PREDATION OF THE GLASSHOUSE RED SPIDER-MITE BY *PHYTOSEIULUS PERSIMILIS* A.-H.

by

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ABSTRACT

In the present studies, the biology of P. persimilis was investigated, but not that of its prey, T. urticae. The functional responses of all the predatory stages of P. persimilis with all the immature prey stages of T. urticae were studied. The results were analysed with the 'random predator equation' to show the variation of 'search-rate' and 'handling-time' with the size of the prey and the predator. Also studied were the responses of the three predatory stages to two prey situations when the different stages of the prey were found in combination. The effect of predator density on the searching efficiency of all three predatory stages were investigated both on a leaf-disc arena and a trifoliate bean leaf. The behavioural responses of the adult female predators to the spatial variation of the prey density was observed on five leaf experimental systems.

Finally, the population interactions of P. persimilis and T. urticae were studied in a small ecosystem of ten bean plants each with only a single trifoliate leaf.

CHAPTER 1

GENERAL INTRODUCTION

This thesis is concerned with an experimental study on the interaction of two species of mites, Tetranychus urticae Koch (Acarina: Tetranychidae) and its predator, Phytoseiulus persimilis Athias-Henriot (Acarina: Phytoseiidae). Tetranychus urticae, often referred to as the glasshouse red spider mite in the United Kingdom, is more commonly known as the two-spotted spider mite in other parts of the world. It is one of the most widespread and destructive mites of word agriculture and is a serious pest in both glasshouse and field crops. It is known to damage a large number of fruit and vegetable crops, and a wide range of flowers, ornamentals, weeds and pasture plants (Unwin 1971). Damage results in reduction in yields of fibre, flowers, fruits and seeds, and even death of plants (Powell & Landis 1966; Huffaker, van de Vrie & McMurtry 1969).

Within glasshouses, biological control of T. urticae by P. persimilis has proved promising, especially on beans (Chant 1961a), cucumbers (Bravenboer & Dosse 1962; Hussey, Parr & Gould 1965; and Markkula, Tiittanen & Nieminen 1972), white clover (Mori & Moriyama 1970), ivy (Gould & Light 1971), and roses (Boys & Burbutis 1972; Simmonds 1972). In all these cases, the help of any supplementary control has been unnecessary.

In this thesis, T. urticae and P. persimilis are used as experimental subjects in a detailed analysis of some components of predation outlined below. These studies aim primarily to provide some basic insights that are applicable to predator-prey theory and may also relate indirectly to the use of P. persimilis as a biological control agent.

1.1 Components of predation

Hassell, Lawton & Beddington (1976) distinguished between two fundamental aspects of predation: the prey death rate (due to predation)

and the predator rate of increase. They suggest that the former is considerably affected by three general components: the predators' response to prey density, the response to predator density, and the response to the distribution of prey. The predator's rate of increase, in turn, hinges upon its ability to find and consume prey which will effect its developmental rate, survival rate and fecundity. It is clear, therefore, that this distinction parallels to some extent, that between functional and numerical responses (Solomon 1949; Holling 1959a) described below. It is however, a broader classification since prey density is now only one of the independent variables affecting predator performance.

1.1.1 The Prey Death Rate (Prey Density)

The predator's response to prey density is customarily defined as its functional response, a term introduced by Solomon (1949) to describe the relationship between the number of prey eaten per predator (Na/P) and prey density (N). This term was only widely used following Holling's (1959a, b) classic paper in which he distinguishes between three fundamentally different kind of response, types I, II and III. In the type I response, the term Na/P increases linearly with prey density, at least to some upper limit when the predator is satiated. Type II responses are quite different in rising at a decreasing rate towards some upper asymptote. This is primarily due to the influence of "handling time" (Holling 1959b), the time not spent in searching that is associated with a prey being eaten, but may be considerably influenced by satiation. Finally, Type III responses show a sigmoid rise to the upper asymptote. Originally widely thought to be characteristic of vertebrate predators, it is now clear that they may also be shown by parasitoids and invertebrate predators (Murdoch & Oaten 1975; Hassell et al. 1976, 1977).

A number of workers, Chant (1961b), Mori & Chant (1966a), Sandness & McMurtry (1970), Pruszynski (1973), and Takafuji & Chant (1976), have

studied functional responses of several different species of predatory mites in simple laboratory experimental systems. Most of these experimental results conformed approximately to the type II response described above. An extensive series of responses have been carried out in this study (Chapter 4) to determine the influence of (a) the stage of predator, (b) the size of prey, and (c) the duration of the experimental interaction.

1.1.2 The Prey Death Rate (Predator Density)

A likely outcome of increasing the density of searching predators, is that the frequency of encounter between the predators will increase. Hassell (1971a, b) and Rogers (1970), studying the ichneumonid parasitoid, Nemeritis canescens (Grav.) found that encounters between adults or between an adult and a parasitised host tended to lead to a reduction in time available for search. Such "mutual interference" is the likely explanation for the several experimental results where searching efficiency declines with increasing predator or parasitoid density (Hassell & Varley, 1969; Hassell et al. 1976).

Experiments are described in Chapter 5 where interference has been studied for some of the different developmental stages of P. persimilis. Interference in relation to dispersal and prey distribution is discussed in Chapter 6.

1.1.3 The Prey Death Rate (Prey Distribution)

Phytophagous prey are generally confined to those areas of the plant on which they feed and seek shelter. Therefore, their spatial distribution is heterogenous and uneven. Mathematical models of predator-prey interactions are based on the assumption that predators search at random with respect to their prey (Holling 1959b; Rogers 1972; Hassell & Rogers 1972). Realistically, they do not search at random often showing a marked response to local areas of high prey density. Due to the nature

of this response, there is a tendency for predators to aggregate in areas of prey abundance, and hence to show a density dependent behavioural response (Hassell 1966). Several types of behaviour may be involved. For example, predators may be attracted by biological exudates and secretions of prey (Spradbery 1970; Mitchell & Mau 1971; Wood 1972) or they may change their behaviour on successfully encountering a prey and tend to spend a longer time searching more intensively in that area, by increased turning rate or reduced speed of movement (Laing 1937; Fleschner 1950; Wylie 1958; Murdie & Hassell 1973). The spatial interactions of T. urticae and P. persimilis are discussed in Chapter 6.

1.2 The Predator Rate of Increase

Solomon (1949), Holling (1961) and Huffaker, Kennett, Matsumoto & White 1968, considered the survival rate, reproductive rate, and aggregative response as basic aspects of predator increase or its numerical response.

The simple linear function which describe the numerical increase of parasitoids in terms of the number of hosts parasitised does not hold for predators, since they normally require several prey to complete development and reproduce. In P. persimilis, for example, which has three immature stages of which only the last two are predatory, each predator stage has to consume several prey to complete its development. Even as an adult it has a pre-ovipositional stage during which prey are eaten. Therefore, the development of each stage depend on availability of prey for consumption.

