by the replicates for successive values of N (one card for each prey density). The data matrix (DATA) has dimensions of (100,4) and so, unless this is altered, not more than 100 data points can be input. Each set of data has a title, input in A format, which is printed at the top of the page of results for that set of data.

On the first occasion that subroutine EVAL is called for each set of data, the value of IRUN results in the model used being printed from function XNEWTR.

Other models can be fitted to data using this programme by changing the function XNEWTR. For example, one of the other functions described in Section A1.2 could be used. Obviously, if more (or less) than two parameters are being fitted, the main programme has to be altered to allow for this. Thus, the more complex functional response models described in this work (Chapters 2 & 3) can be fitted by this means.

Using the resultant best parameters, an analysis of variance is performed.

```
1      PROGRAM BESTFIT (INPUT,OUTPUT,TAPE5=INPUT,TAPE6=OUTPUT)
      C
      C      PROGRAMME BESTFIT
      C
      C      THIS PROGRAMME FINDS THE PARAMETERS (A - SEARCH EFFICIENCY; TH (B)
      C      - HANDLING TIME) OF THE RANDOM PREDATOR EQUATION (ROGERS, 1972),
      C      WHICH GIVE THE BEST FIT TO AN INPUT SET OF DATA, BY A LEAST
      C      SQUARES DIFFERENCE APPROACH.
      C
      C      THIS PROGRAM CALLS SUBROUTINE EVAL WHICH CALLS FUNCTION XNEATR.
      C      XNEATR CAN BE CHANGED TO FIT ALTERNATIVE MODELS (E.G. HOLLING DISC
      C      EQUATION).
      C
      C      INPUT:
      C
      C      1. NPROB - PROBLEM NUMBER (OPERATES AS PER THAT OF R.G. DAVIES)
      C      2. TITLE(10) - TITLE FOR THE PROBLEM.
      C      3. AMIN,AMAX - MINIMUM + MAXIMUM VALUE FOR SEARCH EFFICIENCY
      C      4. BMIN,BMAX - MINIMUM + MAXIMUM VALUE FOR HANDLING TIME
      C      5. C - TOTAL TIME (NOTE HANDLING TIME WILL BE IN THE SAME UNITS)
      C      6. NP - NUMBER OF PREY DENSITIES
      C      7. TYPE - OF DATA INPUT :
      C
      C          TYPE=1 DATA IS A SET OF PREY DENSITIES WITH THE
      C          CORRESPONDING NUMBERS OF PREY EATEN
      C      8. DATA(J,1),J=1,NP - PREY DENSITIES
      C      9. DATA(J,2),J=1,NP - NUMBERS EATEN
      C
      C          TYPE=2 DATA IS A SET OF PREY DENSITIES WITH VARYING
      C          NUMBERS OF REPLICATES OF THE NUMBER OF PREY
      C          EATEN
      C      8. DATA(J,3),J=1,NP - PREY DENSITIES
      C      9. DATA(J,4),J=1,NP - NUMBER OF REPLICATES OF NUMBER EATEN FOR
      C          EACH PREY DENSITY
      C      9+. DATA(J,2) - REPLICATES OF NUMBER OF PREY EATEN - NEW CARD FOR
      C          FOR EACH PREY DENSITY
      C
      C
      C      DIMENSION TITLE(10)
      C      COMMON DATA(100,4),IRUN
      C
      C      DATA(J,3) WILL CONTAIN THE CALCULATED VALUES OF THE NUMBER EATEN
      C      FOR SUCCESSIVE PARAMETER VALUES.
      C      DATA(J,4) WILL CONTAIN THE CORRESPONDING SQUARE OF THE DIFFERENCES
      C      BETWEEN THE OBSERVED AND THE CALCULATED VALUES OF THE NUMBER EATEN
      C
      C
      C      3005 READ(5,1000)NPROB
      C      IF(NPROB.EQ.0)STOP
      C      IRUN=0
      C      READ(5,1001)(TITLE(J),J=1,10)
      C      WRITE(6,2000)NPROB,(TITLE(J),J=1,10)
      C      READ(5,1002)AMIN,AMAX
      C      READ(5,1002)BMIN,BMAX
      C      WRITE(6,2001)AMIN,AMAX,BMIN,BMAX
      C      AINT=(AMAX-AMIN)/10.
      C      BINT=(BMAX-BMIN)/10.
      C      READ(5,1003)C
      C      WRITE(6,2002)C
      C      READ(5,1000)NP
      C      READ(5,1003)TYPE
      C      IF(TYPE.EQ.2.)GOTO3020
      C
      C      MATCHING VALUES OF THE PREY DENSITY AND NUMBER OF PREY EATEN ARE
      C      READ IN :
      C
      C      19 READ(5,1005)(DATA(J,1),J=1,NP)
      C      20 READ(5,1005)(DATA(J,2),J=1,NP)
      C      21 WRITE(6,2003)
      C      22 WRITE(6,2003)(DATA(J,1),J=1,NP)
      C      23 WRITE(6,2004)
      C      24 WRITE(6,2008)(DATA(J,2),J=1,NP)
      C      25 GOTO3023
      C      3020 WRITE(6,2020)
      C
      C      REPLICATED VALUES OF THE NUMBER OF PREY EATEN ARE INPUT, AND THE
      C      VALUES ARE ADJUSTED WITHIN THE MATRIX DATA :
      C
      C      27 READ(5,1005)(DATA(J,3),J=1,NP)
      C      28 READ(5,1005)(DATA(J,4),J=1,NP)
```

```

29      NA=1  &  NB=0
30      DO 3021 J=1,NP
31      NB=DATA(J,4)
32      NB=NB*N)
33      READ(5,1005) (DATA(K,2),K=NA,NB)
34      DO 3022 K=NA,NB
35      3022 DATA(K,1)=DATA(J,3)
36      SUMX=0.  &  SUMXSQ=0.
37      DO 3040 JA=NA,NB
38      SUMX=SUMX+DATA(JA,2)
39      3040 SUMXSQ=SUMXSQ+DATA(JA,2)*DATA(JA,2)
40      XX=NB-NA+1.
41      VAR=(SUM XSQ-SJM X*SUMX/XX)/(XX-1.)
42      WRITE(5,2021) DATA(J,3),VAR,(DATA(K,2),K=NA,NB)
43      NA=NA+NB
44      3021 CONTINUE
45      NP=NB
46      3023 CONTINUE
47      COUNT=0.

C
C      PROGRAM RETURNS TO 3000 WITH NEW VALUES FOR VARYING THE PARAMETERS
C      A + B.
C
48      3000 CONTINUE
49      COUNT=COUNT+1.0
50      COUNTER=0.

C
C      VARY THE PARAMETERS A + B :
C
51      A=AMIN-AINT
52      2999 A=A+AINT
53      B=BMIN-BINT
54      2998 B=B+BINT
55      CALL EVAL (NP,A,B,C)
56      COUNTER=COUNTER+1.

C
C      IN THE NEXT SECTION THE SQUARES OF THE DIFFERENCES ARE SUMMED
C
57      SUM=0.
58      DO 3003 J=1,NP
59      3003 SUM=SUM+DATA(J,4)
60      IF (COUNTER.EQ.1)GOTO3002
61      IF (SUM.GT.BSUM)GOTO3004

C
C      IF SUM OF SQUARES OF DIFFERENCES IS LESS THAN PREVIOUS LOWEST,
C      THE VALUES OF A + B ARE STORED AS BA + BB.
C
62      3002 HA=A  &  HB=B  &  BSUM=SUM
63      3004 CONTINUE
64      IF (B.LT.BMAX)GOTO2998
65      IF (A.LT.AMAX)GOTO2999
66      WRITE(5,2006) COUNT,HA,HB
67      IF (COUNT.GE.10.)GOTO3006

C
C      COUNT CONTROLS THE NUMBER OF APPROXIMATIONS MADE (I.E. 10)
C
68      IF (BA.EQ.AMIN.OR.BA.GE.AMAX.OR.BB.EQ.BMIN.OR.BB.GE.BMAX)GOTO3007
69      3007 AMIN=BA-AINT  &  AMAX=BA+AINT  &  AINT=(AMAX-AMIN)/10.
70      BMIN=BB-BINT  &  BMAX=BB+BINT  &  BINT=(BMAX-BMIN)/10.
71      GOTO3000
72      3006 CONTINUE

C
C      CALCULATE THE BEST VALUES OF THE NUMBER EATEN AND OUTPUT THEM :
C
73      CALL EVAL (NP,BA,BB,C)
74      IF (TYPE.EQ.2.)GOTO3010
75      WRITE(6,2007)
76      WRITE(6,2008) (DATA(J,3),J=1,NP)
77      WRITE(6,2009)
78      WRITE(6,2008) (DATA(J,4),J=1,NP)
79      GOTO2999
80      3010 WRITE(6,2030)
81      N=1
82      DO 3030 J=1,NP
83      L=J+1
84      IF (DATA(J,1).EQ.DATA(L,1))GOTO3030
85      WRITE(6,2031) (DATA(J,K),K=1,3,2)
86      WRITE(6,2032) (DATA(M,4),M=N,J)

```

```

87      N=L
88      3030 CONTINUE
89      3099 CONTINUE
C
C      PERFORM ANALYSIS OF VARIANCE :
C
90      DFR=NP-2. $ DFT=NP-1. $ DFM=1.
91      SUM=0. $ SUMSQ=0.
92      DO 4000 J=1,NP
93      SUM=SUM+ATA(J,2)
94      4000 SUMSQ=SUMSQ+DATA(J,2)*DATA(J,2)
95      SSR=SUM*
96      SST=SUMSQ-SUM*SUM/NP
97      SSM=SST-SSR
98      SM=SSM/DFM
99      SR=SSR/DFR
100     ST=SST/DFT
101     F=SM/SP
102     WRITE(5,2100)
103     2100 FORMAT(//,* ANALYSIS OF VARIANCE :*,
104             1//,* SOURCE : DF . SS . MS .
105             2F .*)
104     WRITE(5,2101)DFM,SSM,SM,F
105     2101 FORMAT(//,* MODEL : *,F4.0,3X,3(E14.6,3X))
106     WRITE(5,2102)DFR,SSR,SR
107     2102 FORMAT(* RESIDUAL : *,F4.0,3X,2(E14.6,3X))
108     WRITE(5,2103)DFT,SST,ST
109     2103 FORMAT(//,* TOTAL : *,F4.0,3X,2(E14.6,3X))
110     WRITE(5,2010)BA,BB
111     GOTO3005
112     3007 CONTINUE
113     IF(COUNT.ST.1.0)GOTO3009
C
C      BEST FIT IS AT LIMIT OF ONE OF THE PARAMETERS - (ONLY POSSIBLE ON
C      FIRST RUN THROUGH), PROGRAM MOVES ON TO NEXT PROBLEM.
C
114     WRITE(5,2011)
115     GOTO3003
C
C      INPUT FORMATS :
C
116     1000 FORMAT(I2)
117     1001 FORMAT(10A8)
118     1002 FORMAT(2F10.5)
119     1003 FORMAT(F10.5)
120     1005 FORMAT(15F5.0)
C
C      OUTPUT FORMATS :
C
121     2000 FORMAT(1-1,* PROBLEM NUMBER :*,I3,/,10A8)
122     2001 FORMAT(//,* PARAMETER A - INITIAL LIMITS :*,2(5X,E14.6),
123             1//,* PARAMETER B - INITIAL LIMITS :*,2(5X,E14.6))
124     2002 FORMAT(* CONSTANT C :*,E14.6)
125     2003 FORMAT(//,* FIRST VARIABLE :*)
126     2004 FORMAT(//,* SECOND VARIABLE :*)
127     2006 FORMAT(F12.0,10X,2(5X,E14.6))
128     2007 FORMAT(//,* SEQUENCE HAS CONVERGED*,
129             1//,* CALCULATED VALUES OF SECOND VARIABLE*)
130     2008 FORMAT(1X,5X,10F8.3)
131     2009 FORMAT(//,* SQUARES OF DIFFERENCES FROM ACTUAL VALUES*)
132     2010 FORMAT(/////,* BEST VALUES :*,
133             1//,* PARAMETER A :*,E14.6,8X,* PARAMETER B :*,E14.6)
134     2011 FORMAT(* BEST FIT IS AT LIMIT OF ONE OF THE PARAMETERS*)
135     2020 FORMAT(//,* INDEPENDANT VARIABLE - VARIANCE - REPLICATES OF
136             10DEPENDANT VARIABLE*)
137     2021 FORMAT(5X,F8.3,5X,E14.6,5X,10F5.0)
138     2030 FORMAT(//,* SEQUENCE HAS CONVERGED*,
139             1//,* INDEPENDANT VARIABLE - DEPENDANT VARIABLE - SQUARES OF DIFFERE
140             2NCES*)
141     2031 FORMAT(//,F5.0,4X,E14.6)
142     2032 FORMAT(4)X,5E14.6)
143     END

```

```
1      SUBROUTINE EVAL (NP,A,B,C)
      C
      C      SUBROUTINE EVAL
      C
      C      THIS SUBROUTINE USES FUNCTION XNEWTR TO CALCULATE VALUES OF THE
      C      NUMBER OF PREY EATEN FOR EACH VALUE OF THE PREY DENSITY STORED IN
      C      DATA. THE RESULTANT VALUES ARE STORED IN DATA(J,3) AND THE SQUARE
      C      OF THE DIFFERENCE FROM THE OBSERVED VALUES ARE STORED IN DATA(J,4)
      C
2      COMMON DATA(100,4),IRUN
3      DO 3000 K=1,NP
4      X=DATA(K,1)
5      DATA(K,3)=XNEWTR(X,A,B,C,IRUN)
6      DIFF=DATA(K,2)-DATA(K,3)
7      3000 DATA(K,4)=DIFF*DIFF
8      IF(IRUN.NE.1)RETURN
9      IRUN=2
10     WRITE(5,2000)
11     2000 FORMAT(/,* SUBROUTINE EVAL USES SUM OF SQUARES OF ACTUAL DIFFERENC
      C      IES*,
12     2//,* TIMES THROUGH SEQUENCE - PARAMETER A - PARAMETER B*)
13     RETURN
      END
```

Al.4 Programme PUT

In Chapter 4 the functional responses of Anthocoris nemorum to various distributions of Pieris brassicae eggs in square perspex arenas were examined. Amongst the distributions were two using the negative binomial with values for K of 0.1 and 0.01. The arrangements of the prey using the negative binomial were obtained using this programme.

The square arena is divided into a number of square units. In the experimental arrangement used (Section 4.2) the arena is divided into 15 x 15 units (i.e. a total of 225) each one cm square. This programme is generalized to allow for different arena and unit sizes; K and the total density are input parameters. The arrangement of the input is described in the comment cards.

The calculations are as follows:

1) Calculation of the expected frequencies (see, e.g. Bliss, 1953). The expected frequency of class 0 (ϕ_0) is defined by:

$$\phi_0 = N q^{-K}$$

where N is the total density, K is the constant of the negative binomial distribution (defined as $K = m^2/(s^2 - m)$ where m is the mean density per unit and s^2 is the variance), and q is defined as $1 + m/K$. The expected frequency of successive frequency classes (ϕ_x) can then be calculated, since:

$$\phi_x = R(K + x - 1)/x \cdot \phi(x - 1)$$

where $R = m/(K + m)$ or, if $p = 1 - q$, $R = p/q$.

2) Calculation of the integer frequencies. It is at this stage that rounding off errors may cause the resultant values of K and the total density to differ from the input values. The more units that are available, the better the fit will be. The smaller the value of K is, the worse the fit will be, due to the long tail of high densities at low frequencies being truncated (see Fig. 6.21). Low total densities may also produce large

deviations in K due to rounding off errors. If the actual frequencies are simply rounded off, the resultant total number of units will frequently differ from the actual number of units. To compensate for this, the rounding off factor (initially 0.5) is varied until the correct number of units is obtained.

- 3) The actual prey density and K value are calculated.
- 4) The frequency classes are arranged at random within the arena.
- 5) A random number table for the distribution of prey within each unit is generated.

The control option (NO) determines how many of these operations are done (see listing).


```

1      PROGRAM PUT (INPUT,OUTPUT,TAPES=INPUT,TAPE6=OUTPUT)
C
C      PROGRAMME PUT
C
C      THIS PROGRAMME CALCULATES THE DISTRIBUTION OF FREQUENCY
C      CLASSES BETWEEN AN INPUT NUMBER OF UNITS ACCORDING TO THE
C      NEGATIVE BINOMIAL DISTRIBUTION.
C      THE PARAMETERS K + TOTAL DENSITY ARE INPUT, AND CAN BE VARIED
C      IN A LOGARITHMIC OR ARITHMETIC SERIES.
C
C      THE TERMINATION POINT IS DETERMINED BY THE INPUT PARAMETER NO
C      NO=1 : EXPECTED FREQUENCIES
C      NO=2 : INTEGER FREQUENCIES
C      NO=3 : RANDOM DISTRIBUTION OF FREQUENCIES AMONGST THE UNITS
C      NO=4 : RANDOM NUMBER TABLE FOR INTRA-JUNIT ARRANGEMENT OF
C      INDIVIDUALS.
C
2      DIMENSION F(100), IN(100), MC(50,50)
C
C      F(100) WILL CONTAIN THE CALCULATED CLASS FREQUENCIES
C      IN(100) WILL CONTAIN THE INTEGER CLASS FREQUENCIES
C      MC(50,50) WILL BE USED TO DISTRIBUTE THE UNITS AT RANDOM
C
3      READ(5,1002)PRIMER
4      READ(5,1000)XKMIN,XKINT,XKMAX,K
5      READ(5,1000)XNMIN,XNINT,XNMAX,N
6      READ(5,1001)NO,NREP
7      READ(5,1002)XNUMB
8      IF(NO.EQ.4)READ(5,1003)IS
9      V=RNSET(PRIMER)
C
C      INPUT :
C
C      1. PRIMER(F10.5) - PRIMER FOR THE RANDOM NUMBER GENERATOR.
C      RANDOM NUMBER SEQUENCE INITIALIZED AT 9
C      2. XKMIN,XKINT,XKMAX,K(3F10.5,I1) -
C      K OF THE NEGATIVE BINOMIAL DISTRIBUTION -
C      MINIMUM VALUE,INTERVAL LENGTH + MAXIMUM VALUE -
C      K=0 : PROGRESSION IS LOGARITHMIC
C      K=1 : PROGRESSION IS ARITHMETIC
C      3. XNMIN,XNINT,XNMAX,N(3F10.5,I1) - TOTAL PREY DENSITY -
C      MINIMUM VALUE,INTERVAL LENGTH + MAXIMUM VALUE -
C      N=0 : PROGRESSION IS LOGARITHMIC
C      N=1 : PROGRESSION IS ARITHMETIC
C      4. NO,NREP(I1,I2) - NO=CONTROL PARAMETER (SEE ABOVE)
C      NREP=NUMBER OF REPLICATES FOR ARRANGEMENT OF
C      PREY FREQUENCIES
C      5. XNUMB(F10.5) - TOTAL NUMBER OF UNITS AVAILABLE
C      6. IS(I3) - LENGTH OF SIDE OF AN INDIVIDUAL UNIT -
C      ONLY READ IF NO=4
C
10     WRITE(6,2000)PRIMER
11     IF(K.EQ.0)WRITE(6,2001)XKMIN,XKINT,XKMAX
12     IF(K.EQ.1)WRITE(6,2002)XKMIN,XKINT,XKMAX
13     IF(N.EQ.0)WRITE(6,2003)XNMIN,XNINT,XNMAX
14     IF(N.EQ.1)WRITE(6,2004)XNMIN,XNINT,XNMAX
15     IF(NO.GT.1)WRITE(6,2005)XNUMB
16     IF(NO.EQ.4)WRITE(6,2006)IS
17     NUMB=XNUMB
18     NREP=
C
C      VARY XK AND XN IN A LOGARITHMIC (IF K OR N = 0) OR ARITHMETIC
C      (IF K OR N = 1) PROGRESSION :
C
19     IF(K.EQ.0)XK=XKMIN/XKINT
20     IF(K.EQ.1)XK=XKMIN-XKINT
21     101 IF(N.EQ.0)XN=XNMIN*XNINT
22     IF(N.EQ.1)XN=XNMIN-XNINT
23     IF(N.EQ.0)XN=XNMIN/XNINT
24     IF(N.EQ.1)XN=XNMIN-XNINT
25     100 IF(N.EQ.0)XN=XN*XNINT
26     IF(N.EQ.1)XN=XN+XNINT
27     NR=NR+1
28     WRITE(6,2007)
29     WRITE(6,2008)NR,XK,XN

```

```

30      DO 3000 J=1,100
31      F(J)=0.
32      3000 IN(J)=0
C
C          CALCULATE THE FREQUENCY OF CLASS 0 AND STORE IN F(1) :
C
33      XM=XN/XNUMB
34      P=XM/XK
35      Q=1.+P
36      X=XNUMB+1/J**XK
37      F(1)=X
C
C          CALCULATE SUCCESSIVE FREQUENCY CLASSES AND STORE IN F :
C
38      DO 3001 I=1,100
39      XI=I
40      X=X*(P/Q)*(XI+XK-1.)/XI
41      F(I+1)=X
42      IF(F(I+1).LT.0.1)GOTO3002
43      3001 CONTINUE
44      3002 CONTINUE
45      IF(N0.NE.1)GOTO3023
C
C          N0=1 : EXPECTED FREQUENCY CLASSES OUTPUT AND RUN TERMINATES.
C
46      WRITE(6,2009)
47      DO 3024 JA=1,(I+1)
48      J=JA-1
49      3024 WRITE(6,2010) J,F(JA)
50      GOTO4000
51      3023 CONTINUE
C
C          CHANGE EXPECTED FREQUENCIES TO INTEGERS AND SUM INTEGER
C          FREQUENCIES :
C
52      NN=0
53      DO 3003 J=1,100
54      I(J)=F(J)+0.5
55      3003 NN=NN+IN(J)
56      IF(NN.E0.NUMB)GOTO3008
C
C          IF SUM OF INTEGER FREQUENCIES EQUALS XNUMB GO TO 3008
C          OTHERWISE ADJUST ROUNDING OFF FACTOR UNTIL IT DOES :
C
57      IF(NN.GT.NUMB)GAP=-1.
58      IF(NN.LT.NUMB)GAP=1.
59      ADD=0.5 $ ESS=0.2
60      3012 NN=0
61      DO 3004 J=1,100
62      IN(J)=F(J)+ADD+ESS*GAP
63      NN=NN+IN(J)
64      IF(IN(J).LE.0)GOTO3005
65      3004 CONTINUE
66      3005 IF(NUMB-NN)3007,3008,3009
67      3007 IF(GAP)3010,3008,3011
68      3009 IF(GAP)3011,3008,3010
69      3010 ESS=ESS+ESS/2. $ GOTO3012
70      3011 ESS=ESS/2. $ GOTO3012
71      3008 CONTINUE
72      DO 3027 L=J,100
73      3027 IN(L)=0
C
C          EXPECTED FREQUENCIES AND INTEGER FREQUENCIES ARE OUTPUT.
C
74      WRITE(6,2019)
75      DO 3025 JA=1,(I+1)
76      J=JA-1
77      3025 WRITE(6,2011) J,F(JA),IN(JA)