Once a predator becomes an adult the rate of increase depends on its fecundity. In invertebrate predators, mainly in prey-specific ones (e.g. P. persimilis, see review by McMurtry, Huffaker & van de Vrie 1970), the predator must consume prey in excess of its maintenance threshold for reproduction to occur (Takafuji & Chant 1976). Rivard (1962)

found that in the predatory mite Melichares dentriticus (Berl.) the rate of oviposition depends on the prey consumed only during oviposition and not during development. Similar results were obtained by Chant (1961b) and Smith & Newson (1970) for the predatory mites Typhlodromus occidentalis Nesbitt and Amblyseius fallacis (Garman), respectively. In situations of very low prey densities the increase of predators could be further affected by predators resorting to cannibalism (Chant 1961b; Laing 1968; Smith & Newson 1970). The oviposition rates of Typhlodromus occidentalis (Chant 1961b), and Amblyseius largoensis Muma (Sandness & McMurtry 1970) reached maximum, at a point below their maximum rate of consumption.

Lawton, Hassell & Beddington (1975) and Beddington, Hassell & Lawton (1976) considered the predators rate of increase to be largely determined by those factors affecting the predator's:

(i) rate of development

(ii) survival, and

(iii) fecundity.

In particular, they focussed on how the response to prey density can influence each of these.

Despite the obvious importance of the predator rate of increase to the dynamics of any predator-prey interaction, the emphasis in this study has been primarily on the basic components of predation affecting the prey's death rate as outlined in the previous sections. In particular, it was considered valuable to study the responses to prey density, predator density and prey distribution for a single predator species, an approach which is largely lacking in the current literature.

CHAPTER 2

REVIEW OF LITERATURE

2.1 The Prey - Tetranychus urticae Koch

Tetranychus urticae is one of the most polyphagous of tetranychid mites. In many countries, vast sums of money are lost annually as a result of its damage to crops, and the expenditure incurred in its control. Due to this economic importance, there is a considerable amount of information available on the work done in different countries on various aspects of this pest.

2.1.1 Taxonomy

Taxonomically, T. urticae belong to the order Acarina: sub-order Trombidiformes and family Tetranychidae. Earlier there was much confusion about its taxonomic position. This is due to the existence of a large number of closely related species, especially the linden mite and the carmine mite. Pritchard and Baker (1955) included both carmine mite and red spider mite in the polytypic species, Tetranychus telarius L., 1758. In current usage linden mite is named as Eotetranychus tiliarium Hermann 1804 (Pritchard & Baker (1955); Boisduval 1867 (Tuttle & Baker 1968); and red spider mite (or two-spotted mite) as Tetranychus urticae Koch 1836 (Boudreaux & Dosse 1963; Tuttle & Baker 1968). The older synonym Tetranychus bimaculatus Harvey 1893, is not used now. In literature, T. telarius could refer to either red spider mite or carmine mite.

2.1.2 Biology and Ecology

The biology of T. urticae has been discussed in detail by Cagle (1949), Iglinsky & Rainwater (1954), Hussey, Parr & Crocker (1957). Its life cycle has five different stages: egg, larva, protonymph,

deutonymph and adult. The larval stage is six-legged while other stages are all eight-legged. Each of the three immature stages spends almost half its time in a quiescent state prior to moulting to the next stage. During this period the mite anchors itself to a leaf or to its webbing and assumes a characteristic pose. The legs are bent upon themselves and a new cuticle is formed before casting off the exuvia (Boudreaux 1963).

The life history and the multiplication of red spider mite are influenced by the factors of the environment and the condition of its host plant. The most important environmental factors are temperature and humidity, while other factors such as light, rain and wind are also known to affect their abundance.

The temperature has a profound effect on the development, survival and reproduction of T. urticae. The mean incubation period has been found to vary from 2.5 days at 34° to 38°C to 20.5 days at 12° to 15°C (Cagle 1949; Inglinsky & Rainwater 1954; Laing 1969). The developmental periods of immature stages, over the same temperature ranges, varied from 3 to 21 days (Cagle 1949; Gasser 1951; van Marle 1951; Hussey, Parr & Crocker 1957).

Mating in T. urticae takes place immediately after the last moult of the female and sometimes even before the female has freed herself from the old exoskeleton. For this purpose the male remains close to the quiescent deutonymph after locating it by contact (Helle 1962; Boudreaux 1963; Laing 1969). Though multiple mating is observed, single impregnation is sufficient to produce diploid eggs for the rest of her life (Helle 1962). Like most other tetranychids, virgin females produce only male progeny; mated females produce both sexes, but usually a high percentage of females. The pre-oviposition period of this species may last from 0.5 days at 27° to 33° and to 5 days at 13.5°C (Cagle 1949).

The total number of eggs per female may exceed 100, but the mean is closer to 40 (Cagle 1949; van de Bund & Helle 1960). The mean number of days on which females laid eggs at 20.6° to 28.3°C were 14.7 (Lehr & Smith 1957), and at 20.3°C were 15.7 (Laing 1969). The sex ratio recorded by Lehr & Smith (1957) was 2.3 females : 1 male and by Laing (1969) was 2.9 females : 1 male.

It is evident that the number of generations of T. urticae are correlated with the temperature. Boudreaux (1963) observed that the most rapid development of phytophagous mites occurs at temperatures from 23.9° to 29.4°C at which the life cycle is completed within 7-12 days.

The humidity is also an important factor in the life history of spider mites. Boudreaux (1958) and Nickel (1960) observed increased egg production, increased survival of newly hatched larvae and a higher rate of development of mites at low humidities. Boudreaux (1958) postulated that, this may be due to an increased intake of nutrients as a result of increased feeding at low humidities to compensate for the loss of water to the atmosphere. Rodriguez (1964) observed a change in the physiology of plants under dry conditions which make them more favourable for reproduction of mites feeding on them. Thus, the common observation of increased damage to crops by mites during hot dry weather conditions may be a result of increased feeding of mites in trying to adjust their water balance, and of the favourable nutritional quality of the host plants which make them reproduce faster.

T. urticae over-winters as diapausing adult females. It is established that all the over-wintering females are fertilised before entering into diapause (Nuber 1961). Apparently, the males all die during winter. The summer forms of T. urticae are dark green due to feeding on chloroplasts while the diapausing ones are orange-red or orange in colour, and hence the name red-spider mite.

The effect of changing photoperiod, temperature and nutritive condition in inducing diapause is well documented (Wilde 1962). From the start of Autumn the decrease in the daily photoperiod and the daily average temperature induces the developing young females to become diapausing adults which stop feeding and egg-laying until the following spring. The most important factor inducing diapause is a change in the photoperiod which may be modified by different temperatures (Lees 1953; van de Bund & Helle 1960; Helle 1962, 1968; Parr & Hussey 1966). Exhaustion of healthy food plants and senescent leaves also could induce diapause (Pritchard & Baker 1952; Lees 1953; Parr & Hussey 1966).

The advantage of diapause to over-wintering females is that they can withstand low temperatures provided air humidity is high (Helle 1962; Parr & Hussey 1966). Even the susceptibility to acaricides is reduced in diapausing mites as observed by Parr & Hussey (1966).

On the dispersal of the red-spider mites on host plants, Helle (1962) stated that the females of the pre-oviposition stage migrate to fresh leaves higher up on the plants. According to Hussey & Parr (1963b) they disperse by migration of teneral females to new oviposition sites, dropping off from heavily infested plants, and migrating on the soil surface in accordance with the plane of polarised light. As with most other tetranychids, T. urticae has not been observed to suspend from silken threads for dispersal by wind (Fleschner et al. 1956; Hussey & Parr 1963b). They may be washed off by heavy rains or carried away by strong winds (Boyle 1957).

General observations and some detailed records reveal that the potential reproductive rate of the mites is influenced by the condition and the species of the host plant; due to variations in the plant nutrient status (van de Vrie et al. 1972). This may influence the fecundity, egg viability, mortality and rate of development of different stages in a given environmental condition. Thus, even within a given plant species, the

populations of red-spider mites are affected by, the variety of the host plant (Leigh 1963; Gentile et al. 1969; Schuster et al. 1972), the level of fertilisers (Le Roux 1954; Hamstead & Gould 1957; Henneberry 1962a, 1962b & 1963; Watson 1964; Storms 1969), the seasonal change in the plant physiology (Boudreaux 1958), the chemical constitution of the leaf tissue (Rajinder & Cutkomp 1966; Rodriguez et al. 1970), and also by such physical features of the leaf surface as the presence of hairs which help in webbing, and ridges and depressions which provide ovipositional sites and hiding places (Finney 1953; Huffaker 1958). The interactions of these factors with the meteorological conditions, and the inherent reproductive potentials of the strain of the red-spider mite greatly affect their abundance (Huffaker et al. 1969).

There is a positive correlation of mite populations with the N_2 and reducing sugar contents in plants up to certain upper limits (Garman & Kennedy 1949; Hamstead & Gould 1957; Rodriguez et al. 1957; Henneberry 1962a, b). It has been shown experimentally, that the proteins, reducing sugars and hormones, are induced in plants following the application of pesticides (Huffaker & Spitzer 1950; Rodriguez et al. 1960a, b; Chaboussou 1967, 1969). The increased mite populations observed by Klostermeyer & Rasmussen (1953) and Bartlett (1968) following the application of pesticides could have been due to the pesticide-induced improvement in mite nutrition, or growth factors in the leaves. At the same time there is evidence to show increase of fecundity in mites due to direct effects of DDT application (Locher 1958; Seifert 1961).

2.1.3 Economic Importance

Injury to plants by red-spider mite is related to its method of feeding, which is primarily on the foliage and mostly on the under surfaces. There is no positive evidence to show transmission of any plant viruses by T. urticae (Slykhuis 1963; Oldfield 1970; Orlob & Takahashi 1970, 1971).

Liesering (1960) observed that T. urticae punctured and sucked out the contents of palisade and spongy parenchyma cells and even stomatal guard cells, at the rate of 18-22 cells per minute. This feeding was done in a circular pattern which is characteristic of feeding by T. urticae. During feeding, the epidermis itself is not ruptured, but the punctured epidermal cells collapsed. Radioactive tracer techniques ($^{14}CO_2$) have indicated that T. urticae, and even other spider mites, inject some substances into the plants during feeding (Rodriguez 1954; Liesering 1960; Avery & Briggs 1968; Storms 1971). Weismann (1968) demonstrated that the substances injected by T. urticae dissolve the cell contents and so facilitate feeding. Damaged leaves were also found to have an increased transpiration rate, reduced photosynthesis, and altered pigmentation.

The effect of red-spider mite damage on some crops has been well documented (Svazdarg 1957; Powell & Landis 1966; Oatman 1970). Furr & Pfrimmer (1968) and Klostermeyer (1961) reported that only early and mid-season infestations reduced the yields of cotton and corn, respectively. A detailed study of damage symptoms and associated reduction in yield of cucumbers in glasshouses was done by Parr & Hussey (1962) and Hussey & Parr (1963a, b, 1965). They used a damage index on foliage and found no reduction in yield until foliage damage rose to 30% of total leaf area. Similar work was reported for roses (Henneberry et al. 1961), and sugar beet (Reynolds et al. 1967).

2.1.4 Control Measures

All available methods of arthropod pest management have been tried for the control of T. urticae, but no single method has proved a panacea.

The conventional cultural methods of control of red-spider mite involve the removal of heavily infested, senescent leaves (Oatman et al. 1967), destruction of such winter host plants as cover crops and weeds

(Pritchard & Baker 1952; Dosse 1964; Rota 1967), the prevention of diapause in glasshouses (Hussey 1968), and the use of resistant varieties, which is now widely practiced. There are several examples of crop varieties which are either tolerant or resistant to mite attack: Varieties of cotton (Leigh 1963; Schuster et al. 1972), egg plant (Soans et al. 1973), strawberries (Rodriguez et al. 1971), and tomatoes (Stoner et al. 1967; Gentile et al. 1969; Rodriguez et al. 1972). Some workers have tried to characterise this resistance. Thus, Stoner et al. (1968), Gentile et al. (1969), and Aina et al. (1972) found that in tomatoes there is both tolerance and resistance, the latter being due to the high density of glandular hairs. In strawberries certain morphological characteristics such as open, erect, up-cupped leaves with less pubescence appear also to be connected with resistance (Kishaba et al. 1972), and Soans, Pimental & Soans (1973) have reported that varieties of cucumbers with a high content of bitter principle (cucurbitacin) are more resistant than others.

At present the use of pesticides remains the most realistic method of mite control. But, this method is limited by the usual problems associated with pesticide use. In brief, these are:

(a) selection of resistance to pesticides in the pest population

(b) resurgence of treated populations

(c) out of breaks of secondary pests

(d) toxicity hazards

(e) destruction of beneficial species including parasites and predators, and pollinating insects, and

(f) the expense of pesticides, also involving recurrent costs of equipment, labour and materials.

Jeppson (1965) reviewed the factors peculiar to the acarina which are responsible for success or failure of chemical control. The most important is the development of resistance to chemicals, especially to the Phosphorus-based insecticides which were once very effective against adult mites (Helle 1965). Resistance and tolerance of T. urticae to different pesticides has also been reported by Hussey (1965), Powell & Landis (1966), Unwin (1973), and Overmeer et al. (1975).

The mechanism of resistance of T. urticae is due either to Cholinesterase insensitivity (Smissaert 1964; Voss & Matsumura 1964; Overmeer & Harrison 1969) or to detoxification of the chemical (Matsumura & Voss 1964; Herne & Brown 1969). The relative importance of each has not been clearly established.

On an experimental scale, chemo-sterilisation (Jalil & Morrison 1969,a,b; Redfern 1970), and radiation induced sterilisation (Henneberry 1964; Nelson & Stafford 1972), have been tried for mite control, but with an arrhenotokous species such as T. urticae there is little scope for this technique.

2.1.5 Natural Enemies

In unsprayed orchards and in undisturbed environments the mite injury seen is much below economic levels. One theory for this has already been mentioned: that the increase in mite populations in well attended crops is due to the favourable conditions provided by modern crop husbandry, and not alone due to the destruction of natural enemies by the use of pesticides (Post 1959, 1962; Chaboussou 1963a, b, 1965). An alternative view held by DeBach et al. (1950), Collyer (1964), and Huffaker & Flaherty (1966), places great emphasis on the control of mites by their natural enemies. There are data from laboratory population interactions (Collyer 1958; Smith et al. 1963; McMurtry & Scriven 1966; Laing & Huffaker 1969; Mori 1975), and from glasshouses (Chant 1961a;

Hussey 1964; Hussey et al. 1965; Mori 1975), which strongly support the efficiency of predators in suppressing mite populations. This work is well reviewed by Huffaker et al. (1970), and McMurtry et al. (1970).