```

```
C
C          ACTUAL K AND TOTAL PREY DENSITY ARE CALCULATED AND PRINTED :
C
70      DO 3013 J=1,100
71      3013 F(J)=IN(J)
80      S=0.  S  SS=0.
81      DO 3014 J=1,100
82      X=J-1
83      S=S+F(J)*X
84      3014 SS=SS+F(J)*X*X
85      V=(SS-S**2/XNUMB)/(XNUMB-1.)
86      XM=S/XNUMB
87      XKA=XM*X**2/(V-XM)
88      WRITE(6,2012) S,XKA

C
C          NO=2 : RUN IS TERMINATED.
C
89      IF(NO.EQ.2)GOTO4000
90      WRITE(6,2013)
91      NSU=SQRT(XNUMB)

C
C          NSU=LENGTH OF SIDE OF SQUARE MATRIX.
C          I.E. ARENA CONSISTS OF NSU X NSU UNITS
C
C          DISTRIBUTE THE FREQUENCY CLASSES AT RANDOM WITHIN NSU X NSU
C          OF THE MATRIX MC, AND PRINT OUT THE RESULTANT DISTRIBUTION :
C
92      DO 3015 JJ=1,NREP
93      WRITE(6,2014) JJ
94      DO 3016 L=1,NSU
95      DO 3016 J=1,NSU
96      3016 MC(J,L)=0
97      DO 3018 J=2,100
98      NJ=IN(J)
99      IF(NJ.LT.1)GOTO3026
100     DO 3018 L=1,NJ
101     3019 IX=IRAND(NSU)-1  S  IY=IRAND(NSU)-1
102     IF(MC(IX,IY).NE.0)GOTO3019
103     3016 MC(IX,IY)=J-1
104     3026 CONTINUE
105     DO 3020 J=1,NSU
106     3020 WRITE(6,2015) (MC(J,L),L=1,NSU)
107     3015 CONTINUE
108     4000 CONTINUE
109     IF(XN.LT.XNMAX)GOTO100
110     IF(XK.LT.XKMAX)GOTO101
111     WRITE(6,2007)

C
C          NO.LT.4 TERMINATE JOB
C          NO=1 : GENERATE RANDOM NUMBER TABLE FOR INTRA UNIT
C          ARRANGEMENT OF PREY.
C          LENGTH OF SIDE OF UNIT INPUT AS IS
C
112     IF(NO.NE.4)STOP
113     WRITE(6,2016)
114     DO 3022 K=1,50
115     DO 3021 J=1,30
116     3021 IN(J)=IRAND(15)-1
117     IF(15.GT.10)WRITE(6,2018) (IN(J),J=1,30)
118     IF(15.LE.10)WRITE(6,2017) (IN(J),J=1,30)
119     3022 CONTINUE
120     WRITE(6,2007)
```

```
C
C          INPUT FORMATS :
C
121      1000 FORMAT(3F10.5,I1)
122      1001 FORMAT(I1,I2)
123      1002 FORMAT(F10.5)
124      1003 FORMAT(I3)
C
C          OUTPUT FORMATS :
C
125      2000 FORMAT(1H1,* PRIMER FOR THIS JOB =*E14.6)
126      2001 FORMAT(//,* K OF THE NEGATIVE BINOMIAL VARIES FROM *,E14.6,/,
127      1* IN MULTIPLES OF *,E14.6,* TO A MAXIMUM VALUE OF *,E14.6)
127      2002 FORMAT(//,* K OF THE NEGATIVE BINOMIAL VARIES FROM *,E14.5,/,
128      1* AT INTERVALS OF *,E14.6,* TO A MAXIMUM VALUE OF *,E14.6)
128      2003 FORMAT(/,* THE TOTAL PREY DENSITY VARIES FROM *,E14.0,/,
129      1* IN MULTIPLES OF *,E14.6,* TO A MAXIMUM VALUE OF *,E14.6,/)
129      2004 FORMAT(/,* THE TOTAL PREY DENSITY VARIES FROM *,E14.6,/,
130      1* AT INTERVALS OF *,E14.6,* TO A MAXIMUM VALUE OF *,E14.6,/)
130      2005 FORMAT(* TOTAL NUMBER OF ENVIRONMENT UNITS =*E14.6)
131      2006 FORMAT(* LENGTH OF SIDE OF INDIVIDUAL UNITS =*,I4)
132      2007 FORMAT(//,34(2H-),//)
133      2008 FORMAT(* RUN NUMBER *I3,
134      1//,* K IS SET TO *,E14.6,
135      2//,* PREY DENSITY IS SET TO *,E14.6)
134      2009 FORMAT(/,* PREY DENSITY . EXPECTED FREQUENCY .*)
135      2010 FORMAT(I9,I2X,F9.2)
136      2011 FORMAT(I9,I2X,F8.2,I4X,I4)
137      2012 FORMAT(//,* TOTAL PREY DENSITY : *,E14.6,
138      1//,* ACTUAL K = *,E14.6,*)
138      2013 FORMAT(//,* DISTRIBUTION OF UNITS :*)
139      2014 FORMAT(/,* REPLICATE :*I3)
140      2015 FORMAT(5X,50I2)
141      2016 FORMAT(///,* RANDOM NUMBER TABLE :*)
142      2017 FORMAT(5X,15(I3,I1))
143      2018 FORMAT(5X,15(I4,I2))
144      2019 FORMAT(/,* PREY DENSITY . EXPECTED FREQUENCY . ACTUAL FREQUENCY .*
145      1,/)
145      STOP
146      END
```

Al.5 Programme PREDICT

This programme was written to predict the predation in the situation of two prey types mixed together, from the parameters of the functional responses to the individual prey types.

The Random Predator Equations (Rogers, 1972) used to describe the individual functional responses are:

$$N_e = N(1 - \exp(- a(T - T_h N_e)))$$

$$N_{e'} = N'(1 - \exp(- a'(T - T_h' N_{e'})))$$

where N_e is the number of prey eaten, N is the prey density, a is the search efficiency, T is the total time available, T_h is the handling time for one prey, and the primed symbols refer to the second prey type. The predator density (P) is assumed to be unity in this programme (as in the rest of this work) and the programme would have to be altered to allow for the inclusion of P . These equations are readily modified to describe the two prey situation:

$$N_e = N(1 - \exp(- a(T - T_h N_e - T_h' N_{e'})))$$

$$N_{e'} = N'(1 - \exp(- a'(T - T_h' N_{e'} - T_h N_e))).$$

If either N_e or $N_{e'}$ are known, the other can be calculated directly using Newton's approximation. In this programme, the value of N_e is found with $N_{e'}$ set to zero; this value of N_e is then used to calculate $N_{e'}$; this value of $N_{e'}$ is used to recalculate N_e , and so on. Thus, after several approximations, the values of N_e and $N_{e'}$ will converge upon the true values.

This programme was used in Section 5.3, while a modified version was used in Section 3.4.4.

```
1      PROGRAM PREDICT (INPUT,OUTPUT,TAPE5=INPUT,TAPE6=OUTPUT)
C
C      PROGRAM PREDICT
C
C      THIS PROGRAM SOLVES THE TWO-PREY-TYPE ROGERS RANOOM PREDATOR
C      EQUATION USING NEWTONS APPROXIMATION IN A DOUBLE CONVERGING LOOP
C
C      INPUT : 1. TOTAL TIME AVAILABLE - (T)
C              2. NUMBER OF PREY DENSITIES FOR PREY TYPE 1 AND
C              PREY TYPE 2 - (NPI,NPV)
C              3. NPI VALUES OF PREY DENSITY FOR TYPE 1.
C              4. NPV VALUES OF PREY DENSITY FOR TYPE 2.
C              5. PROBLEM NUMBER - (PROB)
C              6. SEARCH EFFICIENCY + HANDLING TIME FOR EACH PREY TYPE -
C              (A1,B1,A2,B2)
C              CARDS 5 + 6 ARE REPEATED FOR EACH SET OF PARAMETERS
C
2      DIMENSION XNOI(50),XNOV(50)
3      READ(5,1001)T
4      READ(5,1002)NPI,NPV
5      READ(5,1003)(XNOI(J),J=1,NPI)
6      READ(5,1003)(XNOV(J),J=1,NPV)
7      3001 READ(5,1001)PROB
8      IF(PROB.EQ.0.)STOP
9      READ(5,1000)A1,B1,A2,B2
10     WRITE(6,2000)A1,B1,A2,B2,T
11     WRITE(5,2001)
12     DO 3000 J=1,NPI
13     XN1=XNOI(J)
14     DO 3000 K=1,NPV
15     XNV=XNOV(K)
16     EI1=0.  EV1=0.
17     EI2=100.  EV2=100.
18     3011 IF(XN1.EQ.0.)GOTO3006
19     EI1=XNEIT(B2,A1,B1,XN1,EI1,EV1,T)
20     DI=ABS((EI1-EI2)/EI1)
21     EI2=EI1
22     GOTO3008
23     3006 DI=0.  EV1=0.
24     3008 IF(XNV.EQ.0.)GOTO3009
25     EV1=XNEIT(B1,A2,B2,XNV,EV1,EI1,T)
26     DV=ABS((EV1-EV2)/EV1)
27     EV2=EV1
28     GOTO3010
29     3009 DV=0.  EV1=0.
30     3010 IF(DI.GT.0.00001.OR.DV.GT.0.00001)GOTO3011
31     R=EI1/EV1
32     P=EI1/(EI1+EV1)
33     WRITE(6,2002)XN1,XNV,EI1,EV1,R,P
34     3000 CONTINUE
35     GOTO3001
36     1000 FORMAT(4F10.5)
37     1001 FORMAT(F10.5)
38     1002 FORMAT(2I5)
39     1003 FORMAT(1X,16F5.0)
40     2000 FORMAT(1X,1,* PROGRAM PREDICT : RESULTS :*,
41     1/,* A FOR PREY TYPE 1 : *,E14.6,
42     2/,* B FOR PREY TYPE 1 : *,E14.6,
43     3/,* A FOR PREY TYPE 2 : *,E14.6,
44     4/,* B FOR PREY TYPE 2 : *,E14.6,
45     5/,* TOTAL TIME AVAILABLE *,E14.6)
41     2001 FORMAT(1///,* 1ST PREY PRESENT . 2ND PREY PRESENT . 1ST PREY EATEN
42     1. 2ND PREY EATEN . RATIO . PERCENTAGE .*)
42     2002 FORMAT(6(4X,E14.6))
43     END
```

PROGRAMME PREDICT LISTING PAGE 2

```
1      FUNCTION XNEWT (H2,A1,B1,X,E1,E2,T)
C
C      THIS FUNCTION USES NEWTONS APPROXIMATION TO SOLVE THE ROGERS
C      RANDOM PREDATOR EQUATION.  IT CAN INCLUDE E2 OF A SECOND PREY
C      TYPE.  EACH WITH A HANDLING TIME OF B2 - I.E. THE TWO PREY
C      SOLUTION.  IF E2=B2=0 THE ONE PREY SITUATION IS OBTAINED.
C
2      1 BR=EXP(-A1*(T-B1*E1-B2*E2))
3      SLOPE=1.+A1*B1*X*BR
4      CEE=E1-X*(1.-BR)
5      E=E1-CEE/SLOPE
6      D=ABS((E-E1)/E)
7      E1=E
8      IF(D.GT.0.00001)GOTO1
9      XNEWT=E
10     RETURN
11     END
```

APPENDIX 2

SUPPLEMENTARY MATERIAL FOR CHAPTER 6

A2.1 LISTING OF THE COMPUTER SIMULATION PROGRAMME


```

C      XKA/B - K OF THE NEGATIVE BINOMIAL
C      SJA/B - LENGTH OF SIDE OF UNIT OF ARENA FOR THE NEGATIVE
C      BINOMIAL DISTRIBUTION OF ATTACKS
C      CA/B - IF C=1 ADJUSTMENT OF VALUES OF XN +XK IS MADE TO OBTAIN
C      A GOOD FIT FOR THE DISTRIBUTION
C      FACTOR A/B - ADJUSTMENT FACTOR USED WHEN CA/B=1
C
2     DIMENSION RESULT(50,3),SPARE(50)
C
C      RESULT WILL CONTAIN THE RESULTS FROM NREP REPLICATES :
C      RESULT(N,1) IS FOR THE NUMBER OF PREY TYPE A EATEN (EATA)
C      RESULT(N,2) IS FOR THE NUMBER OF PREY TYPE B EATEN (EATB)
C      RESULT(N,3) IS FOR THE TIME WASTED (TW)
C      RESULT(N,4) IS FOR THE PERCENTAGE TIME WASTED (PER)
C      RESULT(N,5) IS FOR THE TOTAL TIME SPENT IN THE ARENA (TTIME)
C      RESULT(N,6) IS FOR THE TOTAL TIME SPENT SEARCHING (TS)
C      RESULT(N,7) IS FOR THE LN S VALUES OF PREY TYPE A
C      RESULT(N,8) IS FOR THE LN S VALUES OF PREY TYPE B
C
C      SPARE IS USED TO STORE RESULTS OF ONE TYPE FOR USE IN CALCULATING
C      THE MEAN AND S.E.
C
3     COMMON/A1/ARENA(50,50),LENGTH
C      LENGTH IS THE LENGTH OF SIDE OF THE ARENA
4     COMMON/A2/EATA,EATB,PER,TW,TTIME,TT,TS,UP
5     COMMON/A3/ITA,JTA,THA1,THA2,THA3,THA,ITB,ITB,THB1,THB2,THB3,THB
6     COMMON/A4/ISA,ISA,SA1,SA2,SA3,SA,ISB,ISB,SB1,SB2,SB3,SB,IC
7     COMMON/A5/LSS,TSS,LLS,TLS,H
8     COMMON/A6/LA,LA,LC
9     COMMON/A7/MQ,NENC(100,3),NEN,ISTORE(100,3),NFEED
C
C      NEN ENCOUNTERS WILL BE STORED IN NENC(100,3) AND NFEED PREDATIONS
C      WILL BE STORED IN ISTORE(100,3) FOR THE CONSTRUCTION OF A MAP
C
C      READ IN AND PRINT OUT DATA :
C
10    READ(5,100)NRUNS,NREPS,PRIMER
11    CALL RANSET(PRIMER)
12    READ(5,1001)TT,JP
13    IF(TT.GT.0.)UP=TT
14    IF(TT.EQ.0.)WRITE(6,2000)UP
15    IF(TT.GT.0.)WRITE(6,2001)TT
16    READ(5,1002)ITA,JTA,THA1,THA2,THA3
17    READ(5,1002)ITB,ITB,THB1,THB2,THB3
18    READ(5,1002)ISA,ISA,SA1,SA2,SA3
19    READ(5,1002)ISB,ISB,SB1,SB2,SB3
20    IC=0 S X=0.
21    READ(5,1003)IS
22    WRITE(6,2002)
23    IF(ITA.EQ.1)WRITE(6,2007)
24    IF(ITA.EQ.2)WRITE(6,2008)
25    CALL FIX (IC,JTA,THA1,THA2,THA3,THA,X)
26    WRITE(6,2003)
27    IF(ITB.EQ.1)WRITE(6,2007)
28    IF(ITB.EQ.2)WRITE(6,2008)
29    CALL FIX (IC,ITB,THB1,THB2,THB3,THB,X)
30    WRITE(6,2004)
31    IF(ISA.EQ.1)WRITE(6,2007)
32    IF(ISA.EQ.2)WRITE(6,2008)
33    IF(IS.GE.4)WRITE(6,2006)SA1,SA2
34    IF(IS.LT.4)CALL FIX (IC,ISA,SA1,SA2,SA3,SA,X)
35    WRITE(6,2005)
36    IF(ISB.EQ.1)WRITE(6,2007)
37    IF(ISB.EQ.2)WRITE(6,2008)
38    IF(IS.GE.4)WRITE(6,2006)SB1,SB2
39    IF(IS.LT.4)CALL FIX (IC,ISB,SB1,SB2,SB3,SB,X)
40    IC=1
41    IF(IS.EQ.4)READ(5,1004)LSS,LLS,TSS,TLS,H
42    IF(IS.EQ.5)READ(5,1005)LA,LA,LC
43    WRITE(6,2010)IS
44    IF(IS.EQ.4)WRITE(6,2011)H,LSS,LLS,TSS,TLS
45    IF(IS.EQ.5)WRITE(6,2012)LC,LA,LA
46    WRITE(6,2013)
47    LENGTH=50
48    DO 3000 J=1,NRUNS
49    READ(5,1100)NA,IDA,MOA,XNA,XKA,SQA,CA,FACTORA
50    READ(5,1100)NB,IDB,MOB,XNB,XKB,SQB,CB,FACTORB

```

```

51      MQ=0
52      IF (MQA.EQ.1.AND.MQB.EQ.1)MQ=1
53      SCHA=0.  $  SCHB=0.
54      DO 2999 NREP=1,NREPS
C
C      EMPTY ARENA :
C
55      DO 3018 M=1,LENGTH
56      DO 3018 N=1,LENGTH
57      3018 ARENA(M,N)=0.
C
C      ARRANGE PREY TYPE A :
C
58      SNA=0.
59      IF (XNA.EQ.0.)GOTO3005
60      GOTO(3001,3002,3003,3004)IDA
61      3001 CALL RANPJT (XNA,NREP,SNA,NA)
62      GOTO3005
63      3002 CALL RANPJT (XNA,NREP,NA)
64      SNA=XNA
65      GOTO3005
66      3003 CALL AGGPJT (XNA,NREP,XKA,SQA,CA,FACTORA,SNA,NA)
67      IF (CA.EQ.10.)GOTO3000
68      GOTO3005
69      3004 CALL CLUPJT (XNA,NREP,SNA,NA)
70      3005 CONTINUE
C
C      ARRANGE PREY TYPE B :
C
71      SNB=0.
72      IF (XNB.EQ.0.)GOTO3010
73      GOTO(3006,3007,3008,3009)IDB
74      3006 CALL RANPJT (XNB,NREP,SNB,NB)
75      GOTO3010
76      3007 CALL RANPJT (XNB,NREP,NB)
77      SNB=XNB
78      GOTO3010
79      3008 CALL AGPJT (XNB,NREP,XKB,SQB,CB,FACTORB,SNB,NB)
80      IF (CB.EQ.10.)GOTO3000
81      GOTO3010
82      3009 CALL CLUPJT (XNB,NREP,SNB,NB)
83      3010 CONTINUE
C
C      DEFINE SEARCHING PARAMETERS IF NECESSARY :
C
84      IF (ITA.EQ.1)CALL FIX (IC,JTA,THA1,THA2,THA3,THA,SNA)
85      IF (ITB.EQ.1)CALL FIX (IC,JTB,THB1,THB2,THB3,THB,SNB)
86      IF (ISA.EQ.1)CALL FIX (IC,JSA,SA1,SA2,SA3,SA,SNA)
87      IF (ISB.EQ.1)CALL FIX (IC,JSB,SB1,SB2,SB3,SB,SNB)
C
C      PREDATION :
C
88      NEN=0  $  NFEED=0
89      GOTO(3011,3011,3011,3012,3013)IS
90      3011 CALL EAT123 (IS,NREP)
91      GOTO3014
92      3012 CALL AG-EAT (NREP)
93      GOTO3014
94      3013 CALL CLUEAT (NREP)
95      3014 CONTINUE
96      IF (NREP.EQ.1.AND.MQ.EQ.1)CALL MAP
C
C      STORE RESULTS FOR REPLICATE :
C
97      RESULT(NREP,1)=EATA  $  RESULT(NREP,2)=EATB
98      RESULT(NREP,3)=TW  $  RESULT(NREP,4)=PER
99      RESULT(NREP,5)=TTIME  $  RESULT(NREP,6)=TS
100     IF (SNA.LE.EATA)GOTO3015
101     RESULT(NREP,7)=ALOG((SNA-EATA)/SNA)
102     GOTO3015
103     3015 RESULT(NREP,7)=0.  $  SCHA=1.
104     3016 IF (SNB.LE.EATB)GOTO3017
105     RESULT(NREP,8)=ALOG((SNB-EATB)/SNB)
106     GOTO2999
107     3017 RESULT(NREP,8)=0.  $  SCHB=1.
108     2999 CONTINUE
C
C      CALCULATE AND PRINT OUT MEANS AND S.E. FOR RUN :

```

```

C
109      DO 3020 K=1,8
110          IF (SCHA.EQ.1.0.AND.K.EQ.7) GOTO3021
111          IF (SCHA.EQ.1.0.AND.K.EQ.8) GOTO3021
112          DO 3022 K=1,NREPS
113      3022 SPARE(KA)=RESULT(KA,K)
114          CALL SUBS(XMEAN,SE,SPARE,NREPS)
115          RESULT(1,K)=XMEAN
116          RESULT(2,K)=SE
117          GOTO3020
118      3021 RESULT(1,K)=0. 5 RESULT(2,K)=0.
119      3020 CONTINUE
120          WRITE(5,2102)(RESULT(1,K),K=1,8)
121          WRITE(5,2103)(RESULT(2,K),K=1,8)
122          WRITE(5,2103)
123      3000 CONTINUE
C
C      FORMATS :
C
124      1000 FORMAT(2I2,F10.5)
125      1001 FORMAT(2F10.5)
126      1002 FORMAT(2I1,3F5.0)
127      1003 FORMAT(I1)
128      1004 FORMAT(2I3,3F5.0)
129      1005 FORMAT(2I3,F6.0)
130      1100 FORMAT(I3,2I1,5F6.0)
131      2000 FORMAT(//,* -*,50(*5-*),//,
132          1* IN THIS JOB AGGREGATIVE RESPONSE DATA IS GENERATED WITH A GIVING
133          2 UP TIME OF *F10.0,//)
134      2001 FORMAT(//,* -*,50(*5-*),//,
135          1* IN THIS JOB FUNCTIONAL RESPONSE DATA IS GENERATED WITH A TIME LI
136          2MIT OF *F10.0,//)
137      2002 FORMAT(* PARAMETER DEFINITION :*,//
138          1* HANDLING TIME FOR PREY TYPE A :*)
139      2003 FORMAT(/,* HANDLING TIME FOR PREY TYPE B :*)
140      2004 FORMAT(/,* SEARCH EFFICIENCY FOR PREY TYPE A :*)
141      2005 FORMAT(/,* SEARCH EFFICIENCY FOR PREY TYPE B :*)
142      2006 FORMAT(* CONSTANT IN NORMAL SEARCH PHASE AT*F10.5,* IN LOCAL SEARCH
143          1* PHASE CONSTANT AT*F10.5)
144      2007 FORMAT(* PARAMETER DEFINED BY INITIAL PREY DENSITY*)
145      2008 FORMAT(* PARAMETER DEFINED BY INSTANTANEOUS NUMBER OF PREY EATEN*)
146      2010 FORMAT(//* IN THIS JOB SEARCH STRATEGY NUMBER*13* IS USED*)
147      2011 FORMAT(* HUNGER FACTOR = *,F5.0,
148          1/* LENGTH OF SHORT STEP = *,I4,
149          2/* LENGTH OF LONG STEP = *,I4,
150          3/* TIME USED FOR SHORT STEP = *,F5.0,
151          4/* TIME USED FOR LONG STEP = *,F5.0)
152      2012 FORMAT(* TIME TO SEARCH CLUMP AREA = *,F5.0,
153          1/* LENGTH OF NORMAL STEP = *,I4,
154          2/* LENGTH OF LONG STEP = *,I5)
155      2013 FORMAT(//,* -*,50(*5-*),//)
156      2102 FORMAT(/,* MEANS :*,/,8(2X,E14.6))
157      2103 FORMAT(* STANDARD ERROR OF MEAN :*,/,8(2X,E14.6))
158          STOP
159          END