The available information thus suggests that natural enemies can be most important mortality factors of red-spider mite populations. Almost all of these natural enemies are arthropod predators, together with a few fungi and viruses. No parasitoids or bacteria infesting T. urticae have been reported (Huffaker et al. 1969).

The important insect predators of mites are mainly found in the Coccinellidae, Endomychidae, and Staphylinidae (order - Coleoptera); Chrysopidae and Coniopterygidae (order - Neuroptera); Anthocoridae and Miridae (order - Hemiptera); Thripidae and Phaleothripidae (order - Thysanoptera); and also in some families of minor importance in the Diptera.

Amongst the acarina the most important predatory mites are found in the Phytoseiidae, Stigmaeidae, Trombidiidae, and Bdellidae.

Of special economic importance are those species which are obligate predators in one or more stages of mites requiring these prey for development and reproduction. The specilised insect predators of mites are species of genera Stethorus (Coccinellidae), and Oligota (Staphylinidae), a few species of Coniopterygidae, species of Scolothrips (Thripidae) and Cryptothrips nigripes Reuter (Phlaeothripidae) (McMurtry et al. 1970). Most of the others are general predators and their feeding on tetranychids is mostly incidental.

The Phytoseiidae includes the largest group of predators of Tetranychidae. Of these, the most important predators of T. urticae are Amblyseius cucumeris (Ouds.) (Cone 1963), Amblyseius fallacis (Garman) (Oatman 1965a), Amblyseius longispinosus (Evans) (Mori 1969), Amblyseius

rademacheri Dosse and Amblyseius tsugawai Ehara (Ehara 1964), Phytoseiulus macropilus (Banks) (Smith & Summers 1949), Phytoseiulus persimilis Athias-Henriot (Dosse 1959; Chant 1961a; Bravenboer & Dosse 1962; Bravenboer 1963; Hussey & Parr 1965; Oatman 1965b; Laing & Huffaker 1969), Typhlodromus caudiglans Schuster (Oatman 1965a), Typhlodromus longipilus Nesbitt (Bravenboer 1959), Typhlodromus occidentalis Nesbitt (Allen 1959a; Laing & Huffaker 1969) and Typhlodromus rhenanus (Ouds.) (Parent 1967).

The species whose preference for alternate food (viz. plant exudates, pollen, fungi, thrips, eriophyds, white flies and insect eggs) results in the neglect of the prey have proved to be of lesser economic value (Huffaker & Flaherty 1966).

Pesticides used for the control of pests and diseases exert a wide variety of influences on predators of mites. Their mode of action on predators is very complex and varied. There are records of many predators of mites which are adversely affected by the use of pesticides. These are extensively reviewed by Huffaker et al. (1969) and McMurtry et al. (1970). As in the case of pest mites, even among predatory mites there are strains of Typhlodromus occidentalis (Morgan & Anderson 1958), Typhlodromus cucumeris (Klostermeyer 1959), Typhlodromus fallacis and Phytoseiulus persimilis (Smith et al. 1963), Amblyseius hibisci (Kennet 1970) and Phytoseiulus persimilis (Schulten et al. 1976) which have shown resistance or tolerance to some of the commonly used insecticides.

There are still, however, no records of any pesticides causing an enhanced fecundity in predators. Pathogens, mainly fungi and viruses, provide another group of natural enemies of tetranychids. The most common species of fungi attacking spider mites are an Entomophthora species and a Hirsutella species (Fisher 1951; Muma et al. 1961). Muma (1955 and 1958) observed that they are most effective during periods of

high humidity or rainfall. The fungus Entomophthora fresenii Nowakowski was seen to infest up to 88% of a population of T. urticae in some cotton fields in Alabama (Carner & Canerday 1968). Steinhaus (1959), Gilmore & Munger (1963), Gilmore (1965), and Shaw et al. (1968) have confirmed the presence of a virus attacking tetranychids both in the laboratory and in the field. The experimental data available on the use of fungi and viruses for the control of tetranychids are insufficient to draw any conclusions regarding their efficiency as a control agent.

2.2 The Predator - P. persimilis A-H

The glasshouse is a closed system with a regulated environment which favours the use of biological agents for the control of pests of crops grown in them. The selection of parasites and predators should be made with due consideration to the environmental factors within the glasshouses. It is seen from the information available that the conditions required for the glasshouse crops favours the breeding of both red-spider mite and its predator, Phytoseiulus persimilis. Recently there has been considerable attention devoted to P. persimilis as a promising predator for the control of red-spider mites in glasshouses and also in the field.

2.2.1 Taxonomy

Phytoseiulus persimilis belongs to the order Acarina: sub-order Mesostigmata, family Phytoseiidae and sub-family Phytoseiinae. Until recently this species was known by three separate names, mainly due to its collection from widely separated geographical areas. In 1957, an Algerian stock of specimens feeding on T. urticae on beans and roses was described as P. persimilis by Athias-Henriot. Another stock collected from water hyacinth in Chile was described by Dosse (1958) as P. riegeli. Lombardini (1959) described a third stock collected from pole beans in Sicily as Amblyseius tardi.

Ehara (1966) working with species of Phytoseiulus placed Lombardini's species, A. tardi, as a species of Phytoseiulus, hence called P. tardi (Lombardini). Kennett and Caltagirone (1968), after making a comparative taxonomic study of Sicilian stock and the original specimens of Athias-Henriot, found them to be conspecific. Thus, P. tardi (Lombardini) is a synonym of P. persimilis A.-H. In addition to morphological studies, they undertook a cross-breeding programme to compare Sicilian and Chilean stocks since they came from widely separated geographic areas, and found them also to be conspecific. Finally, Kennett and Caltagirone (1968) were able to establish that P. persimilis A.-H. (1957), P. riegeli Dosse (1958), and P. tardi (Lombardini) (1959) are synonymous. In general, North American investigators (Chant 1961a; Smith et al. 1963; Oatman 1965b; Oatman & McMurtry 1966) have referred to the Chilean stock as Phytoseiulus persimilis Athias-Henriot, while European workers (Bravenboer & Dosse 1962; Bravenboer 1963; Vogel 1963; Hussey 1964; Hussey & Parr 1965) have referred to it as Phytoseiulus riegeli Dosse.

2.2.2 Biology and Ecology

This species also has five stages in its life cycle: egg, larva, protonymph, deutonymph and adult. Again, the larvae are six-legged while other stages are eight-legged. The larva of P. persimilis does not require to feed in order to transform into the next stage. It generally prefers to remain stationary though it will move when disturbed. There is no quiescent stage seen in any of the immatures. The developmental period of P. persimilis is very much shorter than that of its prey, T. urticae under identical conditions (Bravenboer & Dosse 1962, and Laing 1968). (A detailed discussion of the biology of this species will be dealt with in the next chapter.)

It is found to be very active within certain temperature ranges: 25°-30°C (Bravenboer & Dosse 1962), 20°C (Force 1967), and 25°-35°C (Pruszynski et al. 1970). As this species is not adapted to the climatic conditions of temperate regions, it is not known to diapause or survive during winter. There are examples of other phytoseiids which are capable of overwintering in protected places. Dosse (1957) reported of a species of Typhlodromus which is capable of feeding on a warm winter day. P. persimilis is also sensitive to changes of humidity. Mori & Chant (1966b) found that P. persimilis as well as its prey, T. urticae, was more active and also showed an increase rate of consumption at lower than at higher humidities.

P. persimilis is an obligate predator on tetranychids. It is never known to survive on any other prey or non-prey food (Dosse 1959; Chant 1961a; Oatman & McMurtry 1966; Mori & Chant 1966b; Laing 1968), although some cannibalism has been reported in the absence of prey (Dosse 1955b; Laing 1968). There is no information available on its preference for any species within tetranychids.

Though P. persimilis was collected from pear trees in Algeria (Athias-Henriot 1958), and apple trees in Chile (Gonzalez & Schuster 1962), it is ill-adapted to arboreal life in wind swept areas as it can be easily dislodged by winds as low as 3-4 m.p.h. (Mori & Chant 1966a). They spent most of their time on the under surfaces of the leaves. Chant (1961b), Oatman & McMurtry (1966) found that P. persimilis was rearly seen on leaves which are not infested with its prey, and this associated between predator and prey resulted from its high mobility and its dependency on tetranychids for food.

2.2.3 Economic Importance

There is considerable experimental evidence showing P. persimilis to be a very effective predator for controlling T. urticae in glasshouses and in the field (Chant 1961a; Bravenboer & Dosse 1962; Smith et al. 1963; Hussey et al. 1965; Oatman et al. 1968; Mori & Moriyama 1970; Gould & Light 1970; Simmonds 1971, 1972; Markkula et al. 1972, and Boys & Burbutis 1972). Bravenboer & Dosse (1962) claimed that the effect of using P. persimilis to control T. urticae on cucumbers was equivalent to 3 to 5 applications of pesticides. Begljarov (1967) claimed the possibility of obtaining over 50% higher yields by using P. persimilis than chemicals for control of T. urticae.

Even with a very effective acaricide, 100% kill of mites cannot be obtained as complete foliage coverage with a spray is difficult. At the same time the presence of strains of T. urticae resistant to pesticides could pose a problem for their control, in which case integration of P. persimilis within a chemical pest control programme could be beneficial. Such work has been frequently carried out successfully in glasshouses (Hussey et al. 1965; Begljarov 1967; Binns et al. 1971; Pruszyski et al. 1970). In the preliminary studies of a more sophisticated integrated control programme, Gould (1970) successfully used P. persimilis to control red-spider mites, Encarsia formosa Gahan to control white flies (Trialeurodes vaporariarum Westw.) bed drenches of gamma BHC to control thrips, and Dimethiriniol to control the fungus, Erysiphe cichoracearum. Even in the field the effectiveness of P. persimilis for control of spider mites has been well established. Oatman et al. (1966) and Simmonds (1971) have shown that the predator alone could effectively control red-spider mites in strawberries in the field. Smith et al. (1963) reported similar results for roses grown out doors while Oatman (1970) used P. persimilis together with other natural enemies to control red-spider mites in rhubarb in the field.

With pesticides still forming the core of most pest control systems, it is very important to look for non-persistent and selective pesticides to be used in addition to the release of parasites and predators. Begljarov (1967) and Pruszynski et al. (1970) suggested the use of mild acaricides to control spider mites in order to minimise the harmful effects to the predator. As presented by Riper et al. (1951), the pesticides should be selected in terms of their physiological and ecological selectivity, with emphasis on avoiding food chain toxicity. The availability of insecticide resistant strains of P. persimilis (Smith et al. 1963; Hussey 1968, and Schulten et al. 1976), should enhance the possibilities of its use in integrated programmes.

It is, therefore, likely that predation by P. persimilis can play an important part in suppressing populations of red spider mites whether acting along or in integration with some other practice.

2.2.4 Natural Enemies of P. persimilis

The most extensive study on natural enemies of phytoseiids was done in Germany by Kramer (1961), which was later reviewed by Dosse (1962). Thirty eight species of insects and spiders were observed feeding on various predacious mites. The anthocorid bug Orius minutus L., was seen to attack spider mites and aphids only when Typhlodromus mites (Phytoseiidae) were not available. Next in importance were Chrysopa vulgaris Schneider and Anthocoris nemorum L. Putman (1955) observed the coccinellid Stethorus punctillum Weise to attack phytoseiids in the absence of tetranychids. There are reports of several species of spiders feeding on phytoseiids in apple orchards in England (Chant 1956). Adults of six-spotted thrips, Scolothrips sexmaculatus (Pergande), have also been feeding on eggs of P. persimilis (McMurtry et al. 1970). There are no records of any specific predator feeding on P. persimilis, although at least some of the general predators could be expected to do so. Generally, the information available on natural enemies of phytoseiids is scanty.

CHAPTER 3

BIOLOGY OF PHYTOSEIULUS PERSIMILIS

3.1 Introduction

P. persimilis has five different stages, namely, egg, larva, protonymph, deutonymph and adult. The immature stages do not show any sexual dimorphism. McMurtry et al. (1970) found P. persimilis to have a very short developmental period compared to other phytoseiids. The temperature, and the quality and the quantity of food are known to affect the speed of development (Dosse 1958; Bohm 1966; McClanahan 1968; Pruszynski et al. 1970), the rate of oviposition (Dosse 1958; Begljarov 1967; McClanahan 1968), the longevity (Dosse 1958; Ragusa 1965), and also the general activities (Bravenboer & Dosse 1962; Force 1967; Pruszynski et al. 1970), of this species. Mori & Chant (1966b) found P. perisimilis to have a higher rate of prey consumption and more activity at lower than at higher relative humidities. Begljarov (1967) also found a higher rate of consumption by P. persimilis at low humidity, but a lower rate of oviposition.

The studies reported in this chapter are mainly concerned with the general biology, and with the rate of development and oviposition under very low levels of feeding. Prey and predators for the experiments were collected from the cultures maintained for at least seven days under the same conditions as the experiments.

3.2 Stock Cultures of P. persimilis and T. urticae

The original stock cultures of P. persimilis and T. urticae were obtained from the Glasshouse Crop Research Institute at Littlehampton. At Silwood Park, T. urticae was reared on young French bean plants (Phaseolus vulgaris L.) grown in medium-size flower pots, in a heated

glasshouse at about 20°C and 16 hours of continuous illumination per day with four 65/80 watt flourescent tubes per 15 sq.ft. of bench space. The relative humidity was not controlled. French beans have the advantage that T. urticae thrived on them. At the same time they provide sufficiently large leaf discs of even surface for experiments and also show the slightest mite damage as clearly visible bleached patches on the leaves.

The rearing of the predator was done by introducing a few female P. persimilis onto bean plants infested with T. urticae. The cultures of prey and predators were maintained in separate glasshouses to avoid contamination of the prey cultures with the predator.

The cultures of both T. urticae and P. persimilis could rapidly increase to enormous numbers such that the prey would kill the host plants in the absence of predators, but be itself eliminated with predators present. Hence, it was necessary to start each of the cultures with only a very few specimens, which was done every two weeks on eight plants in two flower pots.

No steps were taken to reduce the risk of inbreeding in the culture, by introducing new stocks.