```

```

1      SUBROUTINE RESPUT (XN,NREP,SN,NN)

```

```

C
C      THIS SUBROUTINE DISTRIBUTES XN PREY WITHIN THE ARENA.
C      IF XN IS NOT A PERFECT SQUARE, IT IS REDUCED TO THE NEAREST
C      PERFECT SQUARE BELOW THE INPUT VALUE. IF NREP=1 THE NUMBER OF
C      PREY DISTRIBUITED IS PRINTED OUT.
C      RESPUT CAN BE ADAPTED TO ARENAS OF DIFFERENT SIZES
C      BY CHANGING THE COMMON/A1/ CARD.
C

```

```

2      COMMON/A1/ARENA(50,50),LENGTH
3      NN=SQRT(XN)
4      N=XN
5      NN=NN+1.
6      GAP=LENGTH/NN
7      XL=0.
8      DO 3000 J=1,NN

```

```

9      XL=XL+GAP
10     L=XL
11     XM=0.
12     DO 3000 K=1,N
13     XM=XM+GAP
14     M=XM
15     3000 ARENA(L,M)=ARENA(L,M)+NN
16     M=M*N
17     SM=N
18     IF(NREP.EQ.1.AND.NN.EQ.1)WRITE(6,2000)N
19     IF(NREP.EQ.1.AND.NN.EQ.100)WRITE(6,2001)N
20     2000 FORMAT(15,' PREY OF TYPE A ARE DISTRIBUTED REGULARLY*')
21     2001 FORMAT(15,' PREY OF TYPE B ARE DISTRIBUTED REGULARLY*')
22     RETURN
23     END

```

C

```

1      SUBROUTINE RANPUT (XN,NREP,NN)
C
C      THIS SUBROUTINE DISTRIBUTES XN PREY IN THE ARENA AT RANDOM.
C      IF NREP=1 THE NUMBER OF PREY DISTRIBUTED IS PRINTED OUT.
C      RANPUT CAN BE ADAPTED TO ARENAS OF DIFFERENT SIZES
C      BY CHANGING THE COMMON/A1/ CARD.
C
2      COMMON/A1/ARENA(50,50),LENGTH
3      N=XN
4      DO 3001 J=1,N
5      IX=I+AND(LENGTH) $ IY=IRAND(LENGTH)
6      3001 ARENA(IX,IY)=ARENA(IX,IY)+NN
7      IF(NREP.EQ.1.AND.NN.EQ.1)WRITE(6,2000)N
8      IF(NREP.EQ.1.AND.NN.EQ.100)WRITE(6,2001)N
9      2000 FORMAT(15,' PREY OF TYPE A ARE DISTRIBUTED AT RANDOM*')
10     2001 FORMAT(15,' PREY OF TYPE B ARE DISTRIBUTED AT RANDOM*')
11     RETURN
12     END

```

C

```

1      SUBROUTINE AGSPUT (XN,NREP,XK,SQ,CORRECT,FACTOR,SP,NNN)
C
C      THIS SUBROUTINE DISTRIBUTES XN PREY IN THE ARENA USING THE
C      NEGATIVE BINOMIAL DISTRIBUTION AND A K VALUE OF XK.
C      IT FUNCTIONS IN A SIMILAR WAY TO PROGRAMME NEWPJT.
C      THE ARENA IS DIVIDED INTO XNUMB UNITS EACH OF SIDE SQ.
C      THE EXPECTED FREQUENCY DISTRIBUTION OF XN PREY AMONGST XNUMB UNITS
C      WITH K SET TO XK IS CALCULATED, AND THE ROUNDING OFF FACTOR IS
C      ADJUSTED TO GIVE EXACTLY XNUMB UNITS. THE UNITS ARE ARRANGED
C      RANDOMLY WITHIN THE ARENA, AS ARE THE PREY WITHIN EACH UNIT.
C      AGSPUT CAN BE ADAPTED TO ARENAS OF DIFFERENT SIZES
C      BY CHANGING THE COMMON/A1/ CARD.
C
2      DIMENSION F(100),IN(100),MC(50,50),SPARE(100)
C
C      F(100) WILL CONTAIN THE GENERATED FREQUENCIES AS REAL NUMBERS
C      IN(100) WILL CONTAIN THE ROUNDED OFF FREQUENCIES
C      MC(50,50) WILL BE USED TO DISTRIBUTE THE UNITS RANDOMLY WITHIN THE
C      ARENA
C
3      COMMON/A1/ARENA(50,50),LENGTH
4      IF(NREP.EQ.1)GOTO3999
C
C      THE FREQUENCIES ARE ONLY CALCULATED FOR THE FIRST REPLICATE.
C      CHECK THAT SQ HAS A SUITABLE VALUE :
C
5      CHECK=0.
6      SK=XK $ SN=XN
7      ISQ=SQ
8      SIUE=LENGTH/SQ
9      I=SIDE

```

```

10         IF (FLOAT(I).NE.SIDE)GOTO4000
11         XNUMB=SIDE*SIDE
12         NUMB=XNUMB
C
C         CALCULATE THE FREQUENCY OF CLASS 0 AND STORE IN F(1) :
C
13         5001 CONTINUE
14         DO 3000 J=1,100
15         F(J)=0.
16         3000 IN(J)=0
17         X4=SN/XNUMB
18         P=X4/SK
19         Q=1.+P
20         X=XNUMB/Q**SK
21         F(1)=X
C
C         CALCULATE SUCCESSIVE FREQUENCY CLASSES AND STORE IN F :
C
22         DO 3001 I=1,99
23         XI=I
24         X=X*(P/Q)*(XI+SK-1.)/XI
25         F(I+1)=X
26         IF (F(I+1).LT.0.1)GOTO3002
27         3001 CONTINUE
28         3002 CONTINUE
C
C         CHANGE EXPECTED FREQUENCIES TO INTEGERS AND SUM INTEGER
C         FREQUENCIES :
C
29         NN=0
30         DO 3003 J=1,100
31         IN(J)=F(J)+0.5
32         3003 NN=NN+IN(J)
33         IF (NN.EQ.NUMB)GOTO3006
C
C         IF SUM OF INTEGER FREQUENCIES EQUALS XNUMB GO TO 3006 .
C         OTHERWISE ADJUST ROUNDING OFF FACTOR UNTIL IT DOES :
C
34         IF (NN.GT.NUMB)GAP=-1.
35         IF (NN.LT.NUMB)GAP=1.
36         ADD=0.5  $  ESS=0.2
37         3012 NN=0
38         DO 3004 J=1,100
39         IN(J)=F(J)+ADD+ESS*GAP
40         NN=NN+IN(J)
41         IF (IN(J).LE.0)GOTO3005
42         3004 CONTINUE
43         3005 IF (NUMB-NN)3007,3008,3009
44         3007 IF (GAP)3010,3008,3011
45         3009 IF (GAP)3011,3008,3010
46         3010 ESS=ESS+ESS/2.  $  GOT03012
47         3011 ESS=ESS/2.  $  GOT03012
48         3008 CONTINUE
49         DO 3027 L=J,100
50         3027 IN(L)=0
51         3006 CONTINUE
C
C         CALCULATE ACTUAL PREY DENSITY AND VALUE OF K :
C
52         DO 3013 J=1,100
53         3013 SPARE(J)=IN(J)
54         S=0.  $  SS=0.
55         DO 3014 J=1,100
56         X=J-1
57         S=S+SPARE(J)*X
58         3014 SS=SS+SPARE(J)*X*X
59         V=(SS-S**2/XNUMB)/(XNUMB-1.)
60         X4=S/XNUMB
61         XKA=X4*X/(V-X4)
62         IF (CORRECT.NE.1.)GOTO5000
C
C         IF CORRECTIONS ARE NOT TO BE MADE GO TO 5000
C
C         IF RESULTANT VALUES OF XN AND XK ARE NOT WITHIN 1/10 OF THE INPUT
C         VALUES, REDUCE XK BY FACTOR AND INCREASE XN BY FACTOR AS
C         NECESSARY :
C
63         DIFFN=(XN-S)/XN

```

```

64      IF (DIFFN.LT.0.1)GOTO5002
65      SN=SN+S1*FACTOR
66      5002 CONTINUE
67      DIFFK=ABS(XK-XKA)/XK
68      IF (DIFFK.LT.0.1)GOTO5003
69      SK=SK-SK*FACTOR
70      5003 CONTINUE
71      IF (DIFFN.LT.0.1.AND.DIFFK.LT.0.1)GOTO5000
72      CHECK=CHECK+1.
73      IF (CHECK.LT.50.)GOTO5001
74      WRITE (5,2011)
75      CORRECT=10.
76      RETJRN
77      5000 CONTINUE
C
C      PRINT OUT ACTJAL PREY DENSITY, VALUE OF K AND CALCULATED FREQUEN-
C      CIES :
C
78      IF (N.NN.EQ.1)WRITE (6,2000)S,XKA
79      IF (N.NN.EQ.100)WRITE (6,2001)S,XKA
80      NSU=SQRT(XNUM3)
C
C      NSU = SQRT(TOTAL NUMBER OF UNITS)
C      I.E. ARENA CONSISTS OF NSU X NSU UNITS
C
81      3999 CONTINUE
C
C      EMPTY MC :
C
82      DO 3016 L=1,50
83      DO 3016 J=1,50
84      3016 MC(J,L)=0
C
C      DISTRIBUTE FREQUENCIES RANDOMLY WITHIN NSU X NSJ OF MC :
C
85      DO 3018 J=2,100
86      NJ=I4(J)
87      IF (NJ.LT.1)GOTO3026
88      DO 3018 L=1,NJ
89      3019 IX=IRAND(NSU) $ IY=IRAND(NSU)
90      IF (MC(IX,IY).NE.0)GOTO3019
91      3018 MC(IX,IY)=J-1
92      3026 CONTINUE
C
C      DISTRIBUTE DENSITIES AT RANDOM WITHIN EACH UNIT :
C
93      DO 4001 J=1,NSU
94      DO 4001 K=1,NSU
95      N=MC(J,K)
96      IF (N.EQ.0)GOTO4001
97      DO 4002 L=1,N
98      IX=J*ISQ+IRAND(ISQ)-ISQ
99      IY=K*ISQ+IRAND(ISQ)-ISQ
100     4002 ARENA(IX,IY)=ARENA(IX,IY)+N.NN
101     4001 CONTINUE
102     SP=S
103     RETJRN
C
C      FORMATS :
C
104     2000 FORMAT(F5.0,* PREY OF TYPE A HAVE BEEN DISTRIBUTED WITH A K VALUE
105     2001 FORMAT(F5.0,* PREY OF TYPE B HAVE BEEN DISTRIBUTED WITH A K VALUE
106     2011 FORMAT(* ADJUSTMENT DOES NOT WORK*)
107     4000 WRITE (5,2010)S0
108     2010 FORMAT(* VALUE OF S0 INPUT(*,F10.5,*) IS UNSUITABLE*)
109     RETJRN
110     END
C

```

1 SUBROUTINE CLJPUT (XN,NRFP,SN,NN)

C

```

C THIS SUBROUTINE DISTRIBUTES RANDOMLY ARRANGED CLUMPS OF EIGHT PREY
C IN THE ARENA. THE CLUMPS ARE A SQUARE OF 2 X 2 WITH 2 PREY IN
C EACH.
C IF NREP=1 THE PREY DENSITY AND ARRANGEMENT IS PRINTED OUT.
C THIS SUBROUTINE CAN BE ADAPTED TO ARENAS OF DIFFERENT SIZES BY
C CHANGING THE COMMON/A1/ CARD.
C
2 COMMON/A1/ARENA(50,50),LENGTH
3 N=XN/R
4 DO 3000 J=1,N
5 IX=IPAND(49) $ IY=IRAND(49)
6 DO 3000 L=IX,IX+1
7 DO 3000 K=IY,IY+1
8 3000 ARENA(L,K)=ARENA(L,K)+2.*NN
9 X=N*A.
10 SN=X
11 IF(NREP.EQ.1.AND.NN.EQ.1)WRITE(6,2000)X
12 IF(NREP.EQ.1.AND.NN.EQ.100)WRITE(6,2001)X
13 2000 FORMAT(F10.0,* PREY OF TYPE A ARE ARRANGED IN RANDOMLY DISTRIBUTED
1 CLUMPS OF EIGHT*)
14 2001 FORMAT(F10.0,* PREY OF TYPE B ARE ARRANGED IN RANDOMLY DISTRIBUTED
1 CLUMPS OF EIGHT*)
15 RETURN
16 END

```

1 SUBROUTINE EAT123 (IS,NREP)

```

C THIS SUBROUTINE CONTAINS THREE SEARCH STRATEGIES FOR THE PREY :
C IS=1 - RANDOM SEARCH
C IS=2 - RANDOM WALK (CALLING SUBROUTINE DIR)
C IS=3 - FORWARD DIRECTED RANDOM WALK (CALLING SUBROUTINE FDIR)
C THE NUMBER OF PREY EATEN OF EACH TYPE (EATA + EATB) AND THE TIME
C WASTED (TW) ARE SUMMED FOR EACH REPLICATE AND THE PERCENTAGE TIME
C WASTED (PER) IS CALCULATED AT THE END. AS EACH LOCATION IN THE
C ARENA IS SEARCHED, ITS VALUE IS SET TO ZERO IF NO PREY REMAIN AT
C THAT LOCATION, SO THAT UNITS PREVIOUSLY SEARCHED CAN BE RECOGNISED
C AND COUNTED.
C THE SEARCH EFFICIENCIES AND HANDLING TIMES CAN BE ALTERED IN
C RESPONSE TO THE NUMBER OF PREY EATEN.
C
2 COMMON/A1/ARENA(50,50),LENGTH
3 COMMON/A2/EATA,EATB,PER,TW,TTIME,TT,TS,UP
4 COMMON/A3/JTA,JTA,THA1,THA2,THA3,THA,ITB,ITB,THB1,THB2,THB3,THB
5 COMMON/A4/ISA,ISA,SA1,SA2,SA3,SA,ISB,ISB,SB1,SB2,SB3,SB,IC
6 COMMON/A7/MQ, VENC(100,3),NEN,ISTOPE(100,3),NFEED
7 EATA=0. $ EATB=0. $ TS=0. $ TW=0. $ L=1 $ LDIR=0
8 TTIME=0. $ TIME=0.
9 5000 IX=IPAND(LENGTH) $ IY=IRAND(LENGTH)
10 4000 IF(ITA.EQ.2)CALL FIX (IC,JTA,THA1,THA2,THA3,THA,EATA)
11 IF(ITB.EQ.2)CALL FIX (IC,ITB,THB1,THB2,THB3,THB,EATB)
12 IF(ISA.EQ.2)CALL FIX (IC,ISA,SA1,SA2,SA3,SA,EATA)
13 IF(ISB.EQ.2)CALL FIX (IC,ISB,SB1,SB2,SB3,SB,EATB)
14 IF(ARENA(IX,IY).LE.0.)GOTO6000
15 CALL ENC (SA,SH,EA,EB,IX,IY,NREP)
16 EATA=EATA+EA $ EATB=EATB+EB
17 TTIME=TTIME+THA*EA+THB*EB
18 IF(TTIME.GE.TT.AND.TT.GT.0.)GOTO7000
19 IF(EA.GT.0.0. OR EB.GT.0.0)TIME=-1.
20 5000 CONTINUE
21 TIME=TIME+1
22 IF(TIME.GE.UP)GOTO8000
23 TTIME=TTIME+1
24 IF(TTIME.GE.TT.AND.TT.GT.0.)GOTO8000
25 IF(ARENA(IX,IY).EQ.-1.)TW=TW+1.
26 TS=TS+1.
27 IF(ARENA(IX,IY).EQ.0.)ARENA(IX,IY)=-1.
28 GOTO(5000,5001,5002)IS
C
C IS=1 : A NEW PAIR OF RANDOM CO-ORDINATES IS SELECTED
C IS=2 : PREDATOR MOVES ONE SQUARE IN ANY DIRECTION
C IS=3 : PREDATOR MOVES ONE SQUARE, NOT TURNING MORE THAN A RIGHT
C ANGLE RELATIVE TO THE LAST DIRECTION OF MOVEMENT

```



```

C
29 5001 CALL DIR (IX,IY,L,LENGTH)
30   GOT04000
31 5002 CALL FDIR (IX,IY,L,LDIR,LENGTH)
32   GOT04000
33 7000 IF (EA.EQ.0.)GOTO7001
34   EATA=EATA+(TT-TTIME)/((EA/(EA+EB))*THA)
35 7001 IF (EB.EQ.0.)GOTO3000
36   EATB=EATB+(TT-TTIME)/((EB/(EA+EB))*THB)
37 8000 PER=100.*TW/TS
38   RETJRN
39   END

```

C

1 SUBROUTINE AGSEAT (NREP)

```

C
C THIS SUBROUTINE IMITATES THE INCREASED RATE OF TURN AND REDUCED
C STEP LENGTH OF A PREDATOR IN RESPONSE TO A PREY.
C
C THE NORMAL, LONG-STEP, SMALL-ANGLE-OF-TURN PHASE IS MODELLED BY
C MOVING LLS SQUARES IN ONE DIRECTION (USING SDIR), FOLLOWED BY A
C TURN USING FDIR (I.E. OF NOT MORE THAN A RIGHT ANGLE) AND A FURTHER
C LLS SQUARES IN THE NEW DIRECTION ETC. : EACH STEP USES TLS TIME
C UNITS. IF A PREY IS ENCOUNTERED, THE PREDATOR ALTERS ITS BEHAV-
C IOUR TO AN INCREASED-RATE-OF-TURN, REDUCED-STEP-LENGTH PHASE.
C THIS IS IMITATED USING STEP LENGTHS OF LLS, EACH USING TSS TIME,
C AND USING DIR (I.E. RANDOM DIRECTION OF TURN) TO TURN AFTER EACH
C STEP. THIS PHASE IS USED FOR H TIME UNITS ; IF ANOTHER PREY IS
C FOUND, A FURTHER H TIME UNITS ARE USED IN THIS PHASE.
C THE HANDLING TIMES (THA, THB) CAN BE ALTERED IN RESPONSE TO THE
C NUMBER OF PREY EATEN. DIFFERENT SEARCH EFFICIENCIES CAN BE USED
C IN THE TWO SEARCH PHASES.
C

```

```

2 COMMON/A1/ARENA(50,50),LENGTH
3 COMMON/A2/EATA,EATB,PER,TW,TTIME,TT,TS,UP
4 COMMON/A3/ITA,JTA,THA1,THA2,THA3,THA,ITB,JB,THB1,THB2,THB3,THB
5 COMMON/A4/ISA,JSA,SA1,SA2,SA3,SA,ISB,JSB,SB1,SB2,SB3,SB,IC
6 COMMON/A5/LSS,TSS,LLS,TLS,H
7 COMMON/A7/MQ, NENC(100,3),NEN,ISTORE(100,3),VFEEF
8 EATA=0. $ EATB=0. $ TW=0. $ TWO=0. $ L=1
9 S=LLS $ STEP=0. $ LDIR=0 $ SA=SA1 $ SB=SB1
10 TTIME=0. $ TIME=0. $ TS=0.
11 IX=IRAND(LENGTH) $ IY=IRAND(LENGTH)
12 4000 IF (ARENA(IX,IY).LE.0.)GOTO6000
13   CALL ENC (SA,SB,EA,EB,IX,IY,NREP)
14   IF (EA.EQ.0.0.AND.EB.EQ.0.)GOTO6000
15   EATA=EATA+EA $ EATB=EATB+EB
16   IF (ITA.EQ.2)CALL FIX (IC,JTA,THA1,THA2,THA3,THA,EATA)
17   IF (ITB.EQ.2)CALL FIX (IC,JB,THB1,THB2,THB3,THB,EATB)
18   TTIME=TTIME+THA*EA+THB*EB
19   IF (TTIME.GE.TT.AND.TT.GT.0.)GOTO7000
20   TIME=-TS
21   IF (STEP.GT.1.) TIME=-TLS/S
22   TWO=H+1
23 5000 CONTINUE
24   IF (ARENA(IX,IY).EQ.-1.)TW=TW+TSS
25   IF (ARENA(IX,IY).EQ.-1.0.AND.STEP.GT.1.)TW=TW+TLS/S-TSS
26   IF (ARENA(IX,IY).EQ.0.)ARENA(IX,IY)=-1.
27   TWO=TWO-1.
28   IF (TWO.LE.0.)GOTO5000
29   CALL DIR (IX,IY,L,LENGTH)
30   TIME=TIME+TSS
31   IF (TIME.GE.UP)GOTO8000
32   TS=TS+TSS
33   TTIME=TTIME+TSS
34   IF (TTIME.GE.TT.AND.TT.GT.0.)GOTO8000
35   SA=SA2 $ SB=SB2
36   GOT04000
37 5000 STEP=STEP-1.
38   IF (STEP.GT.0.)GOTO9000
39   STEP=S
40   CALL FDIR (IX,IY,L,LDIR,LENGTH)
41   GOT03000