The specimens used in experiments were not taken directly from the stock cultures maintained in the glasshouses as the temperature and relative humidity there were highly variable. The transfer of specimens from this type of environment directly to constant experimental conditions could give erroneous results, especially in short term experiments. (For example, it was observed that protoynmphs of P. persimilis bred in 25°C failed to feed at 20°C). Therefore, the mites used in the experiments were obtained from smaller cultures maintained under the same conditions as the experiments. (i.e., 20°C 55-65% R.H. and 16 hour continuous light period). A few pots of lightly infested bean plants kept under these conditions for about two weeks provided sufficient specimens of T. urticae

for any current experiments. The experimental cultures of P. persimilis was maintained in a slightly different way. A few females of P. persimilis were introduced to heavily infested bean leaves kept on moist cotton wool in small trays (30cm x 15cm x 3cm). Sufficient water was added to the trays to act as a barrier preventing the migration of predators. From these cultures, freshly hatched larvae of the predator were moved onto another set of infested leaves, similarly maintained. Therefore, P. persimilis in each set of cultures were the same age to within one day. This method minimised the handling of the prey and made it easier to examine and handle the predators under the microscope. Whenever the leaves became senescent or the prey mites depleted, another fresh infested leaf was kept beside it to enable the predators to migrate onto it.

3.3 Materials and Methods

The developmental stages of P. persimilis were studied on small discs (1.5cm diameter) cut from French bean leaves. These leaf discs were kept on sponges in 300ml. plastic containers, 9cm in diameter, containing sufficient water to float the sponges. The sponge, 2cm thick, was also cut into discs (8cm diameter) to fit loosely into the containers. Before placing the leaf discs on the sponges, a very thin layer of cotton wool was spread on it and this assured a uniform film of water around the leaf discs which formed an efficient barrier against the migration of the mites. Five leaf discs were arranged in a circle on the sponge, in each container.

Experiment A

Eggs of P. persimilis, immediately after oviposition, were placed carefully with a sable-hair brush one on each of the leaf discs described above. When the resulting larvae were about to moult, first into the protonymph and then into the deutonymph stage, thirty freshly laid eggs of T. urticae were counted onto each leaf disc with a sable-hair brush

under the binocular microscope. Any eggs damaged during transfer were replaced. From the time of moult, the number of eggs fed by protonymphs and deutonymphs at the end of every 12 hour period was counted and replaced with new ones. Hourly observations were made to ascertain the time of egg hatch and time of moult of different stages. The approximate developmental periods of different stages determined in a previous pilot experiment acted as a guide line for this. The records were kept of time of laying, hatching moulting, and periods of resting and the number of prey eggs fed during every 12 hour period.

The studies on oviposition and longevity were carried out on small bean leaflets heavily infested with T. urticae, kept on moist cotton wool. Newly emerged female predators were transferred one on to each leaflet with one or two males. The leaflets were examined daily at the same time and the eggs laid by the predators were removed from the leaves. This examination was continued until the death of all the predators. The records were kept of periods of pre-oviposition, oviposition, post oviposition and longevity, and of daily oviposition.

Experiment B

In this experiment the development of predatory immature stages were studied under four different densities of prey eggs, i.e., 1, 2, 3 and 4 eggs of T. urticae per day. The studies were carried out on small leaf discs as described in the preceeding experiment. As soon as the protonymphs emerged from the larva stage, they were transferred to different leaf discs having the four different densities of eggs. The predators were then observed as in the previous experiments for the first three days and then at every four hours from 8.00a.m. and 10.00p.m. At the end of each day (the day reckoned from the time of moult) the prey eggs eaten were replaced. Records were kept for the time of moulting and number of eggs eaten each day.

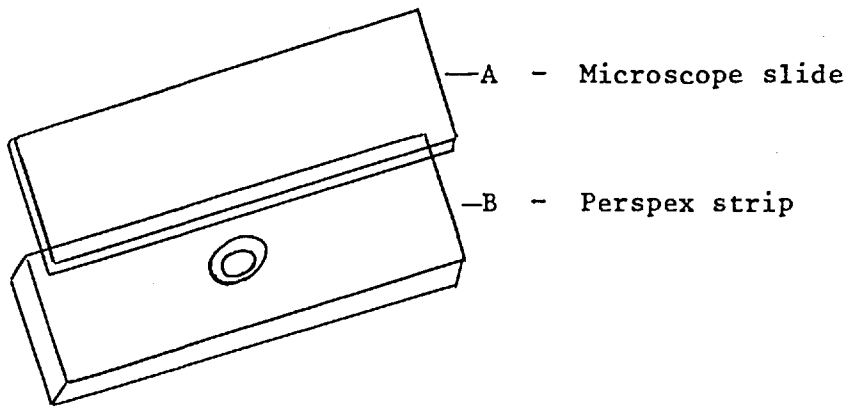


Fig. 3.1 Cage used to study the effect of feeding on different densities of prey eggs on oviposition of *P. persimilis*

Experiment C

This experiment was conducted to determine the effect of feeding on different numbers of prey eggs on the oviposition of P. persimilis. Young gravid females of the predator were allowed to feed on different densities (1, 2, 4, 8 & 16) of prey eggs in cells similar to the type developed by Robertson (1944), (Figure 3.1). It consists of a hole in the form of a truncate cone measuring diameters of 1.5cm at the top and 1.0cm at the bottom drilled through a rectangular strip of perspex (B) about 4.0cm by 7.5cm by 0.3cm. A piece of fine mesh nylon cloth (125 meshes per inch) glued to the lower surface of the perspex provided a permeable base to the cell. This is enclosed above by an ordinary microscope slide (A) secured to the perspex at each end by strips of double sided cellotape. Prey eggs were introduced into the chamber by attaching them to a piece of black paper with a very fine film of vaseline.

At the end of each day the number of eggs laid by the female predator and the number of prey eggs eaten in each cell were recorded. The piece of black paper was replaced by another with the full compliment of prey eggs. For analysis, the eggs laid by the predator during the first 24 hours were discarded to avoid the influence of previous feeding. In this experiment the predators did not have access to water.

3.4 Results

Experiment A

Egg stage

The eggs were laid single and were oval in shape. At laying, they were either creamy, light orange or dark orange in colour. They did not change colour on ageing but remained the same throughout the incubation period. The egg stage lasted an average of 3.28 ± 0.03 days

TABLE 3.1 - Duration of Immature Stages of P. persimilis

Stage	Sex	Number observed	Number of days			S.E. ±
			Maximum	Minimum	Average	
Egg	Male	2	3.32	3.25	3.28	0.03
	Female	25	3.81	3.29	3.42	0.03
Larva	Male	2	1.13	1.04	1.08	0.05
	Female	20	1.33	0.94	1.08	0.02
Protonymph	Male	2	1.67	1.58	1.62	0.05
	Female	18	1.85	1.52	1.70	0.02
Deutonymph	Male	2	2.04	1.96	2.0	0.04
	Female	17	2.31	1.88	1.97	0.02
All Stages	Male	2	8.0	7.99	7.99	-
	Female	17	8.95	7.83	8.14	0.08

TABLE 3.2 - Duration of non-feeding period of P. persimilis before moulting

Stage	Number observed	Number of days			S.E. ±
		Maximum	Minimum	Average	
Protonymph	15	0.83	0.33	0.53	0.04
Deutonymph	11	1.0	0.33	0.68	0.06

TABLE 3.3 - Duration of various stages of adult females of P. persimilis

Stage	Number observed	Number of days			S.E. ±
		Maximum	Minimum	Average	
Pre-oviposition	15	4.5	2.9	3.3	0.1
Oviposition	16	44.0	6.0	37.1	2.2
Post-Oviposition	11	44.0	6.0	22.7	3.4
Total longevity	19	72.0	10.0	50.9	3.9

TABLE 3.4 - Number of T. urticae eggs eaten during development of immature stages of P. persimilis

Stage	Number observed	Number of eggs			S.E. ±
		Maximum	Minimum	Average	
Larva	22	0.0	0.0	0.0	0.0
Protonymph	22	7.0	4.0	5.4	0.21
Deutonymph	20	12.0	8.0	9.3	0.29
TOTAL	20	17.0	13.0	14.55	0.31

TABLE 3.5 - Feeding pattern of immature stages of P. persimilis

Stage	Number observed	Period	% of total number of eggs fed
Protonymph	21	1st 12 hours	68.1
		2nd 12 hours	30.3
		3rd 12 hours	1.7
Deutonymph	17	1st 12 hours	62.37
		2nd 12 hours	33.33
		3rd 12 hours	4.3

TABLE 3.6 - Feeding of adult females on T. urticae eggs. (Average of 3 days)

Period	Number observed	Eggs eaten per female per day			S.E. ±
		Maximum	Minimum	Average	
Pre-oviposition	12	14.0	8.0	11.0	0.5
Oviposition	11	30.0	16.0	22.2	1.4
Post-oviposition	9	7.0	0.0	3.6	0.9

for males and 3.42 ± 0.03 days for females (Table 3.1).

Larva stage

The larvae have the same colour as the eggs. Older larvae could be easily distinguished from these newly hatched by being 'thinner', probably due to loss of water since there is no feeding during the larval period. They generally preferred to remain inactive but were occasionally seen to move around slowly. The males and females remained in the larval stage for an average of 1.08 ± 0.02 and 1.08 ± 0.05 days respectively (Table 3.1).

Protonymph stage

Protonymphs were capable of movement and feeding almost immediately after moulting from the larva stage. The protonymph stage of both male and female lasted for an average of 1.62 ± 0.05 days and 1.70 ± 0.02 days, respectively (Table 3.1). During this stage, an individual ate an average of 5.4 ± 0.21 eggs of T. urticae (Table 3.4). There were no differences in feeding between the males and the females. Protonymphs had a non-feeding period of 0.53 ± 0.04 days with a maximum of 0.83 days and a minimum of 0.33 days just before moulting into the deutonymphal stage (Table 3.2). During this period they were seen to remain resting at the same spot. This was also clearly shown in the pattern of feeding of the protonymphs where 68.1% occurred in the first 12 hours and 30.3% in the second 12 hours (Table 3.5).

Deutonymph stage

This stage lasted for an average of 2.0 ± 0.04 days for males and 1.97 ± 0.02 days for females (Table 3.1). Each of the males and the females ate an average of 9.3 ± 0.29 prey eggs during this period (Table 3.4). As in the protonymph stage, the deutonymph stage also had a non-feeding resting period of 0.68 ± 0.06 days, with a maximum of 1.0 and

TABLE 3.7 - Number of eggs laid by *P. persimilis*

	Number observed	Number of egss laid			S.E. ±
		Maximum	Minimum	Average	
Average number per female per day	16	2.38	1.9	2.11	0.03
Total number per female	16	95.0	12.0	78.8	4.8

TABLE 3.8 - The duration of immature stages of *P. persimilis* under low levels of feeding on *T. urticae* eggs

Stage of predator	Number observed	Prey eggs offered / day	Duration of the stage (days)	Total number of eggs fed
Protonymph	12	1	3.41 ± 0.27 SE	2.75 ± 0.22 SE
	11	2	2.25 ± 0.10 SE	3.45 ± 0.25 SE
	8	3	2.2 ± 0.05 SE	4.12 ± 0.35 SE
	8	4	1.99 ± 0.03 SE	4.25 ± 0.16 SE
	* 18	Surplus	1.70 ± 0.02	5.4 ± 0.21
Deutonymph	9	1	6.88 ± 0.84	5.22 ± 0.81
	10	2	3.07 ± 0.09	4.5 ± 0.34
	8	3	3.18 ± 0.07	6.62 ± 0.37
	8	4	3.03 ± 0.02	7.75 ± 0.41
	* 17	Surplus	1.97 ± 0.02	9.3 ± 0.29

* Taken from TABLE 3.1 for comparison.