```

```

42 9000 CALL SUIV (IX,IY,L,LDIR,LENGTH)
43 3000 SA=SA1 , SB=SB1
44 TIME=TIME+T/S/S $ TS=TS+T/S/S $ TIME=TIME+T/S/S
45 IF (TIME.GE.TT.AND.TT.GT.0.)GOTO8000
46 IF (TIME.GE.UP)GOTO8000
47 GOTO4000
48 7000 IF (EA.EQ.0.)GOTO7001
49 EATA=EATA+(TT-TIME)/((EA/(EA+EB))*THA)
50 7001 IF (EB.EQ.0.)GOTO8000
51 EATB=EATB+(TT-TIME)/((EB/(EA+EB))*THB)
52 8000 PER=100.*TW/TS
53 RETJRN
54 END

```

C

```

1 SUBROUTINE CLJEAT (NREP)
C
C THIS SUBROUTINE MIMICS INTENSIVE LOCAL SEARCH IN RESPONSE TO
C FINDING A PREY.
C
C NORMAL SEARCH INVOLVES STEPS OF LENGTH LA USING 1 TIME UNIT EACH,
C FOLLOWED BY A TURN USING FDIR ( I.E. NOT MORE THAN A RIGHT ANGLE).
C IF A PREY IS FOUND, AN AREA OF 3 X 3 UNITS IMMEDIATELY AROUND IT
C IS SEARCHED, WHEREUPON THE PREDATOR TAKES A STEP OF LENGTH LB ;
C THIS MANOUVRE USES TC TIME UNITS.
C THE HANDLING TIMES (THA,THB) CAN BE ALTERED IN RESPONSE TO THE
C NUMBER OF PREY EATEN. DIFFERENT SEARCH EFFICIENCIES CAN BE USED
C IN THE TWO SEARCH PHASES.
C
2 COMMON/A1/ARENA(50,50),LENGTH
3 COMMON/A2/EATA,EATB,PER,TW,TIME,TT,TS,UP
4 COMMON/A3/ITA,JTA,THA1,THA2,THA3,THA,ITB,ITB,THB1,THB2,THB3,THB
5 COMMON/A4/ISA,JSA,SA1,SA2,SA3,SA,ISB,JSB,SB1,SB2,SB3,SB,IC
6 COMMON/A5/LA,LB,TC
7 COMMON/A7/MG,NENC(100,3),NEN,ISTOPE(100,3),NFEEJ
8 EATA=0. $ EATB=0. $ LDIR=0 $ TW=0. $ TS=0.
9 TIME=0. $ TTIME=0.
10 IX=IRAND(LENGTH) $ IY=IRAND(LENGTH)
11 5000 IF (ARENA(IX,IY).LE.0.)GOTO6000
12 CALL ENC (SA1,SB1,EA,EB,IX,IY,NREP)
13 IF (EA.EQ.0.0.AND.EB.EQ.0.0.)GOTO6000
14 EATA=EATA+EA $ EATB=EATB+EB
15 IF (ITA.E.2)CALL FIX (IC,JTA,THA1,THA2,THA3,THA,EATA)
16 IF (ITB.E.2)CALL FIX (IC,ITB,THB1,THB2,THB3,THB,EATB)
17 TIME=TIME+THA*EA+THB*EB
18 IF (TIME.GE.TT.AND.TT.GT.0.)GOTO7000
19 TIME=0.
20 IXA=IX-1 $ IF (IXA.LT.1)IXA=1
21 IXB=IX+1 $ IF (IXB.GT.LENGTH)IXB=LENGTH
22 IYA=IY-1 $ IF (IYA.LT.1)IYA=1
23 IYB=IY+1 $ IF (IYB.GT.LENGTH)IYB=LENGTH
24 DO 3001 J=IXA,IXB
25 DO 3001 K=IYA,IYB
26 IF (ARENA(J,K).LE.0.)GOTO6001
27 CALL ENC (SA2,SB2,EA,EB,J,K,NREP)
28 IF (EA.EQ.0.0.AND.EB.EQ.0.0.)GOTO6001
29 EATA=EATA+EA $ EATB=EATB+EB
30 IF (ITA.E.2)CALL FIX (IC,JTA,THA1,THA2,THA3,THA,EATA)
31 IF (ITB.E.2)CALL FIX (IC,ITB,THB1,THB2,THB3,THB,EATB)
32 TIME=TIME+THA*EA+THB*EB
33 IF (TIME.GE.TT.AND.TT.GT.0.)GOTO7000
34 TIME=-TC/9.
35 5001 CONTINUE
36 IF (ARENA(J,K).EQ.-1.)TW=TW+TC/9.
37 IF (ARENA(J,K).EQ.0.)ARENA(J,K)=-1.
38 TIME=TIME+TC/9.
39 IF (TIME.GE.UP)GOTO8000
40 TS=TS+TC/9.
41 TIME=TIME+TC/9.
42 IF (TIME.GE.TT.AND.TT.GT.0.)GOTO8000
43 3001 CONTINUE
44 CALL FDIR (IX,IY,LB,LDIR,LENGTH)
45 GOTO5000

```

```

46 6000 IF (ARENA (IX, IY).EQ.-1.) TW=TW+1.
47     IF (ARENA (IX, IY).EQ.0.) ARENA (IX, IY)=-1.
48     TS=TS+1.
49     TIME=TIME+1.
50     IF (TIME.GE.UP) GOTO 8000
51     TTIME=TTIME+1.
52     IF (TTIME.GE.TT.AND.TT.GT.0.) GOTO 8000
53     CALL FDIR (IX, IY, LA, LDIR, LENGTH)
54     GOTO 5000
55 7000 IF (EA.EQ.0.) GOTO 7001
56     EATA=EATA+(TT-TTIME)/((EA/(EA+EB))*THA)
57 7001 IF (EB.EQ.0.) GOTO 8000
58     EATB=EATB+(TT-TTIME)/((EB/(EA+EB))*THB)
59 8000 PER=100.*TW/TS
60     RETURN
61     END

```

C

```

1     SUBROUTINE ENC (SA, SB, EA, EB, IX, IY, NREP)
C
C     THIS SUBROUTINE IS USED EACH TIME A LOCATION IS FOUND WITH A PREY
C     IN IT. IT USES THE SEARCH EFFICIENCY (SA, SB) TO FIND THE NUM-
C     BERS OF EACH PREY TYPE EATEN AT THAT LOCATION. ADJUSTS THE VALUE
C     OF ARENA ACCORDINGLY, AND, IF A MAP IS TO BE CONSTRUCTED, STORES
C     THE LOCATION OF THE ENCOUNTERS AND FEEDS WHICH OCCURRED.
C
2     COMMON/A1/ARENA(50,50), LENGTH
3     COMMON/A7/MQ, NENC(100,3), NEN, ISTORE(100,3), NFEED
4     CHECKA=0.
C
C     FIND NUMBER OF PREY TYPE A (NA) AND B (NB) PRESENT :
C
5     N=ARENA (IX, IY)
6     NB=N/100
7     NA=N-NB*100
8     NAX=NA > NBX=NB
9     IF (NA.EQ.0) GOTO 3012
C
C     FIND NUMBER OF A EATEN :
C
10    DO 3010 J=1, NAX
11    A=РАНF (0,0)
C
C     IF A (=РАНF (0,0)) IS LESS THAN SA A PREY IS FOUND
C
12    IF (A.LT.SA) GOTO 3010
13    NA=NA-1
14    IF (NREP.NE.1.OR.MQ.EQ.0) GOTO 3010
15    IF (CHECKA.EQ.1.) GOTO 3010
C
C     STORE THE LOCATION OF UNSUCCESSFUL ENCOUNTERS :
C
16    NEN=NEN+1
17    IF (NEN.GT.100) GOTO 3010
18    NENC(NEN,1)=IX & NENC(NEN,2)=IY & NENC(NEN,3)=1
19    CHECKA=1.
C
C     CHECKA IS USED TO PREVENT MULTIPLE STORAGE OF UNSUCCESSFUL ENC-
C    OUNTERS
C
20    3010 CONTINUE
21    3012 IF (NB.EQ.0) GOTO 3013
22    CHECKB=0.
C
C     FIND NUMBER OF B EATEN (AS FOR A ABOVE) :
C
23    DO 3011 J=1, NBX
24    B=РАНF (0,0)
25    IF (B.LT.SB) GOTO 3011
26    NB=NB-1
27    IF (NREP.NE.1.OR.MQ.EQ.0) GOTO 3011
28    IF (CHECKA.EQ.1.) GOTO 3001
29    IF (CHECKB.EQ.1.) GOTO 3011

```

```

30      IF (NEN.GE.100)GOTO3011
31      NEN=NEN+1
32      NENC(NEN,1)=IX $ NENC(NEN,2)=IY $ NENC(NEN,3)=2
33      CHECK=1.
34      GOTO3011
35      3001 NENC(NEN,3)=3
36      3011 CONTINUE
37      3013 ARENA(IX,IY)=ARENA(IX,IY)-NA-NB*100
38      EA=NA $ EB=NB
C
C      RETURN IF NO PREY EATEN, OR IF NO MAP IS TO BE CONSTRUCTED :
C
39      IF (EA.EQ.0.0.AND.EB.EQ.0.0)RETURN
40      IF (NREP.NE.1.OR.MQ.EQ.0)RETURN
C
C      STORE LOCATION OF FEEDS :
C
41      NFEED=NFEED+1
42      IF (NFEED.GT.100)RETURN
43      ISTORE(NFEED,1)=IX $ ISTORE(NFEED,2)=IY
44      IF (NA.GT.0)ISTORE(NFEED,3)=1
45      IF (NB.GT.0)ISTORE(NFEED,3)=2
46      IF (NA.GT.0.AND.NB.GT.0)ISTORE(NFEED,3)=3
47      RETURN
48      END
C

1      SUBROUTINE FIX (J,I,A,B,C,Y,X)
C
C      THIS SUBROUTINE DEFINES THE PARAMETER Y AS A FUNCTION OF X
C      IF J=0 THE MODEL USED (AS DEFINED BY I) IS PRINTED OUT
C      THE MODEL USED IS SELECTED BY THE PARAMETER I :
C      I=1 : Y=A
C      I=2 : Y=AX+B
C      I=3 : Y=A LOGX + B
C      I=4 : Y=A IF X.GT.C Y=B
C      I=5 : Y=ABX/(1+ACX)
C      I=6 : Y=EXP(A.LN(X)+B)+C
C
C      FURTHER MODELS CAN EASILY BE ADDED
C
2      IF (J.EQ.0)GOTO3999
3      GOTO(3000,3001,3002,3003,3004,3005)I
4      3000 Y=A
5      RETURN
6      3001 Y=A*X+B
7      RETURN
8      3002 Y=A*ALOG(X)+B
9      RETURN
10     3003 Y=A
11     IF (X.GT.C)Y=B
12     RETURN
13     3004 Y=A*B*X/(1.+A*C*X)
14     RETURN
15     3005 Y=EXP(A*ALOG(X)+B)+C
16     RETURN
17     3999 GOTO(4000,4001,4002,4003,4004,4005)I
18     4000 WRITE(6,2000)A
19     RETURN
20     4001 WRITE(6,2001)A,B
21     RETURN
22     4002 WRITE(6,2002)A,B
23     RETURN
24     4003 WRITE(6,2003)A,C,B
25     RETURN
26     4004 WRITE(6,2004)A,B,C
27     RETURN
28     4005 WRITE(6,2005)A,B,C
29     FORMAT(* PARAMETER REMAINS CONSTANT AT *.F10.5)
30     2001 FORMAT(* PARAMETER DEFINED BY Y=AX+B : A = *F10.5,5X,* B = *F10
31     1.5)
31     2002 FORMAT(* PARAMETER DEFINED BY Y=A LOG(X) +B : A=*F10.5,5X,* B = *
31     1F10.5)

```

```

32 2003 FORMAT(* PARAMETER CONSTANT AT *F10.5,* UNLESS X IS GREATER THAN*F
    110.5,* IN WHICH CASE PARAMETER = *F10.5)
33 2004 FORMAT(* PARAMETER DEFINED BY Y=ABX/(1+ACX) (I.E. ANALAGOUS TO HOL
    1LING DISC EQUATION)*,/
    2*A = *F10.5,* B = *F10.5,* C = *F10.5)
34 2005 FORMAT(* PARAMETER OEFINEO BY Y = EXP(A.LN(X) + B) + C :*,
    15X,* A = *,F10.5,* B = *,F10.5,* C = *,F10.5)
35     RETURN
36     END

```

C

```

1     SUBROUTINE FDIR (IX,IY,L,LOIR,LENGTH)
C
C     THIS SUBROUTINE TAKES A STEP OF LENGTH L IN A RANOOM OIRECTION NOT
C     GREATER THAN A RIGHT ANGLE. IF THE PREDATOR MOVES BEYOND THE EDGE
C     OF THE ARENA, ITS RECORUED LAST DIRECTION OF MOVEMENT IS REVERSED
C
2     X=L
3     S=SQRT(X*X/2.)
4     LS=S*0.5
5     IF(LDIR.EQ.0)LDIR=IRAND(8)
6     ND=IRAND(5)
7     GOTO(11,12,13,14,15,16,17,18)LDIR
8     11 GOTO(7,8,1,2,3)ND
9     12 GOTO(8,1,2,3,4)ND
10    13 GOTO(1,2,3,4,5)ND
11    14 GOTO(2,3,4,5,5)ND
12    15 GOTO(3,4,5,6,7)ND
13    16 GOTO(4,5,6,7,8)ND
14    17 GOTO(5,6,7,8,1)ND
15    18 GOTO(5,7,8,1,2)ND
16    1 LX=IX $ LY=IY+L $ LDIR=1 $ GOTO50
17    2 LX=IX+LS $ LY=IY+LS $ LDIR=2 $ GOTO50
18    3 LX=IX+L $ LY=IY $ LDIR=3 $ GOTO50
19    4 LX=IX+LS $ LY=IY-LS $ LDIR=4 $ GOTO50
20    5 LX=IX $ LY=IY-L $ LDIR=5 $ GOTO50
21    6 LX=IX-LS $ LY=IY-LS $ LDIR=6 $ GOTO50
22    7 LX=IX-L $ LY=IY $ LDIR=7 $ GOTO50
23    8 LX=IX-LS $ LY=IY+LS $ LDIR=8
24    50 IF(LX.LT.1.OR.LX.GT.LENGTH.OR.LY.LT.1.OR.LY.GT.LENGTH)GOTO30
25    IX=LX $ IY=LY
26    RETURN
27    30 IF(LOIR.LT.5)GOTO 60
28    IF(LDIR.GE.5)LOIR=LOIR-4
29    GOTO40
30    60 LDIR=LDIR+4
31    GOTO40
32    END)

```

C

```

1     SUBROUTINE SDIR (IX,IY,L,LDIR,LENGTH)
C
C     THIS SUBROUTINE CAUSES THE PREDATOR TO MOVE L UNITS (NORMALLY L=1)
C     IN THE SAME DIRECTION AS IT WAS PREVIOUSLY MOVING. IF IT MOVES
C     BEYOND THE ARENA, THE DIRECTION IS REVERSED AND FDIR IS CALLED.
C
2     GOTO(1,2,3,4,5,6,7,8)LDIR
3     1 LX=IX $ LY=IY+L $ GOTO10
4     2 LX=IX+L $ LY=IY+L $ GOTO10
5     3 LX=IX+L $ LY=IY $ GOTO10
6     4 LX=IX+L $ LY=IY-L $ GOTO10
7     5 LX=IX $ LY=IY-L $ GOTO10
8     6 LX=IX-L $ LY=IY-L $ GOTO10
9     7 LX=IX-L $ LY=IY $ GOTO10
10    8 LX=IX-L $ LY=IY+L
11    10 IF(LX.LT.1.OR.LX.GT.LENGTH.OR.LY.LT.1.OR.LY.GT.LENGTH)GOTO20
12    IX=LX $ IY=LY
13    RETURN

```

```
14      20  IF(LDIR.LT.5)GOTO40
15      IF(LDIR.GE.5)LDIR=LDIR-4
16      GOTO30
17      40  LDIR=LDIR+4
18      30  CALL FDIR (IX,IY,L,LDIR,LENGTH)
19      RETJRN
20      END
```

C

```
1      SUBROUTINE DIR (IX,IY,L,LENGTH)
```

C

C THIS SUBROUTINE CAUSES THE PREDATOR TO TAKE A STEP OF LENGTH L IN
C ANY DIRECTION. IF IT MOVES BEYOND THE ARENA, A NEW DIRECTION IS
C SELECTED UNTIL IT REMAINS WITHIN THE ARENA

C

```
2      X=L
3      S=SQRT(X*X/2.) $ LS=S*0.5
4      500 ID=IPAND(8)
5      GOTO(1,2,3,4,5,6,7,8)ID
6      1 LX=IX $ LY=IY+L $ GOTO400
7      2 LX=IX-LS $ LY=IY+LS $ GOTO400
8      3 LX=IX-L $ LY=IY $ GOTO400
9      4 LX=IX-LS $ LY=IY-LS $ GOTO400
10     5 LX=IX $ LY=IY-L $ GOTO400
11     6 LX=IX+LS $ LY=IY-LS $ GOTO400
12     7 LX=IX+L $ LY=IY $ GOTO400
13     8 LX=IX+LS $ LY=IY+LS
14     400 IF(LX.LT.1.OR.LX.GT.LENGTH.OR.LY.LT.1.OR.LY.GT.LENGTH)GOTO500
15     IX=LX $ IY=LY
16     RETJRN
17     END
```

C

```
1      SUBROUTINE MAP
```

C

C THIS SUBROUTINE PROVIDES A MAP OF THE ARENA AFTER THE PREDATOR HAS
C SEARCHED IN IT.

C

C AREAS SEARCHED MORE THAN ONCE, AND LOCATIONS WHERE MORE THAN ONE
C PREDATION OCCURRED ARE NOT DISTINGUISHED.

C

```
2      COMMON/A1/ARENA(50,50),LENGTH
3      COMMON/A7/MQ,NENC(100,3),NEN,ISTORE(100,3),NFEEED
4      DATA BLANK,STAR,DOT,CIRCLE/1H,1H*,1H.,1H0/
5      DATA A,B,C,X/1HA,1HB,1HC,1HX/
6      DATA PLUS,SUB,PORM/1H+,1H-,1HE/
7      IF(NEN.GT.100.OR.NFEEED.GT.100)GOTO4000
8      DO 3000 J=1,LENGTH
9      DO 3000 K=1,LENGTH
10     N=ARENA(J,K)
11     NB=N/100
12     NA=N-NB*100
13     IF(ARENA(J,K).EQ.0.)ARENA(J,K)=BLANK
14     IF(NA.GT.0)ARENA(J,K)=X
15     IF(NB.GT.0)ARENA(J,K)=STAR
16     IF(NA.GT.0.AND.NB.GT.0)ARENA(J,K)=CIRCLE
17     IF(ARENA(J,K).EQ.-1.)ARENA(J,K)=DOT
18     3000 CONTINUE
19     IF(NEN.EQ.0)GOTO3005
20     DO 3004 M=1,NEN
21     J=NENC(M,1)
22     K=NENC(M,2)
23     IF(NENC(M,3).EQ.1)ARENA(J,K)=PLUS
24     IF(NENC(M,3).EQ.2)ARENA(J,K)=SUB
25     IF(NENC(M,3).EQ.3)ARENA(J,K)=PORM
26     3004 CONTINUE
27     3005 IF(NFEEED.EQ.0)GOTO3005
28     DO 3001 M=1,NFEEED
```

```

29      J=ISTORE(M,1)
30      K=ISTORE(M,2)
31      IF(ISTORE(M,3).EQ.1)ARENA(J,K)=A
32      IF(ISTORE(M,3).EQ.2)ARENA(J,K)=B
33      IF(ISTORE(M,3).EQ.3)ARENA(J,K)=C
34      3001 CONTINUE
35      3006 CONTINUE
36      WRITE(6,2000)
37      DO 3002 X=1,50
38      3002 WRITE(6,2004)(ARENA(J,K),J=1,50)
39      WRITE(6,2002)
40      2000 FORMAT(/,10X,39HS A M P L E M A P F O R T H E R U N ,
1//, 3X,60HKEY: . - LOCATION SEARCHED BY PREDATOR (ONE OR MORE TI
2MES).
3/,10X,54HX - POSITION OF ONE OR MORE INDIVIDUALS OF PREY TYPE A.
4/,10X,54H* - POSITION OF ONE OR MORE INDIVIDUALS OF PREY TYPE B.
5/,10X,85H0 - POSITION OF ONE OR MORE INDIVIDUALS OF PREY TYPE A AN
6D ONE OR MORE OF PREY TYPE B.
7/,10X,55HA - POSITION OF PREDATION OF ONE OR MORE OF PREY TYPE A.
8/,10X,55HB - POSITION OF PREDATION OF ONE OR MORE OF PREY TYPE B.
9/,10X,86HC - POSITION OF PREDATION OF ONE OR MORE OF PREY TYPE A A
1ND ONE OR MORE OF PREY TYPE B.
2/,10X,56H+ - POSITION OF UNSUCCESSFULL ENCOUNTER WITH PREY TYPE A.
3/,10X,56H- - POSITION OF UNSUCCESSFULL ENCOUNTER WITH PREY TYPE B.
4/,10X,72HE - POSITION OF UNSUCCESSFULL ENCOUNTER WITH PREY TYPE A
5AND PREY TYPE B,/,10X,1HI,50(1H-,),1HI,)
41      2002 FORMAT(10X,1HI,50(1H-,),1HI,)
42      2004 FORMAT(10X,1HI,50A1,1HI,)
43      2010 FORMAT(/,10X,86HTHERE IS INSUFFICIENT STORAGE FOR LOCATION OF ENC
1OUNTERS AND/OR PREDATION TO DO A MAP.,)
44      RETJRN
45      4000 WRITE(6,2010)
46      RETJRN
47      END

```

C

```

1      SUBROUTINE SUMS (XB,XS,X,N)
C
C      THIS SUBROUTINE CALCULATES THE MEAN (XB), AND STANDARD ERROR OF
C      THE MEAN (XS), FOR N VALUES STORED IN X
C
2      DIMENSION X(50)
3      R=N $ SUMX=0. $ SUMXS=0.
4      DO 3000 J=1,N
5      SUMX=SUMX+X(J)
6      3000 SUMXS=SUMXS+X(J)*X(J)
7      XB=SUMX/R
8      XVAR=(SUMXS-SUMX*SUMX/R)/(R-1.)
9      IF(XVAR.LE.0.)GOTO3001
10     XS=SQRT(XVAR)/SQRT(R)
11     RETJRN
12     3001 XS=0.
13     RETJRN
14     END

```

C

```

1      FUNCTION IRAND (I)
C
C      THIS FUNCTION FINDS A UNIFORMLY DISTRIBUTED RANDOM INTEGER BETWEEN
C      1 AND THE INPUT I.
C
2      XI=I
3      X=RANF(0.0)*XI+1.
4      IRAND=X
5      RETJRN
6      END

```

A2.2 SIMULATION RESULTS

The tables of simulation results are arranged as follows:

Appendix Table	Number of parts	Simulation results for Section
A2.1	2	6.3
A2.2	15	6.4
A2.3	8	6.5
A2.4	9	6.6
A2.5	4	6.7
A2.6	4	6.8

APPENDIX TABLE A2.1 Results of the simulations for Section 6.3

The aggregative walk ($IS = 4$) uses steps of length LLS in the normal searching phase. In this table are given the results of using a number of values of LLS to search for prey at two densities (about 40 and 480), arranged in four different distributions. The following distributions are used: random, using the negative binomial distribution with K values of 1.0 and 0.05, and in regularly arranged clumps of ten. The larger arena of 100 x 100 is used. The time taken to move LLS (i.e. TLS) is held equal to LLS, whilst the other parameters are held constant ($LSS = TSS = 1$, $H = 5$). The total time available (T) is 1000 time units, the handling time (THA) is 50 time units, and all encounters with prey are successful ($SA = 1.0$). Thirty replicates of each combination were run; the results given for each value of LLS are the mean number of prey eaten (\bar{N}_e) and the mean percentage time wasted ($\overline{\%TW}$), together with the standard error of the mean for each. The table is in two parts:

N	LLS	$\bar{N}_e \pm S.E.$	$\% TW \pm S.E.$	N	LLS	$\bar{N}_e \pm S.E.$	$\% TW \pm S.E.$
40 RANDOM	1	2.4 .27	30.8 1.70	490 RANDOM	1	12.7 .31	27.9 1.57
	2	2.8 .42	22.6 1.12		2	13.3 .31	20.1 1.35
	3	3.4 .40	14.8 .94		3	13.2 .27	15.3 1.35
	4	2.9 .26	14.1 1.13		4	13.2 .22	14.9 1.52
	5	3.3 .26	12.0 1.38		5	13.7 .27	12.3 .76
	6	3.0 .33	11.9 1.20		6	14.0 .26	14.7 1.24
	7	3.4 .35	12.7 1.04		7	13.7 .31	13.6 1.10
	8	2.3 .19	12.2 .96		8	13.6 .22	11.6 .74
	9	2.9 .26	10.1 .51		9	13.5 .24	11.2 1.27
	10	3.4 .35	10.9 1.49		10	14.0 .26	11.2 .75
	12	2.8 .33	12.1 1.29		12	14.0 .24	12.1 1.02
	14	2.8 .37	10.8 .76		14	13.5 .26	11.6 .82
	16	2.9 .31	9.7 .78		16	13.7 .16	9.8 .75
	18	3.0 .35	10.7 .79		18	13.3 .25	9.9 1.02
20	2.3 .25	10.9 .81	20	13.6 .21	10.1 .70		
39 NEGATIVE BINOMIAL K = 1.5	1	2.5 .26	31.2 1.69	487 NEGATIVE BINOMIAL K = 1.1	1	12.6 .26	30.1 1.57
	2	2.5 .34	22.1 1.20		2	13.3 .22	18.4 1.22
	3	2.9 .27	17.0 1.70		3	13.3 .23	14.2 1.06
	4	3.2 .35	12.1 .50		4	13.3 .32	12.9 1.06
	5	2.8 .23	12.3 1.13		5	13.4 .21	12.5 1.18
	6	2.9 .38	11.7 .91		6	13.9 .29	11.7 1.04
	7	3.1 .35	11.4 .90		7	13.6 .33	11.5 .89
	8	2.7 .27	11.0 .84		8	13.9 .26	11.5 .65
	9	2.7 .32	12.1 1.45		9	13.9 .25	11.6 1.04
	10	2.5 .22	10.9 .92		10	13.5 .31	12.6 1.00
	12	2.5 .32	9.9 .80		12	14.0 .27	13.3 .97
	14	2.9 .34	11.7 1.22		14	13.7 .27	12.3 1.04
	16	2.3 .26	9.8 .76		16	13.8 .27	10.4 .66
	18	2.5 .32	10.9 1.41		18	13.8 .41	10.6 .82
20	2.7 .34	11.6 1.44	20	13.4 .21	14.3 1.33		

APPENDIX TABLE A2.1 - part 1

The results for the prey arranged at random and using the negative binomial distribution with $K \approx 1.0$.

N	LLS	$\bar{N}_e \pm S.E.$		$\% TW \pm S.E.$		N	LLS	$\bar{N}_e \pm S.E.$		$\% TW \pm S.E.$	
44 NEGATIVE BINOMIAL K = 0.054	1	3.6	.42	29.9	1.94	463 NEGATIVE BINOMIAL K = 0.053	1	10.7	.91	27.1	1.92
	2	2.6	.35	20.7	1.22		2	13.0	.72	17.5	1.48
	3	4.3	.58	15.9	1.63		3	14.5	.60	15.2	1.49
	4	3.1	.37	14.1	1.00		4	13.3	.68	12.4	1.15
	5	3.6	.39	11.3	.94		5	14.8	.47	10.1	.87
	6	3.6	.37	11.8	.88		6	13.9	.42	10.0	1.08
	7	2.4	.25	11.1	.86		7	13.7	.48	9.5	.83
	8	4.2	.32	10.3	.86		8	14.2	.49	8.4	1.19
	9	3.0	.46	11.8	1.27		9	14.1	.67	8.4	.71
	10	3.7	.50	10.5	.99		10	14.6	.52	9.2	1.16
	12	2.5	.40	9.9	.71		12	14.2	.74	8.9	.70
	14	3.6	.37	9.3	.91		14	14.7	.56	8.2	.72
	16	3.5	.37	12.7	1.38		16	14.4	.58	11.7	1.76
	18	3.6	.37	11.1	.95		18	14.5	.46	9.3	1.06
20	3.4	.29	10.0	.95	20	14.2	.41	9.4	1.06		
40 CLUMPED	1	3.5	.76	29.1	1.41	490 CLUMPED	1	13.1	.49	27.8	1.92
	2	2.2	.66	21.9	1.72		2	14.5	.55	18.7	1.89
	3	3.8	.82	14.5	1.04		3	15.2	.32	13.4	.89
	4	3.1	.64	15.4	1.25		4	14.5	.46	12.3	1.06
	5	2.9	.79	11.9	.76		5	14.1	.48	11.7	.81
	6	3.1	.70	11.7	.94		6	14.1	.35	11.5	1.25
	7	4.4	.81	8.4	.59		7	14.3	.49	11.3	1.21
	8	3.6	.68	10.6	.95		8	14.6	.46	11.0	1.22
	9	3.7	.76	9.8	1.02		9	14.0	.62	10.3	.83
	10	4.3	.71	9.3	.82		10	13.6	.49	11.0	1.13
	12	3.2	.66	12.1	1.54		12	14.1	.55	11.0	1.27
	14	2.7	.50	11.5	1.24		14	13.9	.65	11.5	1.19
	16	3.7	.79	7.9	.71		16	13.1	.49	10.3	1.39
	18	3.7	.70	11.8	1.23		18	12.5	.62	9.9	1.00
20	3.3	.75	10.8	.80	20	12.4	.65	9.5	.90		

APPENDIX TABLE A2.2 - part 2 The results with the prey arranged using the negative binomial distribution with $K \approx 0.05$ and in regularly arranged clumps of ten.

APPENDIX TABLE A2.2 Results of the simulations for Section 6.4

The functional response results given were obtained using each of the search strategies to search for four different prey arrangements. The total time available (T) was 1000 time units, the handling time (THA) was 50 time units, and all encounters with prey were successful (SA = 1.0). In this section the larger arena of 100 x 100 was used. The four prey distributions were: regular, random, using the negative binomial distribution with K approximately 0.05. and in regularly arranged clumps of ten; in the following table these distributions are referred to as regular, random, neg. bin. K = 0.05, and clumps respectively. Eight prey densities of up to about 1000 were used. Thirty replicates were run for each combination (parts 1 - 8), and supplementary replicates were run for some combinations (parts 9 - 15). The results given for each prey density (N) are the mean number of prey eaten (\bar{N}_e) and the mean logarithm of the proportion of the prey surviving ($\overline{\ln S}$), together with the standard error of the mean for each. The table is divided into 15 parts, and the search strategies used in each are as follows:

part	search strategy and parameters
1	totally random search (IS = 1)
2,11	random walk (IS = 2)
3	forward directed random walk (IS = 3)
4,9,12	forward directed random walk with a step length of three (IS = 4a) - (TLS = LLS = 3, TSS = LSS = 0, H = 0)
5,10,13,14	forward directed random walk with a step length of ten (IS = 4b) - (TLS = LLS = 10, TSS = LSS = 0, H = 0)
6	aggregative walk with a long step length of three (IS = 4c) - (TLS = LLS = 3, TSS = LSS = 1, H = 5)
7,15	aggregative walk with a long step length of ten (IS = 4d) - (TLS = LLS = 10, TSS = LSS = 1, H = 5)
8	systematic local search in response to finding a prey (IS = 5) - (LB = 3, TC = 8, area of 5 x 5 is searched)

REGULAR				RANDOM					
N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$		N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$	
9	.85	.17	-.1056	.0208	8	.60	.16	-.0858	.0235
16	1.13	.16	-.0749	.0106	16	1.57	.17	-.1056	.0119
25	1.77	.23	-.0746	.0099	32	2.50	.25	-.0823	.0087
64	4.54	.31	-.0740	.0052	64	4.15	.32	-.0674	.0054
121	7.27	.35	-.0621	.0031	128	7.26	.30	-.0585	.0025
256	10.65	.29	-.0425	.0012	256	11.41	.23	-.0456	.0009
529	14.25	.21	-.0273	.0004	512	13.90	.22	-.0275	.0004
1024	16.48	.11	-.0162	.0001	1024	16.56	.13	-.0163	.0001
Neg. Bin. K = 0.05				C L U M P S					
N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$		N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$	
8	.77	.12	-.1051	.0175	10	1.06	.18	-.1177	.0212
17	1.44	.19	-.0909	.0124	40	3.21	.26	-.0844	.0072
29	2.76	.27	-.1016	.0106	90	5.16	.31	-.0592	.0037
63	4.59	.25	-.0758	.0043	160	8.75	.31	-.0563	.0020
128	7.49	.36	-.0604	.0030	250	10.79	.28	-.0442	.0012
245	10.40	.31	-.0434	.0013	490	13.75	.26	-.0285	.0005
462	13.77	.29	-.0303	.0006	810	16.07	.15	-.0200	.0002
828	15.78	.23	-.0192	.0003	1000	16.65	.14	-.0168	.0001

APPENDIX TABLE A2.2 - part 1 Functional response results from thirty replicates using the strategy of completely random search (IS = 1).

R E G U L A R			R A N D O M		
N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$	N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$
9	.32 .09	-.0372 .0100	8	.32 .11	-.0434 .0145
16	.92 .12	-.0603 .0081	16	.72 .14	-.0477 .0095
25	1.31 .16	-.0545 .0068	32	1.37 .19	-.0443 .0064
64	2.47 .24	-.0396 .0039	64	2.29 .22	-.0366 .0035
121	4.53 .26	-.0382 .0022	128	4.03 .35	-.0322 .0028
256	6.81 .23	-.0270 .0009	256	7.30 .38	-.0290 .0015
529	11.19 .22	-.0214 .0004	512	10.36 .35	-.0204 .0007
1024	14.50 .19	-.0143 .0002	1024	14.43 .24	-.0142 .0002
Neg. Bin. K = 0.05			C L U M P S		
N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$	N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$
8	.30 .11	-.0414 .0153	10	.50 .28	-.0794 .0493
17	.45 .15	-.0279 .0093	40	2.01 .56	-.0548 .0158
29	.96 .22	-.0346 .0080	90	3.19 .60	-.0369 .0071
63	2.58 .36	-.0424 .0061	160	5.82 .63	-.0373 .0041
128	4.35 .56	-.0349 .0046	250	7.04 .71	-.0286 .0029
245	6.55 .85	-.0273 .0036	490	11.03 .53	-.0228 .0011
462	9.26 .83	-.0202 .0021	810	12.63 .45	-.0157 .0006
828	12.66 .71	-.0154 .0009	1000	13.77 .58	-.0139 .0006

APPENDIX TABLE A2.2 - part 2 Functional response results from thirty replicates using the strategy of the random walk (IS = 2).

R E G U L A R					R A N D O M				
N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$		N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$	
9	.66	.14	-.0804	.0172	8	.44	.12	-.0636	.0172
16	1.00	.13	-.0656	.0086	16	1.11	.16	-.0737	.0112
25	1.51	.19	-.0631	.0082	32	1.86	.19	-.0603	.0064
64	3.92	.26	-.0634	.0043	64	3.60	.29	-.0583	.0048
121	6.02	.27	-.0511	.0023	128	5.88	.39	-.0472	.0032
256	9.55	.23	-.0380	.0010	256	9.37	.26	-.0373	.0011
529	13.47	.19	-.0258	.0004	512	12.94	.25	-.0256	.0005
1024	15.80	.16	-.0156	.0002	1024	16.38	.16	-.0161	.0002
Neg. Bin. K = 0.05					C L U M P S				
N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$		N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$	
8	.33	.10	-.0452	.0137	10	2.50	.20	-.0412	.0338
17	1.14	.20	-.0720	.0131	40	2.65	.56	-.0718	.0150
29	1.77	.22	-.0640	.0082	90	4.90	.53	-.0565	.0062
63	3.85	.48	-.0641	.0084	160	6.66	.58	-.0428	.0038
128	6.28	.61	-.0506	.0050	250	10.28	.55	-.0421	.0023
245	8.66	.64	-.0361	.0027	490	12.44	.46	-.0257	.0010
462	11.59	.65	-.0253	.0015	810	15.60	.27	-.0194	.0003
828	14.79	.68	-.0180	.0008	1000	16.05	.31	-.0162	.0003

APPENDIX TABLE A2.2 - part 3

Functional response results from thirty replicates using the strategy of the forward directed random walk (IS = 3).

R E G U L A R			R A N D O M		
N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$	N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$
9	.52 .10	-.0622 .0124	8	.90 .18	-.1291 .0265
16	1.30 .16	-.0861 .0108	16	1.54 .22	-.1048 .0154
25	2.14 .19	-.0906 .0086	32	2.48 .31	-.0823 .0107
64	4.32 .32	-.0703 .0054	64	4.26 .34	-.0694 .0058
121	7.01 .30	-.0598 .0027	128	7.06 .34	-.0568 .0028
256	13.36 .30	-.0536 .0013	256	10.66 .25	-.0425 .0010
529	13.47 .21	-.0258 .0004	512	13.88 .22	-.0275 .0004
1024	18.33 .10	-.0181 .0001	1024	16.64 .13	-.0164 .0001
Neg. Bin. K = 0.05			C L U M P S		
N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$	N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$
8	.41 .12	-.0566 .0165	10	.66 .26	-.0829 .0337
17	1.02 .20	-.0639 .0130	40	3.04 .47	-.0815 .0128
29	1.95 .19	-.0703 .0071	90	5.68 .55	-.0658 .0066
63	4.77 .39	-.0793 .0067	160	7.76 .57	-.0499 .0037
128	7.33 .52	-.0593 .0043	250	10.17 .51	-.0416 .0021
245	9.43 .58	-.0394 .0025	490	13.47 .42	-.0279 .0009
462	13.31 .42	-.0292 .0009	810	15.54 .26	-.0194 .0003
828	15.1 .46	-.0184 .0006	1000	16.20 .28	-.0163 .0002

APPENDIX TABLE A2.2 - part 4 Functional response results from thirty replicates using the strategy of the forward directed random walk with the step length of three (IS = 4a).

R E G U L A R			R A N D O M		
N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$	N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$
9	.88 .19	- .1116 .0251	8	.71 .17	- .1020 .0259
16	3.07 .40	- .2269 .0315	16	1.41 .24	- .0963 .0168
25	2.18 .31	- .0941 .0139	32	2.73 .23	- .0899 .0080
64	4.96 .35	- .0812 .0059	64	4.83 .32	- .0789 .0055
121	9.73 .33	- .0840 .0030	128	7.50 .26	- .0605 .0021
256	13.79 .33	- .0554 .0014	256	10.76 .31	- .0430 .0013
529	16.11 .24	- .0309 .0005	512	14.03 .19	- .0278 .0004
1024	17.51 .25	- .0173 .0003	1024	16.34 .12	- .0161 .0001
Neg. Bin. K = 0.05			C L U M P S		
N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$	N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$
8	.51 .13	- .0706 .0198	10	.82 .28	- .1037 .0390
17	1.19 .20	- .0748 .0129	40	2.36 .36	- .0621 .0098
29	2.36 .28	- .0864 .0104	90	5.83 .66	- .0678 .0079
63	4.65 .38	- .0772 .0065	160	10.48 .55	- .0679 .0037
128	7.84 .44	- .0634 .0037	250	9.53 .44	- .0389 .0018
245	9.93 .49	- .0414 .0021	490	14.00 .41	- .0290 .0009
462	12.35 .59	- .0271 .0013	810	17.31 .23	- .0216 .0003
828	14.32 .46	- .0175 .0006	1000	17.54 .18	- .0177 .0002

APPENDIX TABLE A2.2 - part 5

Functional response results from thirty replicates using the strategy of the forward directed random walk with the step length of ten (IS = 4b).

R E G U L A R				R A N D O M			
N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$		N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$	
9	.67 .13	-.0806 .0161		8	.77 .14	-.1065 .0201	
16	1.20 .18	-.0804 .0129		16	.96 .20	-.0642 .0134	
25	1.64 .19	-.0689 .0083		32	1.96 .19	-.0638 .0066	
64	4.06 .26	-.0658 .0043		64	4.78 .27	-.0779 .0046	
121	6.35 .31	-.0540 .0027		128	7.30 .25	-.0588 .0021	
256	9.67 .26	-.0385 .0011		256	10.54 .23	-.0420 .0009	
529	13.34 .16	-.0255 .0003		512	13.36 .24	-.0265 .0005	
1024	15.41 .15	-.0152 .0002		1024	16.18 .11	-.0159 .0001	
Neg. Bin. K = 0.05				C L U M P S			
N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$		N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$	
8	.70 .14	-.0972 .0201		10	1.40 .44	-.1418 .0490	
17	1.23 .19	-.0774 .0122		40	5.10 .58	-.1403 .0165	
29	2.13 .24	-.0776 .0092		90	6.94 .65	-.0811 .0079	
63	3.93 .42	-.0652 .0073		160	9.68 .62	-.0627 .0041	
128	7.88 .59	-.0639 .0049		250	11.32 .55	-.0464 .0023	
245	10.76 .59	-.0450 .0025		490	15.02 .37	-.0311 .0008	
462	13.78 .59	-.0303 .0013		810	15.81 .22	-.0197 .0003	
828	15.73 .50	-.0192 .0006		1000	16.49 .28	-.0166 .0002	

APPENDIX TABLE A2.2 - part 6 Functional response results from thirty replicates using the strategy of the aggregative walk with the long step length of three (IS = 4c).

R E G U L A R				R A N D O M			
N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$		N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$	
9	.99 .16	-.1223 .0208		8	.64 .14	-.0896 .0207	
16	1.37 .19	-.0923 .0136		16	1.60 .20	-.1081 .0145	
25	1.75 .23	-.0741 .0100		32	2.56 .27	-.0844 .0092	
64	4.29 .36	-.0698 .0056		64	4.62 .29	-.0752 .0048	
121	5.51 .34	-.0467 .0029		128	6.72 .34	-.0541 .0029	
256	7.77 .36	-.0309 .0015		256	10.52 .30	-.0420 .0012	
529	10.80 .29	-.0206 .0005		512	13.70 .20	-.0271 .0004	
1024	12.20 .27	-.0120 .0003		1024	16.35 .12	-.0161 .0001	
Neg. Bin. K = 0.05				C L U M P S			
N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$		N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$	
8	.70 .14	-.0970 .0194		10	.65 .27	-.0838 .0375	
17	1.26 .19	-.0789 .0124		40	4.19 .61	-.1150 .0170	
29	2.48 .31	-.0916 .0121		90	7.15 .66	-.0837 .0079	
63	5.11 .43	-.0854 .0075		160	9.34 .65	-.0604 .0043	
128	7.95 .55	-.0644 .0046		250	12.09 .53	-.0497 .0022	
245	11.96 .66	-.0502 .0028		490	14.52 .40	-.0301 .0008	
462	14.33 .38	-.0315 .0008		810	15.25 .37	-.0190 .0005	
828	16.56 .40	-.0202 .0005		1000	16.13 .23	-.0163 .0002	

APPENDIX TABLE A2.2 - part 7

Functional response results from thirty replicates using the strategy of the aggregative walk with the long step length of ten (IS = 4d).

R E G U L A R				R A N D O M					
N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$		N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$	
9	.47	.12	-.0560	.0140	8	.71	.14	-.0991	.0212
16	.80	.16	-.0528	.0104	16	.80	.17	-.0532	.0115
25	1.93	.20	-.0814	.0090	32	2.17	.21	-.0708	.0073
64	3.71	.30	-.0601	.0050	64	4.13	.32	-.0671	.0054
121	6.28	.25	-.0534	.0022	128	6.32	.33	-.0507	.0028
256	9.05	.26	-.0360	.0011	256	10.59	.33	-.0423	.0013
529	12.71	.18	-.0243	.0003	512	14.24	.24	-.0282	.0005
1024	15.61	.17	-.0154	.0002	1024	17.33	.15	-.0171	.0001
Neg. Bin. K = 0.05				C L U M P S					
N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$		N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$	
8	.80	.19	-.1179	.0308	10	1.34	.61	* -.1439	
17	1.11	.24	-.0714	.0163	40	5.42	.82	-.1537	.0239
29	2.11	.28	-.0770	.0106	90	7.72	.85	-.0911	.0102
63	5.27	.71	-.0896	.0124	160	11.68	.55	-.0759	.0038
128	8.26	.78	-.0673	.0065	250	13.70	.57	-.0565	.0024
245	12.80	.73	-.0538	.0031	490	16.65	.35	-.0346	.0008
462	14.95	.69	-.0329	.0015	890	17.97	.25	-.0224	.0003
828	16.79	.36	-.0205	.0004	1000	18.28	.34	-.0185	.0004

APPENDIX TABLE A2.2 - part 8

Functional response results from thirty replicates using the strategy of systematic local search in response to finding a prey ($IS = 5$). (* - a value of $\overline{\ln S}$ is given since $\overline{\ln S}$ can not be evaluated due to total predation in one or more replicates.)

SECOND 30 REPLICATES					60 REPLICATES		
N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$		N	\bar{N}_e	$\overline{\ln S}$
8	.78	.17	-.1122	.0263	8	.60	-.0844
17	1.35	.17	-.0842	.0110	17	1.19	-.0741
29	1.78	.22	-.0643	.0080	29	1.87	-.0673
63	3.86	.32	-.0636	.0054	63	4.32	-.0715
128	6.41	.40	-.0515	.0032	128	6.87	-.0554
245	9.51	.45	-.0396	.0019	245	9.47	-.0395
462	11.84	.58	-.0260	.0013	462	12.58	-.0277
828	14.89	.59	-.0182	.0007	828	15.00	-.0183

APPENDIX TABLE A2.2 - part 9 Functional response results from
an extra thirty replicates using
the strategy of the forward directed random walk with a step
length of three to search for prey arranged using the negative
binomial distribution with $K = 0.05$.

SECOND 30 REPLICATES				60 REPLICATES		
N	$\bar{N}_e \pm \text{S.E.}$	$\overline{\ln S} \pm \text{S.E.}$		N	\bar{N}_e	$\overline{\ln S}$
8	.93 .17	-.1333 .0259		8	.72	-.1020
17	1.21 .18	-.0759 .0113		17	1.20	-.0754
29	2.13 .24	-.0776 .0090		29	2.24	-.0820
63	3.79 .29	-.0624 .0050		63	4.22	-.0698
128	7.61 .36	-.0614 .0030		128	7.73	-.0624
245	10.09 .40	-.0421 .0017		245	10.01	-.0418
462	13.47 .44	-.0296 .0010		462	12.91	-.0284
828	15.92 .28	-.0194 .0004		828	15.12	-.0185

APPENDIX TABLE A2.2 - part 10 Functional response results from
an extra thirty replicates using
the search strategy of the forward directed random walk with a step
length of ten (IS = 4b) to search for prey arranged using the neg-
ative binomial distribution with K = 0.05.

SECOND 30 REPLICATES					60 REPLICATES		
N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$		N	\bar{N}_e	$\overline{\ln S}$
10	0	0	0	0	10	.15	-.0206
40	2.16	.56	-.0589	.0157	40	2.18	-.0593
90	4.34	.65	-.0502	.0076	90	3.36	-.0388
160	4.93	.64	-.0315	.0041	160	5.38	-.0344
250	5.99	.74	-.0244	.0030	250	6.52	-.0266
490	9.34	.69	-.0193	.0014	490	10.19	-.0211
810	13.39	.47	-.0167	.0006	810	13.01	-.0162
1000	14.30	.40	-.0144	.0004	1000	14.04	-.0142

APPENDIX TABLE A2.2 - part 11 Functional response results from
an extra thirty replicates using
the search strategy of the random walk (IS = 2) to search for
prey in regularly distributed clumps of ten.

FIRST 30 REPLICATES					SECOND 30 REPLICATES				
N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$		N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$	
9	.52	.10	-.0622	.0124	9	.86	.16	-.1066	.0201
16	1.30	.16	-.0861	.0108	16	1.23	.19	-.0824	.0131
25	2.14	.19	-.0906	.0086	25	1.97	.26	-.0841	.0118
64	4.32	.32	-.0703	.0054	64	4.10	.25	-.0665	.0041
121	7.01	.30	-.0598	.0027	121	7.18	.28	-.0612	.0025
256	13.36	.30	-.0536	.0013	256	13.51	.22	-.0542	.0009
529	13.47	.21	-.0258	.0004	529	13.38	.24	-.0256	.0005
1024	18.33	.10	-.0181	.0001	1024	18.22	.10	-.0180	.0001
THIRD 30 REPLICATES					90 REPLICATES				
N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$		N	\bar{N}_e	$\overline{\ln S}$		
9	.53	.11	-.0639	.0140	9	.64	-.0776		
16	1.38	.17	-.0923	.0119	16	1.30	-.0869		
25	2.06	.21	-.0870	.0093	25	2.06	-.0872		
64	3.86	.27	-.0624	.0045	64	4.09	-.0664		
121	6.72	.30	-.0573	.0026	121	6.97	-.0594		
256	12.95	.22	-.0519	.0009	256	13.27	-.0532		
529	13.61	.18	-.0261	.0004	529	13.49	-.0258		
1024	18.40	.08	-.0181	.0001	1024	18.32	-.0181		

APPENDIX TABLE A2.2 - part 12 Functional response results from an extra sixty replicates using the search strategy of the forward directed random walk with a step length of three ($IS = 4a$) to search for regularly arranged prey.

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FIRST 30 REPLICATES					SECOND 30 REPLICATES				
N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$		N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$	
9	.88	.19	-.1116	.0251	9	.80	.15	-.0986	.0198
16	3.07	.40	-.2269	.0351	16	3.01	.40	-.2230	.0322
25	2.18	.31	-.0941	.0139	25	2.12	.32	-.0915	.0143
64	4.96	.35	-.0812	.0059	64	4.83	.41	-.0792	.0068
81	10.16	.75	-.1356	.0103	81	12.64	.60	-.1707	.0085
121	9.73	.35	-.0840	.0030	121	9.23	.51	-.0796	.0045
256	13.79	.33	-.0554	.0014	256	14.68	.33	-.0591	.0014
529	16.11	.24	-.0309	.0005	529	15.30	.33	-.0294	.0006
1024	17.24	.25	-.0173	.0003	1024	17.73	.23	-.0175	.0002
THIRD 30 REPLICATES					90 REPLICATES				
N	$\bar{N}_e \pm S.E.$		$\overline{\ln S} \pm S.E.$		N	\bar{N}_e	$\overline{\ln S}$		
9	.67	.17	-.0844	.0222	9	.78	-.0982		
16	1.93	.36	-.1391	.0280	16	2.67	-.1963		
25	1.93	.27	-.0823	.0121	25	2.08	-.0893		
64	4.30	.29	-.0670	.0048	64	4.70	-.0758		
81	11.17	.69	-.1498	.0098	81	11.32	-.1520		
121	9.85	.50	-.0852	.0045	121	9.60	-.0829		
256	14.08	.33	-.0566	.0014	256	14.18	-.0570		
529	15.64	.23	-.0300	.0005	529	15.68	-.0301		
1000	17.45	.25	-.0172	.0003	1000	17.56	-.0173		

APPENDIX TABLE A2.2 - part 13 Functional response results from an extra sixty replicates using the search strategy of the forward directed random walk with a step length of ten ($IS = 4b$) to search for regularly arranged prey. An extra prey density of 81 has also been included.

FIRST 30 REPLICATES				SECOND 30 REPLICATES			
N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$		N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$	
10	.82 .28	-.1037 .0390		10	.63 .21	-.0739 .0254	
40	2.36 .36	-.0621 .0098		40	2.78 .58	-.0758 .0167	
90	5.83 .66	-.0678 .0079		90	5.46 .51	-.0631 .0061	
160	10.48 .55	-.0679 .0037		160	10.32 .70	-.0670 .0047	
250	9.53 .44	-.0389 .0018		250	10.17 .64	-.0416 .0027	
490	14.00 .41	-.0290 .0009		490	14.37 .38	-.0298 .0008	
810	17.31 .23	-.0216 .0003		810	17.29 .17	-.0216 .0002	
1000	17.54 .18	-.0177 .0002		1000	17.48 .19	-.0176 .0002	
THIRD 30 REPLICATES				90 REPLICATES			
N	$\bar{N}_e \pm S.E.$	$\overline{\ln S} \pm S.E.$		N	\bar{N}_e	$\overline{\ln S}$	
10	.75 .27	-.0945 .0365		10	.73	-.0907	
40	2.85 .44	-.0761 .0120		40	2.66	-.0713	
90	5.38 .42	-.0620 .0049		90	5.56	-.0643	
160	10.44 .46	-.0676 .0031		160	10.41	-.0675	
250	9.84 .47	-.0402 .0019		250	9.85	-.0402	
490	14.06 .35	-.0291 .0007		490	14.14	-.0293	
810	17.54 .14	-.0219 .0002		810	17.38	-.0217	
1000	17.75 .17	-.0179 .0002		1000	17.59	-.0177	

APPENDIX TABLE A2.2 - part 14 Functional response results from an extra sixty replicates using the search strategy of the forward directed random walk with a step length of ten ($IS = 4b$) to search for regularly arranged clumps of ten prey.

FIRST 30 REPLICATES					SECOND 30 REPLICATES				
N	$\bar{N}_e \pm \text{S.E.}$		$\overline{\ln S} \pm \text{S.E.}$		N	$\bar{N}_e \pm \text{S.E.}$		$\overline{\ln S} \pm \text{S.E.}$	
9	.99	.16	-.1223	.0208	9	.85	.17	-.0102	.0231
16	1.37	.19	-.0923	.0136	16	1.52	.24	-.1039	.0173
25	1.75	.23	-.0741	.0100	25	1.67	.21	-.0703	.0093
64	4.29	.36	-.0698	.0056	64	4.15	.30	-.0673	.0050
121	5.51	.34	-.0467	.0029	121	6.49	.28	-.0552	.0025
256	7.77	.36	-.0309	.0015	256	8.07	.29	-.0320	.0012
529	10.80	.29	-.0206	.0005	529	10.39	.23	-.0198	.0005
1024	12.20	.27	-.0120	.0003	1024	12.37	.32	-.0122	.0003
THIRD 30 REPLICATES					90 REPLICATES				
N	$\bar{N}_e \pm \text{S.E.}$		$\overline{\ln S} \pm \text{S.E.}$		N	\bar{N}_e	$\overline{\ln S}$		
9	.47	.10	-.0553	.0126	9	.77	-.0946		
16	1.63	.16	-.1094	.0110	16	1.51	-.1019		
25	1.77	.25	-.0752	.0111	25	1.73	-.0732		
64	4.64	.26	-.0755	.0045	64	4.36	-.0709		
121	5.82	.28	-.0494	.0024	121	5.94	-.0504		
256	8.09	.26	-.0321	.0011	256	7.98	-.0317		
529	10.46	.25	-.0200	.0005	529	10.55	-.0201		
1024	12.75	.27	-.0125	.0003	1024	12.44	-.0122		

APPENDIX TABLE A2.2 - part 15 Functional response results from
an extra sixty replicates using
the search strategy of the aggregative walk with a long step
length of ten (IS = 4d) to search for regularly arranged prey.

APPENDIX TABLE A2.3 Results of the simulations for Section 6.5

In this table the functional response results using various models of the parameters, handling time and encounter success rate, are given. The search strategy used is that of completely random search ($IS = 1$), and the prey are arranged at random. The smaller arena of 50×50 is used, the total time available is 1000 time units, and 50 replicates were run for each prey density. Results are given as the mean number eaten (\bar{N}_e), and the mean of the logarithmic values of the proportion of prey surviving ($\overline{\ln S}$), together with their standard errors of the mean. By substituting for the prey density and \bar{N}_e into the Random Predator Equation, mean values of the parameter affected by the model used can be obtained. Thus, when the encounter success rate is varied, the effective value of the mean search efficiency (\bar{a}) can be obtained, and when the handling time is varied, the mean handling time (\bar{T}_h) can be evaluated. Results for the following models are given:

part	reference	model	parameters
1	S1	$\bar{s} = a N + b$	$a = 0.02, b = 0.2$
2	S2	$s = a N_e + b$	$a = 0.2, b = 0.2$
3	S3	$\bar{s} = a b N / (1 + a c N)$	$a = 0.05, b = 1.0, c = 1.0$
4	S5	$\bar{s} = a \ln N + b$	$a = 0.3, b = -0.4$
5	S12	$\bar{T}_h = a \text{ If } N \text{ } b, T_h = c$	$a = -40, b = 60, c = 4$
6	D1A	$\bar{s} = a N + b$	$a = -0.0002, b = 1.0$
7	D1B	$\bar{s} = a N + b$	$a = -0.0004, b = 2.0$
8	D2	$\bar{s} = a \ln N + b$	$a = -0.11, b = 1.0$

where s is the encounter success rate, T_h is the handling time and a, b & c are input parameters. When the encounter success rate is defined by a model, the handling time used is 50 time units, and when the handling time is defined, the encounter success rate of 0.5 is used.

PREY DENSITY	NUMBER EATEN		$\overline{\ln S}$		CALCULATED \bar{a} (x 1000)
	MEAN	S.E.	MEAN	S.E.	
5	0.43	.10	- .106	.026	.092
8	1.00	.12	- .141	.018	.141
10	1.36	.16	- .156	.020	.157
12	1.85	.15	- .173	.015	.184
14	2.33	.19	- .189	.017	.206
16	2.88	.21	- .205	.017	.232
20	3.67	.21	- .207	.013	.248
24	4.80	.22	- .226	.012	.294
28	5.40	.24	- .217	.011	.293
32	6.17	.24	- .216	.009	.310
64	10.87	.19	- .187	.004	.408
128	14.01	.14	- .116	.001	.387
256	16.44	.10	- .066	.000	.373
500	18.17	.05	- .037	.000	.405
1000	19.03	.03	- .019	.000	.396
2000	19.52	.02	- .010	.000	.409
4000	19.74	.01	- .005	.000	.381

APPENDIX TABLE A2.3 - part 1 Sigmoid functional response
 results obtained using the
 model S1.

PREY DENSITY	NUMBER EATEN		$\overline{\ln S}$		CALCULATED \bar{a} (x 1000)
	MEAN	S.E.	MEAN	S.E.	
5	0.26	.07	- .059	.016	.054
8	0.64	.12	- .090	.018	.085
10	1.21	.17	- .139	.021	.137
12	1.32	.21	- .127	.022	.125
14	2.02	.26	- .169	.024	.173
16	1.59	.22	- .111	.016	.114
20	2.54	.27	- .142	.016	.156
24	2.63	.26	- .120	.013	.134
28	3.70	.34	- .147	.014	.174
32	4.20	.34	- .145	.012	.178
64	7.95	.41	- .134	.007	.220
128	12.82	.21	- .106	.002	.294
256	15.47	.15	- .062	.001	.275
500	17.46	.09	- .036	.000	.280
1000	18.69	.05	- .019	.000	.288
2000	19.31	.03	- .010	.000	.281
4000	19.67	.01	- .005	.000	.299

APPENDIX TABLE A2.3 - part 2 Sigmoid functional response results obtained using the model S2.

PREY DENSITY	NUMBER EATEN		$\overline{\ln S}$		CALCULATED \bar{a} (x 1000)
	MEAN	S.E.	MEAN	S.F.	
5	0.28	.08	-.065	.018	.058
8	0.82	.13	-.117	.019	.113
10	1.46	.13	-.164	.016	.170
12	1.37	.13	-.125	.012	.130
14	1.79	.17	-.142	.015	.150
16	2.18	.17	-.151	.013	.164
20	3.17	.22	-.177	.013	.205
24	4.08	.25	-.190	.013	.234
28	4.33	.24	-.171	.010	.214
32	5.29	.28	-.184	.010	.246
64	9.36	.20	-.158	.004	.297
128	13.56	.16	-.112	.001	.348
256	16.28	.10	-.066	.000	.353
500	17.96	.06	-.037	.000	.359
1000	19.05	.03	-.019	.000	.405
2000	19.51	.01	-.010	.000	.400
4000	19.77	.01	-.005	.000	.431

APPENDIX TABLE A2.3 - part 3 Sigmoid functional response results obtained using the model S3.

PREY DENSITY	NUMBER EATEN		$\overline{\ln s}$		CALCULATED \bar{a} (x 1000)
	MEAN	S.E.	MEAN	S.E.	
5	0.22	.07	- .050	.015	.045
8	0.86	.12	- .121	.017	.119
10	0.98	.13	- .109	.015	.108
12	1.30	.13	- .119	.013	.123
14	1.51	.18	- .119	.015	.123
16	2.20	.18	- .152	.013	.166
20	2.87	.19	- .158	.011	.181
24	3.99	.22	- .185	.011	.227
28	4.50	.20	- .177	.009	.226
32	5.95	.21	- .207	.008	.293
64	9.64	.26	- .164	.005	.315
128	13.85	.18	- .115	.002	.372
256	16.58	.09	- .067	.000	.392
500	18.10	.05	- .037	.000	.388
1000	19.02	.03	- .019	.000	.392
2000	19.50	.02	- .010	.000	.392
4000	19.75	.01	- .005	.000	.396

APPENDIX TABLE A2.3 - part 4 Sigmoid functional response results obtained using the model S5.

PREY DENSITY	NUMBER EATEN		$\overline{\ln s}$		CALCULATED \overline{Th}
	MEAN	S.E.	MEAN	S.E.	
5	0.76	.13	- .193	.037	+ 231.1
8	1.36	.15	- .201	.025	+ 50.3
10	2.34	.18	- .280	.024	- 142.3
12	2.51	.17	- .243	.019	- 69.1
14	2.80	.22	- .233	.020	- 41.3
16	3.18	.24	- .230	.019	- 33.9
20	4.17	.29	- .243	.019	- 40.6
24	4.56	.32	- .218	.017	- 11.8
28	5.33	.25	- .214	.011	- 10.5
32	6.41	.26	- .226	.010	- 18.4
64	10.17	.20	- .173	.004	+ 13.2
128	14.80	.24	- .123	.002	+ 26.1
256	18.37	.17	- .075	.001	+ 34.2
500	21.24	.10	- .043	.000	+ 36.9
1000	23.38	.12	- .024	.000	+ 37.7
2000	24.24	.13	- .012	.000	+ 38.7
4000	25.08	.13	- .006	.000	+ 38.6

APPENDIX TABLE A2.3 - part 5 Sigmoid functional response results obtained using the model Sl2.

PREY DENSITY	NUMBER EATEN		$\overline{\ln S}$		CALCULATED \bar{a} (x 1000)
	MEAN	S.E.	MEAN	S.E.	
8	2.39	.14	- .379	.028	.403
16	4.23	.17	- .313	.015	.389
32	7.11	.21	- .253	.008	.390
64	10.76	.21	- .184	.004	.398
128	13.89	.15	- .115	.001	.376
256	16.41	.09	- .066	.000	.369
500	17.95	.06	- .037	.000	.357
1000	18.81	.04	- .019	.000	.319
1500	19.09	.02	- .013	.000	.282
2000	19.18	.02	- .010	.000	.235
2500	19.23	.03	- .008	.000	.201
3000	19.17	.03	- .006	.000	.154
3500	19.06	.02	- .005	.000	.116
4000	18.78	.03	- .005	.000	.077
4250	18.58	.04	- .004	.000	.062
4500	17.85	.06	- .004	.000	.037
4750	16.40	.09	- .003	.000	.019

APPENDIX TABLE A2.3 - part 6 Dome-shaped functional re-
 sponse results obtained
 using the model D1A.

PREY DENSITY	NUMBER EATEN		$\overline{\ln S}$		CALCULATED \bar{a} (x 1000)
	MEAN	S.E.	MEAN	S.E.	
8	2.61	.17	- .422	.033	.454
16	4.51	.20	- .339	.018	.428
32	7.22	.23	- .258	.009	.400
64	10.72	.21	- .184	.004	.395
128	14.06	.14	- .116	.001	.392
256	16.55	.09	- .067	.000	.387
500	18.13	.05	- .037	.000	.395
1000	19.02	.03	- .019	.000	.392
1500	19.33	.02	- .013	.000	.387
2000	19.51	.01	- .010	.000	.400
2500	19.59	.01	- .008	.000	.384
3000	19.59	.01	- .007	.000	.320
3500	19.55	.02	- .006	.000	.249
4000	19.38	.03	- .005	.000	.157
4250	19.24	.02	- .005	.000	.119
4500	18.93	.03	- .004	.000	.079
4750	18.08	.05	- .004	.000	.040

APPENDIX TABLE A2.3 - part 7 Dome-shaped functional re-
 sponse results obtained
 using the model D1B.

PREY DENSITY	NUMBER EATEN		$\overline{\ln S}$		CALCULATED \bar{a} (x 1000)
	MEAN	S.E.	MEAN	S.E.	
8	2.12	.16	- .329	.029	.344
16	3.34	.21	- .241	.017	.281
32	5.58	.23	- .194	.009	.266
64	7.86	.25	- .132	.005	.216
128	10.15	.17	- .083	.001	.168
256	12.81	.19	- .051	.001	.143
500	15.11	.14	- .031	.000	.126
1000	16.53	.08	- .017	.000	.096
1500	16.94	.08	- .011	.000	.074
2000	17.29	.08	- .009	.000	.064
2500	17.42	.06	- .007	.000	.054
3000	17.63	.07	- .006	.000	.050
3500	17.53	.08	- .005	.000	.041
4000	17.59	.07	- .004	.000	.037
4250	17.40	.07	- .004	.000	.032
4500	17.41	.09	- .004	.000	.030
4750	17.30	.08	- .004	.000	.027

APPENDIX TABLE A2.3 - part 8 Dome-shaped functional re-
 sponse results obtained
 using the model D2.

APPENDIX TABLE A2.4 Results of the simulations for Section 6.6

The results of the simulations of the aggregative responses are given here. All eight search strategies are used to search for four different prey distributions. These prey distributions are: random, using the negative binomial distribution with values for K of 2.0 and 0.05, and in randomly distributed clumps of eight. In the following tables these distributions will be referred to as random, neg. bin. K = 2.0, neg. bin. K = 0.05, and clumps, respectively. A range of initial prey densities is used, and 50 replicates are run for each combination. A giving up time of 250 time units is used. The encounter success rate is defined for each search strategy below.

The first eight parts of this table give the results of the mean number of prey eaten (N_e), the mean time spent searching (T_s), and the mean percentage of this time wasted (%TW), with their standard errors, and the mean number of prey surviving (i.e. $N - N_e$). The final part gives the overall searching efficiency (N_e/T_s) for each combination of prey density and predator search strategy.

The search strategies and their parameters are:

- 1 completely random search - SA (the chance of a prey encounter being successful) = 0.5
- 2 random walk - SA = 0.5
- 3 forward directed random walk - SA = 0.5
- 4a forward directed random walk with a step length of three -
 TLS = LLS = 3, TSS = LSS = 0, H = 0, SA = 0.5
- 4b forward directed random walk with a step length of ten -
 TLS = LLS = 10, TSS = LSS = 0, H = 0, SA = 0.5
- 4c aggregative walk with a long step length of three -
 TLS = LLS = 3, TSS = LSS = 1, H = 5, SA1 (the chance of a successful prey encounter when using the normal searching phase) = 0.5, SA2 (the chance of a successful prey encounter when using the second searching phase in response to a prey) = 0.75
- 4d aggregative walk with a long step length of ten -
 TLS = LLS = 10, TSS = LSS = 1, H = 5, SA1 = 0.5, SA2 = 0.75
- 5 systematic local search in response to finding a prey -
 LB = 3, TC = 8, area of 3 x 3 is searched, SA1 = 0.5, SA2 = 0.75

prey	Prey Density	Number Eaten		Time Spent		% Time Wasted		Number Surviving
		Mean	S.E.	Mean	S.E.	Mean	S.E.	
random	8	.5	.1	318	16	6.1	.3	7.5
	16	1.5	.2	415	30	7.8	.5	14.5
	32	3.6	.5	584	53	10.5	.9	28.4
	64	12.6	1.2	1151	91	18.9	1.3	51.4
	128	59.8	3.0	3384	198	42.3	1.7	68.2
	256	179.5	3.6	6394	221	60.8	1.1	76.5
	500	422.7	4.5	9562	232	70.2	.7	77.3
	1000	928.9	3.6	13543	237	75.4	.4	71.1
neg bin K = 2.0	8	.4	.1	312	15	6.1	.3	7.6
	16	1.5	.3	417	32	7.8	.6	14.5
	32	3.4	.5	574	52	10.1	.9	28.6
	63	13.7	1.3	1273	114	20.4	1.5	49.3
	128	57.0	2.8	3158	188	40.7	1.6	71.0
	255	175.1	4.5	6166	261	59.2	1.3	79.9
	498	426.7	3.0	9786	188	71.0	.5	71.9
	994	922.2	3.8	13367	246	75.2	.4	71.8
neg bin K = .05	8	.6	.1	321	18	6.4	.4	7.4
	17	.9	.2	339	22	6.4	.4	16.1
	29	3.0	.4	547	36	10.1	.7	26.0
	63	10.5	1.1	1034	86	17.3	1.3	52.5
	128	47.1	3.1	2550	181	35.0	1.8	80.9
	245	152.2	5.1	5124	228	54.4	1.6	92.8
	470	376.1	5.7	8415	256	68.2	.8	93.9
	828	718.0	6.9	10518	264	73.1	.6	110.0
clumps	8	.4	.1	280	12	5.5	.3	7.6
	16	.8	.2	305	15	5.9	.4	15.2
	32	2.2	.4	377	26	6.8	.5	28.8
	64	10.3	1.0	856	67	14.8	1.0	53.7
	128	42.6	3.4	2183	182	30.8	2.0	85.4
	256	166.2	4.0	5434	189	56.7	1.1	89.8
	496	415.6	3.2	9296	179	70.5	.5	80.4
	1000	916.9	4.0	12705	218	74.9	.4	83.1

APPENDIX TABLE A2.4 - part 1 Aggregative response results using the search strategy of completely random search (IS = 1).

Prey	Prey Density	Number Eaten		Time Spent		% Time Wasted		Number Surviving
		Mean	S.E.	Mean	S.E.	Mean	S.E.	
random	8	.3	.1	289	10	50.0	1.0	7.7
	16	.5	.1	291	11	50.4	1.3	15.5
	32	1.8	.3	431	29	53.9	1.0	30.2
	64	5.0	.6	658	57	56.8	1.0	59.0
	128	24.1	1.8	1736	127	61.6	.7	103.9
	256	71.0	4.7	3054	209	68.4	.7	185.0
	500	223.2	12.4	5572	356	71.9	.6	276.8
	1000	578.6	24.4	8384	425	73.4	.5	421.4
neg bin K = 2.0	8	.3	.1	284	10	51.4	1.2	7.3
	16	.5	.1	309	18	49.7	1.0	15.5
	32	1.8	.3	422	34	53.3	1.1	30.2
	63	4.1	.6	622	56	56.4	1.3	58.9
	128	16.8	1.5	1252	97	60.6	.9	111.2
	255	73.7	5.2	3147	230	67.2	.6	181.3
	498	220.0	13.5	5649	395	72.2	.7	278.0
	994	578.6	19.9	8330	375	73.3	.6	415.4
neg bin K = .05	8	.3	.1	283	11	52.5	1.2	7.7
	17	.6	.1	303	15	51.3	1.3	16.4
	29	1.5	.2	374	21	54.5	1.1	27.5
	63	4.3	.7	539	46	55.5	1.2	58.7
	128	12.8	1.5	788	65	57.0	1.1	115.2
	245	35.7	3.8	1317	116	59.9	.9	209.3
	470	65.3	6.8	1502	123	62.0	1.0	404.7
	828	119.4	16.2	1449	174	59.8	1.2	708.6
clumps	8	.3	.2	257	4	50.9	1.2	7.7
	16	.5	.2	272	10	49.8	1.0	15.5
	32	1.3	.4	293	13	49.7	1.0	30.7
	64	3.1	.8	391	32	51.9	1.1	60.9
	128	7.2	1.2	509	43	54.6	1.1	120.8
	256	28.2	3.7	1006	105	57.9	1.1	227.8
	496	134.8	13.1	2913	293	64.0	1.0	361.2
	1000	410.1	28.3	5268	381	70.7	.6	589.9
2000	1287.6	42.6	9817	435	72.3	.5	712.4	

APPENDIX TABLE A2.4 - part 2

Aggregative response results using the random walk (IS = 2).

Prey	Prey Density	Number Eaten		Time Spent		% Time Wasted		Number Surviving
		Mean	S.E.	Mean	S.E.	Mean	S.E.	
random	8	.3	.1	287	10	24.9	1.1	7.7
	16	.9	.2	374	26	27.6	1.2	15.1
	32	3.0	.5	530	51	27.9	1.2	29.0
	64	8.2	1.1	873	92	35.3	1.3	55.8
	128	37.3	2.5	2292	158	46.8	1.1	90.7
	256	143.4	5.2	5329	257	62.1	1.0	112.6
	500	353.2	9.2	7993	303	69.0	.7	146.8
	1000	820.6	12.3	11489	310	73.2	.5	179.4
neg bin K = 2.0	8	.4	.1	287	11	27.9	1.1	7.6
	16	1.0	.2	379	28	28.9	1.0	15.0
	32	2.8	.4	542	45	30.2	1.3	29.2
	63	8.1	.9	926	87	35.6	1.5	54.9
	128	39.9	3.0	2402	186	47.2	1.2	88.1
	255	147.6	5.7	5548	271	62.5	.9	107.4
	498	352.1	7.2	8018	291	68.7	.7	145.9
	994	821.9	9.8	11155	311	72.2	.6	172.1
neg bin K = .05	8	.3	.1	277	10	27.3	1.1	7.7
	17	.9	.2	339	24	28.0	1.1	16.1
	29	2.0	.3	431	31	25.8	1.2	27.0
	63	6.4	.7	685	59	31.6	1.5	56.6
	128	25.8	2.5	1358	123	38.4	1.3	102.2
	245	65.7	6.0	2176	194	45.7	1.4	179.3
	470	216.9	14.7	4244	313	57.0	1.6	253.1
	828	384.9	25.9	4434	350	56.0	1.7	443.1
clumps	8	.4	.2	270	9	27.5	1.4	7.6
	16	.7	.3	282	12	26.3	1.2	15.3
	32	1.9	.5	317	18	27.7	1.1	30.1
	64	4.4	.8	439	39	26.3	1.1	49.6
	128	14.3	1.9	789	75	34.4	1.3	113.7
	256	87.6	6.6	2575	210	47.5	1.4	168.4
	496	300.1	12.3	5920	324	62.5	1.2	195.9
	1000	776.4	19.0	9870	419	70.6	.8	223.6

APPENDIX TABLE A2.4 - part 3

Aggregative response results using the strategy of the forward directed random walk (IS = 3).

Prey	Prey Density	Number Eaten		Time Spent		% Time Wasted		Number Surviving
		Mean	S.E.	Mean	S.E.	Mean	S.E.	
random	8	.4	.1	293	13	14.5	.9	7.6
	16	.8	.2	341	19	15.8	.9	15.2
	32	2.1	.3	451	32	16.9	.9	29.9
	64	12.7	1.3	1200	110	27.3	1.5	51.3
	128	56.9	3.2	3367	209	46.4	1.6	71.1
	256	173.8	3.5	6278	209	62.1	.9	82.2
	500	407.7	5.6	9614	263	70.9	.7	92.3
	1000	912.8	4.1	13457	233	75.5	.4	87.2
neg bin K = 2.0	8	.7	.1	334	17	15.1	1.0	7.3
	16	.9	.2	342	19	16.4	1.0	15.1
	32	4.1	.5	635	49	19.6	.9	27.9
	63	12.8	1.2	1211	107	28.1	1.2	50.2
	128	50.3	2.7	2829	173	42.2	1.4	77.7
	255	171.0	3.4	6159	210	61.7	.9	84.0
	498	408.4	4.1	9619	239	71.0	.6	89.6
	994	892.3	6.1	12976	266	74.8	.4	101.7
neg bin K = .05	8	.4	.1	290	12	13.4	.9	7.6
	17	1.1	.2	369	25	15.9	.8	16.9
	29	2.4	.4	465	38	17.0	1.0	26.6
	63	8.3	1.3	819	89	22.5	1.4	54.7
	128	40.7	3.3	2180	171	36.1	1.7	87.3
	245	124.4	6.2	4090	232	51.0	1.5	120.6
	470	291.3	10.5	5516	288	57.5	1.5	178.7
	828	527.2	24.9	6350	391	59.4	2.0	301.0
clumps	8	.4	.2	273	8	14.0	.9	7.6
	16	.9	.2	302	15	14.3	.9	15.1
	32	2.9	.5	413	27	16.2	.9	29.1
	64	6.0	.9	546	45	19.4	1.0	58.0
	128	26.9	2.7	1351	130	28.2	1.5	101.1
	256	116.1	7.8	3654	298	46.7	2.0	139.9
	496	383.3	7.5	8435	314	67.9	1.0	112.7
	1000	865.1	9.6	11758	340	73.1	.7	134.9

APPENDIX TABLE A2.4 - part 4

Aggregative response results using the forward directed random walk with a step length of three (IS = 4a).

Prey	Prey Density	Number Eaten		Time Spent		% Time Wasted		Number Surviving
		Mean	S.E.	Mean	S.E.	Mean	S.E.	
random	8	.5	.1	293	20	11.1	1.0	7.5
	16	1.1	.2	358	22	10.9	.8	14.9
	32	3.0	.4	539	48	13.4	.9	29.0
	64	10.9	1.1	1120	96	22.6	1.3	53.1
	128	51.9	2.9	3019	185	42.6	1.7	76.1
	256	170.9	4.2	6183	247	60.8	1.3	85.1
	500	408.9	4.6	9533	259	70.6	.7	91.1
	1000	898.3	5.2	12902	260	74.4	.5	101.7
	2000	1889.1	7.2	16541	340	75.0	.5	110.9
neg bin K = 2.0	8	.5	.1	312	17	10.5	.9	7.5
	16	1.0	.2	370	30	10.8	.7	15.0
	32	3.3	.5	540	46	14.1	.9	28.7
	63	12.0	1.1	1163	89	23.6	1.2	51.0
	128	48.0	3.2	2705	208	38.7	1.9	80.0
	255	173.7	3.5	6279	222	61.7	1.0	81.3
	498	401.4	4.7	9149	248	69.6	.7	96.6
	994	899.0	4.8	13220	282	75.1	.5	95.0
	neg bin K = .05	8	.5	.1	299	12	10.4	.6
17		1.3	.2	372	22	11.8	.8	15.7
29		2.4	.4	464	39	12.8	.8	26.6
63		9.9	1.1	927	80	19.1	1.2	53.1
128		32.8	3.5	1814	180	29.6	2.1	95.2
245		118.0	6.2	3885	241	48.0	1.7	125.0
470		318.8	8.6	6564	307	61.6	1.4	151.2
828		599.6	19.4	7702	388	64.8	1.5	228.4
clumps		8	.4	.1	274	9	9.0	.8
	16	.6	.2	293	13	10.2	.7	15.4
	32	2.2	.5	373	30	11.0	.8	29.8
	64	6.6	.8	591	44	15.8	.9	57.4
	128	24.1	2.9	1270	128	24.3	1.5	103.9
	256	128.8	5.9	4071	243	49.3	1.6	127.2
	496	372.4	6.7	7847	267	66.2	.9	123.6
	1000	894.0	5.0	12826	245	75.4	.4	106.0

APPENDIX TABLE A2.4 - part 5

Aggregative response results using the forward directed random walk with a step length of ten (IS = 4b).

Prey	Prey Density	Number Eaten		Time Spent		% Time Wasted		Number Surviving
		Mean	S.E.	Mean	S.E.	Mean	S.E.	
random	8	.4	.1	293	12	14.3	.9	7.6
	16	.6	.1	327	19	14.8	.8	15.4
	32	2.8	.4	500	37	18.3	.9	29.2
	64	10.5	1.0	1046	85	25.1	1.2	53.5
	128	54.8	2.2	3003	138	44.9	1.0	73.2
	256	168.9	3.9	5797	227	60.2	1.0	87.1
	500	408.4	4.9	8833	224	69.8	.6	91.6
	1000	897.0	5.3	11427	238	73.7	.5	103.0
	2000	1893.1	5.8	13877	223	75.9	.3	104.9
neg bin K = 2.0	8	.3	.1	288	12	14.2	.9	7.7
	16	.9	.2	351	21	15.1	.8	15.1
	32	3.3	.5	577	46	18.3	1.1	28.7
	63	13.3	1.2	1298	108	28.3	1.3	49.7
	128	47.1	2.7	2553	153	40.9	1.3	80.9
	255	170.5	4.2	5728	217	59.8	1.0	84.5
	498	410.1	4.8	8881	247	69.9	.7	87.9
	994	895.7	6.3	11569	286	73.9	.5	98.3
	1988	1890.6	6.2	14091	233	76.1	.3	97.4
neg bin K = .05	8	.5	.1	315	14	14.2	.7	7.5
	17	1.4	.2	403	27	16.8	1.0	15.6
	29	3.2	.5	528	52	19.4	1.0	25.8
	63	9.9	1.3	759	76	22.1	1.3	53.1
	128	46.6	3.0	1847	123	34.9	1.2	82.4
	245	116.0	7.1	2755	183	42.6	1.4	129.0
	470	301.7	8.8	4023	179	51.3	1.1	168.3
	828	554.9	23.9	4582	292	52.8	1.7	273.1
	clumps	8	.8	.2	281	9	12.9	.7
16		1.2	.4	295	13	13.5	.8	14.8
32		2.6	.5	322	15	14.8	.8	29.4
64		9.0	1.4	537	53	19.4	1.1	55.0
128		39.4	3.4	1318	110	28.5	1.4	88.6
256		136.9	6.9	3050	199	44.3	1.5	119.1
496		368.9	8.5	5614	236	58.6	1.1	127.1
1000		878.7	9.3	8853	234	68.6	.7	121.3

APPENDIX TABLE A2.4 - part 6

Aggregative response results using the aggregative walk with a long step length of three (IS = 4c).

Prey	Prey Density	Number Eaten		Time Spent		% Time Wasted		Number Surviving
		Mean	S.E.	Mean	S.E.	Mean	S.E.	
random	8	.4	.1	301	15	10.0	.7	7.6
	16	1.0	.2	362	25	11.4	.9	15.0
	32	2.6	.4	527	48	14.3	.9	29.4
	64	11.9	1.3	1138	101	23.4	1.3	52.1
	128	57.8	2.8	3209	179	43.5	1.6	70.2
	256	178.4	3.8	6134	224	60.9	1.0	77.6
	500	416.5	4.4	8850	221	69.4	.7	83.5
	1000	921.6	4.4	12181	214	75.0	.4	78.4
neg bin K = 2.0	8	.4	.1	296	16	10.0	.7	7.6
	16	1.0	.2	352	22	10.5	.7	15.0
	32	2.3	.4	494	40	13.7	.9	29.7
	63	14.9	1.2	1371	102	25.9	1.2	48.1
	128	49.1	2.8	2621	169	38.8	1.6	78.9
	255	182.2	3.2	6272	205	61.6	.9	72.8
	498	412.9	4.7	8815	236	69.3	.7	85.1
	994	904.6	4.9	11418	232	73.6	.5	89.4
neg bin K = .05	8	.5	.1	312	13	10.2	.6	7.5
	17	1.2	.2	353	22	12.2	.7	15.8
	29	2.6	.4	455	31	12.6	.9	26.4
	63	10.3	1.1	839	70	18.9	1.0	52.7
	128	45.3	3.2	1807	141	31.2	1.5	82.7
	245	148.4	4.4	3510	136	46.6	1.1	96.6
	470	328.8	10.4	4585	235	52.5	1.5	141.2
	828	641.6	13.4	5319	204	56.2	1.1	186.4
clumps	8	.8	.2	283	10	9.4	.7	7.2
	16	1.8	.4	327	18	10.7	.7	14.2
	32	4.7	.9	413	35	13.2	1.0	27.3
	64	9.6	1.2	548	29	13.9	.7	54.4
	128	34.0	3.3	1138	103	23.3	1.4	94.0
	256	138.8	7.5	3080	205	41.8	1.8	117.2
	496	406.0	4.7	6722	198	62.9	.8	90.0
	1000	899.0	6.0	9233	243	69.2	.7	101.0

APPENDIX TABLE A2.4 - part 7

Aggregative response results using the aggregative walk with a long step length of ten (IS = 4d).

Prey	Prey Density	Number Eaten		Time Spent		% Time Wasted		Number Surviving
		Mean	S.E.	Mean	S.E.	Mean	S.E.	
random	8	.3	.1	271	11	25.9	1.1	7.7
	16	1.0	.2	338	18	29.8	1.4	15.0
	32	2.6	.4	518	43	30.7	1.4	29.4
	64	8.7	.9	865	68	35.2	1.3	75.3
	128	42.7	3.4	2358	202	49.3	1.4	85.3
	256	139.1	5.4	4137	206	61.7	.8	116.9
	500	365.6	6.6	6280	194	71.0	.6	134.4
	1000	809.2	14.2	7020	232	74.4	.6	190.8
	2000	1774.2	18.9	8193	253	77.4	.5	225.8
neg bin K = 2.0	8	.4	.1	305	14	27.6	1.1	7.6
	16	1.2	.2	377	21	28.9	1.1	14.8
	32	2.1	.3	463	32	29.2	1.1	29.9
	63	11.0	1.2	1059	100	37.7	1.5	52.0
	128	40.8	3.3	2224	190	49.4	1.4	87.2
	255	148.1	5.5	4379	191	61.8	.8	106.9
	498	345.5	10.1	5575	234	68.7	.7	152.5
	994	808.5	12.9	6772	201	73.7	.5	185.5
	1988	1726.6	28.1	7708	277	76.6	.6	261.4
neg bin K = .05	8	.5	.1	293	10	26.6	1.2	7.5
	17	1.1	.2	335	19	27.3	1.1	15.9
	29	2.2	.4	401	28	30.3	1.4	26.8
	63	10.4	1.3	676	49	33.3	1.2	52.6
	128	33.8	2.9	1040	73	38.4	1.2	94.2
	245	111.0	6.7	1886	128	45.4	1.0	134.0
	470	257.3	15.2	2296	153	49.2	1.1	212.7
	828	439.9	23.8	2148	136	48.1	.9	388.1
	clumps	8	1.1	.4	266	7	27.5	1.2
16		2.6	.6	310	16	27.7	1.0	13.4
32		2.6	.6	282	8	26.7	1.0	29.4
64		10.8	1.5	407	24	28.8	1.1	53.2
128		33.5	3.3	778	61	35.0	1.2	94.5
256		88.0	8.3	1230	106	40.5	1.1	168.0
496		291.5	14.6	2722	167	51.8	1.2	204.5
1000		783.9	15.9	4616	180	63.6	.7	216.1
2000		1707.5	31.4	6079	260	69.9	.9	292.5

APPENDIX TABLE A2.4 - part 8

Aggregative response results using the strategy of systematic local search in response to finding a prey (IS = 5).

IS	PREY	EFFICIENCY (N_e/T_s) AT THE INITIAL DENSITY OF :							
		8	16	32	64	128	256	500	1000
1	random	16	36	62	110	177	281	312	686
	K = 2.0	13	36	59	108	181	284	436	690
	K = .05	19	27	55	102	185	297	447	683
	clumps	14	26	58	120	195	306	447	722
2	random	10	17	42	76	139	233	401	690
	K = 2.0	11	16	43	66	134	234	389	695
	K = .05	11	20	40	80	162	271	435	824
	clumps	12	18	44	79	142	280	463	779
3	random	11	24	57	94	163	269	442	714
	K = 2.0	14	26	52	88	166	266	439	737
	K = .05	11	27	46	93	190	302	511	868
	clumps	15	25	60	100	181	340	507	787
4a	random	14	24	47	106	169	277	424	678
	K = 2.0	21	26	65	106	178	278	425	688
	K = .05	14	30	52	101	187	304	528	830
	clumps	15	30	70	110	199	318	454	736
4b	random	17	31	56	97	172	276	429	696
	K = 2.0	16	27	61	103	177	277	439	680
	K = .05	17	35	52	107	181	304	486	779
	clumps	15	21	59	112	190	316	475	697
4c	random	14	18	56	100	183	462	785	1364
	K = 2.0	10	26	57	102	298	462	774	1342
	K = .05	16	35	61	130	252	421	750	1211
	clumps	29	41	81	168	299	449	657	993
4d	random	13	28	49	105	180	291	471	757
	K = 2.0	14	28	47	109	187	291	468	792
	K = .05	16	34	57	123	251	423	717	1206
	clumps	28	55	114	175	299	451	604	934
5	random	11	30	50	101	181	335	582	1153
	K = 2.0	13	32	45	104	184	338	620	1194
	K = .05	17	33	55	154	325	589	1121	2048
	clumps	41	84	92	265	431	715	1071	1698

APPENDIX TABLE A2.4 - part 9 Aggregative response results -
overall efficiencies (N_e/T_s)
multiplied x 10,000 for all search strategies (IS) and prey
distributions.

APPENDIX TABLE A2.5 Results of the simulations for Section 6.7

In this table the results of simulating aggregative responses with different giving up times are given. Three different giving up times (of 50, 100, and 200 time units) are used. Two search strategies (IS = 1, 4d) are used to search for two different prey arrangements (random and in randomly distributed clumps of eight, referred to as clumped). The first three parts of the table give the mean number eaten (N_e), the mean time spent searching (T_s), the mean percentage time wasted (%TW), and their standard errors, and the number of prey surviving (i.e. $N - N_e$), while the final part gives the overall efficiencies (N_e/T_s).

The search strategies and their parameters are:

- 1 completely random search - SA = 0.5
- 4d aggregative walk with a long step length of ten -
 LLS = TLS = 10, LSS = TSS = 1, H = 5, SA1 = 0.5, SA2 = 0.75

IS	ID	Prey Density	Number	Eaten	Time Spent		% Time Wasted		Number Left	
			Mean	S.E.	Mean	S.E.	Mean	S.E.		
completely random search (IS = 1)	random	8	.04	.03	50.3	1.0	1.13	.20	7.96	
		16	.22	.07	54.5	1.9	1.25	.22	15.78	
		32	.30	.10	55.4	2.6	.97	.17	31.70	
		64	.76	.18	68.7	4.8	1.51	.19	63.24	
		128	2.82	.42	102.5	7.8	1.87	.25	125.18	
		256	10.94	1.23	219.1	19.6	4.19	.37	245.06	
		500	88.14	7.96	1000.7	88.0	15.55	1.25	411.86	
		1000	474.12	19.79	3382.7	170.9	37.49	1.52	525.88	
		2000	1454.88	18.37	6648.7	157.1	50.86	.69	545.12	
	4000	3413.89	17.30	9768.2	154.2	51.97	.48	586.11		
	completely random search (IS = 1)	clumped	8	.12	.07	50.1	.7	.82	.16	7.88
			16	.16	.07	51.3	1.2	.87	.20	15.84
			32	.34	.10	55.0	1.7	1.20	.21	31.66
			64	.94	.23	65.1	3.8	1.33	.23	63.06
			128	2.10	.45	82.6	6.4	1.33	.21	125.90
			256	7.56	1.07	147.8	15.6	3.05	.34	248.44
			496	36.68	3.64	394.9	35.0	6.89	.58	459.32
			1000	341.82	22.99	2242.3	172.8	28.11	1.79	658.18
2000			1353.06	27.12	5850.9	180.1	49.37	1.00	646.94	
4000	3392.02	19.11	9597.1	150.5	54.70	.45	607.98			
aggregative walk, ILS = 10 (IS = 4d)	random	8	.06	.03	51.3	.8	3.90	.96	7.94	
		16	.18	.05	54.2	1.5	4.33	.82	15.82	
		32	.34	.11	58.0	3.0	5.54	1.26	31.66	
		64	.78	.15	68.6	4.2	6.27	1.09	63.22	
		128	2.68	.47	108.8	10.5	7.82	.93	125.32	
		256	10.00	1.23	205.2	20.5	11.14	.90	246.00	
		500	67.70	7.46	730.5	82.2	22.52	1.19	432.00	
		1000	471.86	15.41	3004.4	124.8	43.47	.75	528.14	
		2000	1373.06	29.85	5331.5	167.0	53.99	.62	626.94	
	4000	3128.86	48.31	6963.2	201.3	56.46	.57	871.14		
	aggregative walk, ILS = 10 (IS = 4d)	clumped	8	.08	.06	51.5	1.1	4.66	1.41	7.92
			16	.18	.13	50.9	.7	3.49	1.13	15.82
			32	.10	.07	50.8	.5	3.40	1.00	31.90
			64	1.76	.36	68.2	3.6	6.13	1.00	62.24
			128	3.32	.65	74.8	4.4	6.76	.90	124.68
			256	10.22	1.87	125.2	13.7	8.53	.84	245.78
			496	37.34	4.48	259.8	25.8	13.31	.82	458.66
			1000	180.74	18.49	824.7	89.0	24.35	1.05	819.26
2000			1040.36	43.26	3046.3	164.1	42.19	.89	959.64	
4000	2993.70	62.41	5951.4	192.1	52.78	.66	1006.30			

APPENDIX TABLE A2.5 - part 1

Aggregative response results simulated with a giving up time of 50 time units.

IS	ID	Prey Density	Number Eaten		Time Spent		% Time Wasted		Number Left
			Mean	S.E.	Mean	S.E.	Mean	S.E.	
completely random search (IS = 1)	random	8	.14	.06	103.8	2.4	1.95	.16	7.86
		16	.20	.06	109.0	3.1	2.19	.20	15.80
		32	.80	.16	135.0	7.5	2.51	.24	31.20
		64	1.70	.35	157.8	13.3	2.93	.30	62.30
		128	7.94	1.02	349.1	31.9	6.52	.57	120.06
		256	66.78	4.97	1536.6	118.9	23.10	1.54	189.22
		500	270.00	7.93	4107.3	167.1	46.31	1.16	230.00
		1000	767.32	9.72	7500.2	181.6	60.42	.72	232.68
	clumped	8	.30	.11	107.0	3.2	2.13	.22	7.70
		16	.44	.14	113.6	5.4	2.15	.17	15.56
		32	.82	.16	124.0	5.6	2.04	.19	31.18
		64	2.82	.43	190.9	14.5	3.11	.31	61.18
		128	6.94	1.13	284.5	33.1	5.08	.61	121.06
		256	44.96	4.50	982.6	97.8	15.91	1.41	211.04
496		203.64	11.55	2862.1	184.2	36.32	1.72	292.36	
1000		731.18	14.37	6838.2	226.5	58.73	1.08	268.82	
aggregative walk, LLS = 10 (IS = 4d)	random	8	.14	.05	105.8	2.6	5.89	.87	7.86
		16	.28	.07	113.1	3.8	6.74	.93	15.72
		32	1.02	.17	150.9	10.4	7.89	.70	30.98
		64	2.38	.35	191.1	14.3	8.27	.79	61.62
		128	10.06	1.14	403.4	36.1	13.00	.83	117.94
		256	61.72	4.42	1357.0	99.0	26.75	1.20	194.28
		500	264.76	9.46	3772.9	170.5	47.46	1.12	235.24
		1000	749.76	10.27	6549.8	179.9	60.27	.69	250.24
	clumped	8	.26	.15	103.4	1.8	6.32	.80	7.74
		16	.70	.24	109.7	3.7	4.30	.57	15.30
		32	.84	.25	116.7	4.7	6.33	.98	31.16
		64	1.42	.44	121.5	6.2	7.01	.82	62.58
		128	9.34	1.46	223.0	21.0	9.82	.84	118.18
		256	31.34	3.81	465.1	49.0	14.74	1.08	224.66
496		159.72	12.06	1396.5	114.0	27.08	1.20	336.28	
1000		591.48	18.95	3518.2	162.7	45.31	.96	408.52	
2000	1622.36	25.69	6931.2	228.7	58.46	.80	377.64		

APPENDIX TABLE A2.5 - part 2

Aggregative response results simulated with a giving up time of 100 time units.

IS	ID	Prey Density	Number Eaten		Time Spent		% Time Wasted		Number Left
			Mean	S.E.	Mean	S.E.	Mean	S.E.	
completely random search (IS = 1)	random	8	.28	.08	228.3	9.1	4.10	.23	7.72
		16	.80	.16	264.1	16.7	5.06	.31	15.20
		32	2.62	.36	395.1	30.0	7.47	.53	29.38
		64	9.24	1.14	788.1	79.3	13.40	1.20	54.76
		128	36.12	2.96	1851.5	154.5	27.12	1.87	91.88
		256	156.40	5.00	4850.3	209.1	53.01	1.48	99.60
		500	407.02	3.92	8616.4	195.6	67.72	.57	92.98
		1000	899.00	5.23	11765.6	245.7	72.06	.54	101.00
	clumped	8	.34	.10	219.1	6.2	4.23	.22	7.66
		16	.92	.20	251.9	13.2	4.56	.27	15.08
		32	2.40	.35	370.8	28.3	6.68	.54	29.60
		64	6.34	.92	538.2	59.6	9.47	.95	57.66
		128	30.22	2.90	1442.1	128.9	22.34	1.70	97.78
		256	137.78	6.08	4153.3	224.4	47.64	1.84	118.22
496		391.42	4.90	7954.9	196.9	66.25	.74	104.58	
1000		901.32	5.17	11796.4	233.1	73.31	.48	88.68	
aggregative walk, LLS = 10 (IS = 4d)	random	8	.36	.09	226.4	7.4	8.80	.70	7.64
		16	1.10	.18	307.5	18.5	10.15	.73	14.90
		32	1.36	.22	306.7	19.0	11.09	.82	30.64
		64	9.70	1.00	842.0	71.9	19.22	1.05	54.30
		128	35.34	2.77	1758.1	137.4	30.45	1.53	92.66
		256	162.00	3.20	5059.4	167.2	56.05	.86	94.00
		500	406.74	3.86	8224.4	182.3	67.75	.58	93.26
		1000	884.40	4.67	10298.0	189.0	71.40	.41	115.60
	clumped	8	.22	.13	210.8	6.2	9.87	.91	7.78
		16	.80	.24	221.9	6.6	8.94	.63	15.20
		32	2.94	.59	272.3	16.4	9.77	.69	29.06
		64	6.00	.79	364.4	20.0	12.01	.72	58.00
		128	24.06	2.36	726.3	61.7	18.51	.96	103.94
		256	98.18	7.33	1923.8	148.1	31.79	1.63	157.82
496		336.66	10.40	4430.8	231.5	51.11	1.39	159.34	
1000		868.08	5.72	7954.9	152.5	65.87	.50	131.92	

APPENDIX TABLE A2.5 - part 3

Aggregative response results simulated with a giving up time of 200 time units.

GUP	IS	ID	EFFICIENCY (Ne/Ts) at the initial density of :							
			8	16	32	64	128	256	500	1000
50	1	2	8	40	54	111	275	499	881	1402
		4	24	31	62	144	254	512	929	1524
	4d	2	12	33	59	114	254	512	927	1571
		4	16	35	20	258	444	816	1437	2192
100	1	2	13	18	59	108	227	435	657	1023
		4	28	39	66	148	244	458	712	1069
	4d	2	13	25	68	125	249	455	702	1145
		4	25	64	72	117	419	674	1144	1681
200	1	2	12	30	66	117	195	316	472	764
		4	16	37	65	118	210	332	492	764
	4d	2	16	36	44	115	201	320	495	859
		4	10	36	108	165	331	510	760	1091

APPENDIX TABLE A2.5 - part 4 Aggregative response results
with different giving up times
(GUP) - overall efficiencies (Ne/Ts) multiplied x 10,000 for
three giving up times (GUP), two search strategies (IS = 1,
random search; IS = 4d, aggregative walk with a long step
length of ten), and two prey distributions (ID = 2, random;
ID = 4, randomly distributed clumps of eight).

APPENDIX TABLE A2.6 Results of the simulations for Section 6.8

Simulation results to show the effects of the presence of alternative prey upon the aggregative response are given in this table. The prey are arranged either at random (IS = 2), or in clumps of eight distributed at random (IS = 4). In the first three parts of the table, random search (IS = 1) is used to obtain the aggregative response to prey type A with background densities of prey type B of 16 (part 1), 64 (part 2), and 128 (part 3). The encounter success rate is 0.5 for both prey types, and the giving up time is 250 time units. In the final part of the table (part 4) an aggregative walk is used (IS = 4d, LLS = TLS = 10, LSS = TSS = 1, H = 5, SA1 = SB1 = 0.5, SA2 = SB2 = 0.75) with a background density of prey type B of 64. Fifty replicates were run for each combination of prey densities and arrangements. The results given for each density of prey type A (N) are the mean number eaten of type A (\bar{N}_e), the mean number of type A surviving ($\bar{N}_s = N - \bar{N}_e$), the mean number of type B eaten (\bar{N}_e'), the mean time spent searching (\bar{T}_s), and the overall efficiency ($E = (\bar{N}_e + \bar{N}_e')/\bar{T}_s$), together with the relevant standard errors of the mean (SE).

IDa	IDb	N	\bar{N}_e	SE	\bar{N}_s	\bar{N}_e'	SE	\bar{T}_s	SE	E
2	2	8	0.8	0.1	7.2	1.5	.3	479	35	48
		16	1.7	0.3	14.3	1.8	.3	609	60	57
		32	4.0	0.5	28.0	2.1	.3	785	73	78
		64	18.4	1.5	45.6	4.6	.4	1774	143	130
		128	64.4	2.9	63.6	8.3	.5	3741	202	194
		256	187.7	3.7	68.3	11.9	.4	6826	218	292
		500	425.5	4.1	74.5	13.5	.3	9846	240	446
		1000	931.0	3.3	69.0	14.8	.2	13562	224	697
4	2	8	0.6	0.2	7.4	1.1	.2	405	26	42
		16	1.9	0.3	14.1	1.6	.3	545	46	64
		32	4.1	0.6	27.9	1.9	.3	692	68	87
		64	14.3	1.5	49.7	3.6	.4	1330	119	135
		128	57.7	3.5	70.3	7.7	.4	3211	220	204
		256	174.9	4.3	81.1	11.0	.3	6046	228	307
		496	415.7	4.5	80.3	12.7	.3	9154	229	468
		1000	918.0	5.1	82.0	15.0	.1	12838	258	727
2	4	8	0.4	0.1	7.6	1.1	.2	381	26	39
		16	2.0	0.3	14.0	1.7	.3	594	40	62
		32	3.7	0.5	28.3	1.8	.3	723	59	76
		64	13.5	1.3	50.5	4.2	.5	1386	110	128
		128	67.9	2.6	60.1	8.3	.5	3858	183	198
		256	189.8	3.0	66.2	11.8	.3	6994	196	288
		500	427.6	3.4	72.4	13.5	.2	9949	207	443
		1000	926.6	3.4	73.4	14.8	.2	13320	204	707
4	4	8	0.6	0.1	7.4	1.3	.3	424	28	45
		16	1.5	0.3	14.5	1.4	.2	475	36	61
		32	2.7	0.4	29.3	1.4	.3	536	39	76
		64	11.6	1.4	52.3	2.5	.4	1068	112	132
		128	58.2	3.6	69.8	7.0	.6	3198	220	204
		256	178.3	4.6	77.7	11.6	.4	6368	250	298
		496	420.6	4.7	75.4	13.5	.3	9744	256	446
		1000	929.5	2.9	72.5	15.2	.1	13441	170	703

APPENDIX TABLE A2.6 - part 1 Aggregative response results
obtained using random search
(IS = 1) to search for prey type A arranged at random (IDa =
2) or in clumps (IDa = 4) in the presence of 16 of prey type
B arranged at random (IDb = 2), or in clumps (IDb = 4).

IDa	IDb	N	\bar{N}_e	SE	\bar{N}_s	\bar{N}_e'	SE	\bar{T}_s	SE	E
2	2	8	2.2	0.2	5.8	15.7	1.6	1481	133	121
		16	4.8	0.4	11.2	19.1	1.5	1828	131	131
		32	11.4	0.9	20.6	21.6	1.6	2262	163	146
		64	29.2	1.5	34.8	29.8	1.5	3298	184	179
		128	79.8	2.9	48.2	40.4	1.6	5257	248	229
		256	197.6	2.7	58.4	50.0	0.7	7641	214	324
		500	438.6	2.6	61.4	55.8	0.4	10625	184	465
		1000	935.1	3.2	64.9	59.9	0.3	13832	226	719
4	2	8	1.7	0.2	6.3	14.3	1.4	1387	124	115
		16	4.6	0.5	11.4	17.6	1.6	1713	144	130
		32	11.0	0.8	21.0	21.9	1.6	2243	155	147
		64	27.0	1.6	37.0	27.8	1.6	3078	192	178
		128	74.0	3.1	54.0	36.2	1.4	4555	224	242
		256	192.6	2.9	63.4	47.6	0.8	7226	223	332
		496	420.7	4.6	75.3	54.0	0.6	9833	269	483
		1000	924.0	4.1	76.0	59.4	0.4	13313	255	739
2	4	8	1.4	0.2	6.6	10.6	1.0	966	79	124
		16	3.3	0.4	12.7	13.6	1.2	1308	112	129
		32	8.0	0.7	24.0	17.5	1.5	1699	128	127
		64	28.2	1.6	35.8	27.5	1.7	3075	180	181
		128	76.1	2.2	51.9	38.2	1.3	4786	192	239
		256	197.5	2.6	58.5	49.6	0.8	7569	201	326
		500	435.7	3.3	64.3	55.9	0.5	10474	198	469
		1000	929.4	3.4	70.6	59.7	0.4	13461	195	735
4	4	8	1.5	0.2	6.5	12.4	1.2	1112	106	125
		16	3.3	0.4	12.7	12.2	1.4	1124	108	138
		32	8.2	0.8	23.8	16.2	1.6	1573	139	155
		64	21.9	1.6	42.1	21.6	1.6	2259	160	193
		128	64.6	2.9	63.4	32.8	1.5	3839	216	254
		256	187.5	3.4	68.5	46.7	0.9	6980	233	336
		496	423.1	4.0	72.9	53.9	0.6	9871	242	483
		1000	926.1	2.8	73.9	59.4	0.3	13316	202	740

APPENDIX TABLE A2.6 - part 2 Aggregative response results
obtained using random search
(IS = 1) to search for prey type A arranged at random (IDa =
2) or in clumps (IDa = 4), in the presence of 64 of prey type
B arranged at random (IDb = 2), or in clumps (IDb = 4).

IDa	IDb	N	\bar{N}_e	SE	\bar{N}_s	\bar{N}_e'	SE	\bar{T}_s	SE	E
2	2	8	3.5	0.2	4.5	60.8	2.9	3442	195	187
		16	7.7	0.5	8.3	62.5	3.3	3656	223	192
		32	17.9	0.7	14.1	71.2	2.6	4273	194	209
		64	41.0	1.1	23.0	80.6	2.0	5270	205	231
		128	90.9	1.9	37.1	91.3	1.7	6411	221	284
		256	208.3	2.4	47.7	103.6	1.3	8780	216	355
		500	436.6	4.0	63.4	111.4	1.1	10692	288	513
		1000	935.5	3.1	64.5	120.2	0.6	13936	211	758
4	2	8	3.8	0.3	4.2	60.4	3.2	3406	183	188
		16	8.1	0.5	7.9	66.6	3.5	3940	237	190
		32	15.7	0.8	16.3	65.3	2.7	3736	206	217
		64	37.9	1.2	26.1	77.1	2.7	5026	232	229
		128	87.8	2.3	40.2	88.9	2.4	6152	225	287
		256	203.7	2.4	52.3	100.9	1.3	8170	234	373
		496	432.3	3.7	63.7	110.2	1.1	10488	255	517
		1000	930.4	3.4	69.5	119.5	0.7	13702	221	766
2	4	8	3.5	0.3	4.5	52.1	3.2	2781	182	200
		16	7.0	0.5	9.0	55.1	3.4	3052	216	203
		32	15.5	0.8	16.5	63.5	2.8	3640	195	217
		64	37.5	1.7	26.5	75.0	2.9	4613	238	244
		128	89.8	1.7	38.2	89.8	1.9	6269	198	286
		256	202.6	3.2	53.4	103.1	1.6	8148	238	375
		500	446.9	2.3	53.1	114.7	0.8	11320	176	496
		1000	932.1	4.2	67.9	119.4	0.7	13768	242	764
4	4	8	2.9	0.3	5.1	46.7	3.3	2434	193	204
		16	6.0	0.5	10.0	49.2	3.7	2758	220	200
		32	14.5	1.0	17.5	56.3	3.3	3176	206	223
		64	34.5	1.6	29.5	65.1	3.3	3885	218	256
		128	83.7	2.6	44.3	84.5	2.4	5735	249	293
		256	195.5	3.7	62.5	97.8	1.9	7656	255	383
		496	425.5	4.0	70.5	109.9	1.1	9976	218	537
		1000	927.9	4.4	72.1	119.0	0.6	13431	238	779

APPENDIX TABLE A2.6 - part 3 Aggregative response results
obtained using random search
(IS = 1) to search for prey type A arranged at random (IDa =
2) or in clumps (IDa = 4), in the presence of 128 of prey
type B arranged at random (IDb = 2), or in clumps (IDb = 4).

IDa	IDb	N	\bar{N}_e	SE	\bar{N}_s	\bar{N}_e'	SE	\bar{T}_s	SE	F
2	2	8	2.0	0.2	6.0	14.2	1.4	1311	112	124
		16	3.8	0.4	12.2	15.2	1.4	1526	124	125
		32	11.3	0.8	20.7	22.8	1.7	2413	185	141
		64	28.7	1.4	35.3	29.0	1.5	3183	182	181
		128	77.8	2.0	50.2	39.7	1.0	4928	175	238
		256	192.9	2.8	63.1	46.7	0.9	7032	191	341
		500	427.8	4.2	72.2	54.1	0.6	9437	239	511
		1000	927.3	3.8	72.7	58.8	0.4	12356	230	798
4	2	8	2.5	0.4	5.5	14.9	1.6	1423	142	122
		16	4.8	0.6	11.2	15.7	1.5	1485	132	138
		32	12.8	1.2	19.2	18.2	1.5	1713	132	181
		64	24.5	2.1	39.5	18.7	1.6	1960	166	220
		128	67.7	3.7	60.3	26.6	1.5	2956	185	319
		256	179.1	4.7	76.9	37.6	1.2	4723	204	459
		496	415.9	4.8	80.1	48.8	0.7	7163	212	649
		1000	913.4	6.5	86.6	54.4	0.7	9958	225	972
2	4	8	0.9	0.1	7.1	11.5	1.5	710	63	175
		16	2.2	0.3	13.8	13.3	1.3	864	63	179
		32	5.9	0.5	26.1	18.7	1.5	1147	79	214
		64	19.9	1.6	44.1	25.8	1.9	2043	154	224
		128	66.3	2.5	61.7	40.5	1.5	3899	188	274
		256	188.7	3.2	67.3	53.5	0.8	6929	197	350
		500	429.2	2.9	70.8	58.7	0.4	9733	199	501
		1000	924.9	3.7	75.1	60.7	0.3	12306	186	801
4	4	8	1.4	0.3	6.6	10.4	1.3	617	47	191
		16	2.5	0.4	13.5	11.0	1.2	652	44	207
		32	6.6	0.9	25.4	12.4	1.5	757	67	251
		64	18.0	1.7	46.0	17.2	1.6	1189	94	296
		128	59.5	3.5	68.5	30.2	1.8	2402	160	373
		256	165.4	5.7	90.6	42.0	1.8	4097	218	506
		496	408.9	5.0	87.1	52.7	0.9	6966	221	663
		1000	904.1	5.8	95.9	57.9	0.6	9607	224	1001

APPENDIX TABLE A2.6 - part 4 Aggregative response results obtained using an aggregative walk (IS = 4d) to search for prey type A arranged at random (IDa = 2) or in clumps (IDa = 4), in the presence of 64 of prey type B arranged at random (IDb = 2), or in clumps (IDb = 4).