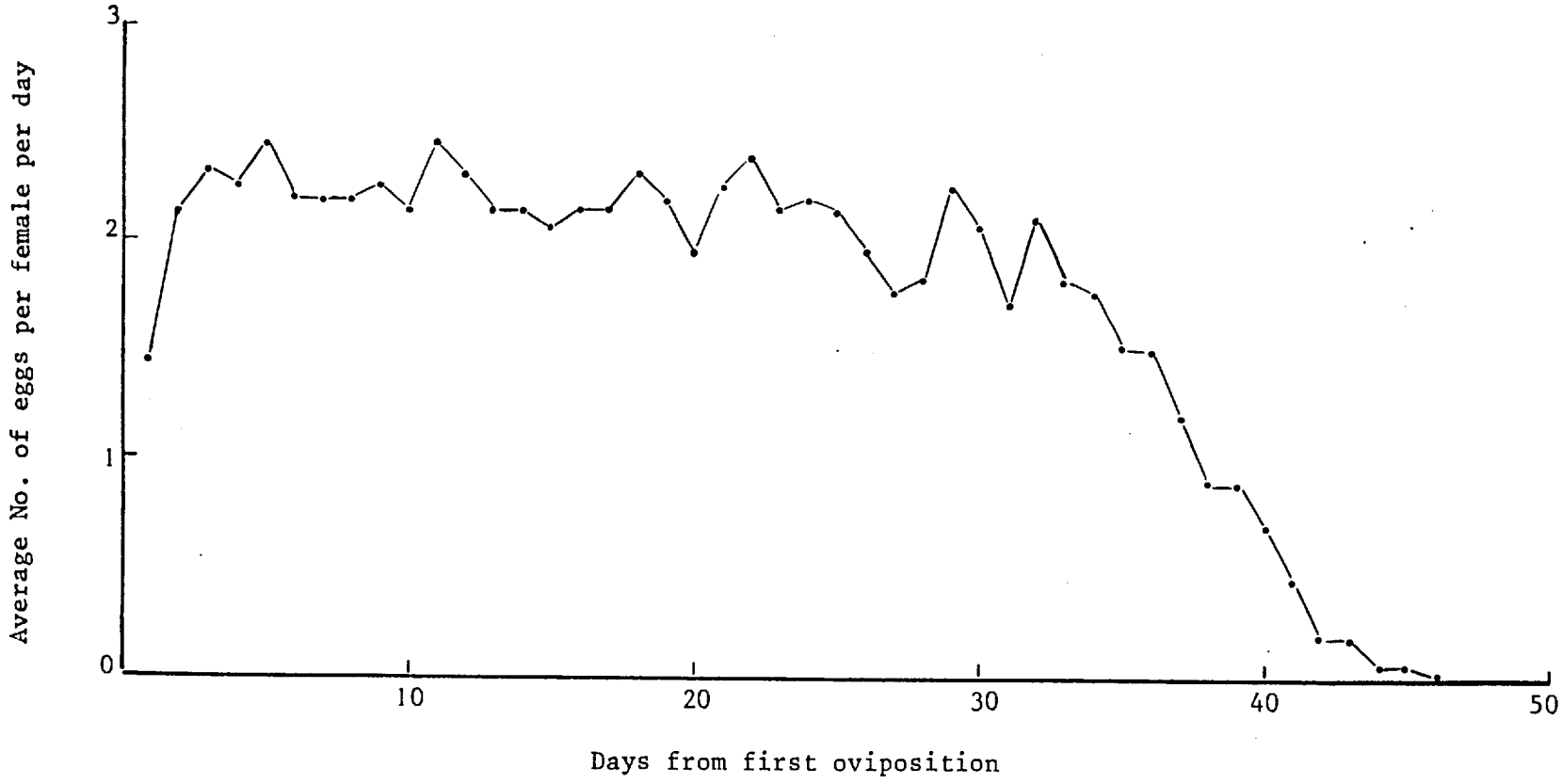


Fig. 3.2 Average daily oviposition of P. persimilis in the presence of abundant prey

minimum of 0.33 days before becoming an adult (Table 3.2). The feeding rate declined during the experiment as shown in Table 3.5.

Under the present experimental conditions the predatory immatures of P. persimilis, males and females combined, each consumed an average of 14.55 ± 0.31 prey eggs within a range of 13 to 17 eggs, to become an adult (Table 3.4).

Adult stage

Though morphologically the same, the adult female has three different stages, pre-ovipositional, ovipositional and post ovipositional, lasting an average of 3.3 ± 0.1, 37.1 ± 2.2 and 22.7 ± 3.4 days, respectively (Table 3.3). The number of prey eggs consumed by the adult depends on the stage of oviposition. The pre-ovipositional adult ate an average of 11.0 ± 0.5 eggs per day (range 8 to 14) but only 3.6 ± 0.9 eggs per day (range 0 to 7) during post oviposition. The maximum feeding was observed during oviposition when adult females consumed an average of 22.2 ± 1.4 eggs per day within a range of 16 to 30 eggs (Table 3.6).

The unmated females did not oviposit. Although multiple matings were common, single mating was observed to be sufficient for complete oviposition. During the whole ovipositional period a female laid an average of 78.8 ± 4.8 eggs with a maximum of 95 and a minimum of 12 eggs. The average number of eggs laid be a female per day during the ovipositional period was 2.11 ± 0.03 eggs (Table 3.7). The maximum number of eggs laid by any female in a day was 4 eggs. The average daily oviposition throughout the ovipositional period is shown in Figure 3.2. This figure reached a maximum around 3 to 5 days after first oviposition, and then decreased slightly until about the 32nd day of oviposition. Thereafter there was a more rapid decrease until oviposition ceased on the 46th day after the first oviposition.

TABLE 3.9 - Comparison of developmental rates at different densities of prey eggs offered to immature stages of P. persimilis

Density of prey eggs offered	Protonymph			Deutonymph		
	d.f.	t*	P	d.f.	t*	P
1, 2	21	3.9	0.001	17	4.77	0.001
1, 3	18	3.62	0.001	15	4.13	0.001
1, 4	18	4.27	0.001	15	4.31	0.001
2, 3	17	0.43	n.s.	16	0.95	n.s.
2, 4	17	2.20	0.05	16	0.30	n.s.
3, 4	14	3.48	0.01	14	2.02	n.s.
Surplus, 4	24	9.49	0.001	23	13.45	0.001

n.s. - not significant

* - Student's "t" test

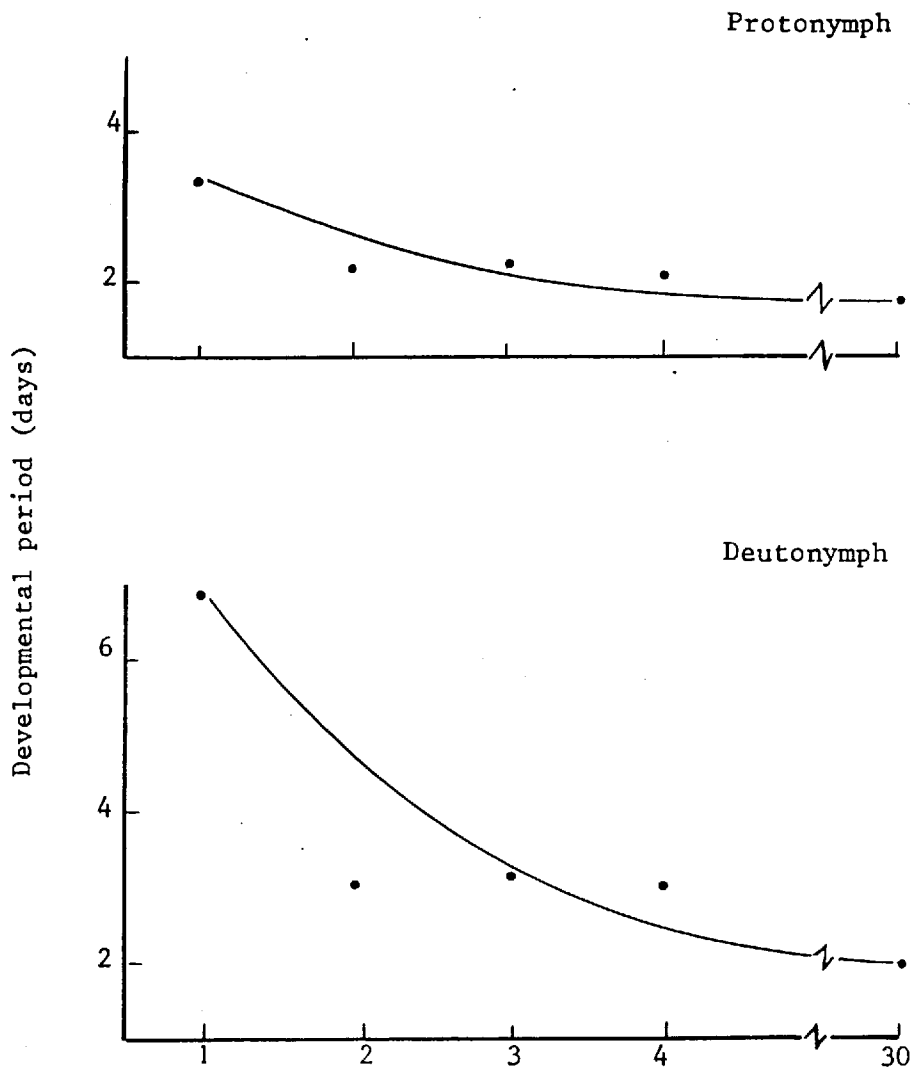


Fig. 3.3 Development of immature stages of P. persimilis under different levels of feeding. (Curves fitted by eye.)

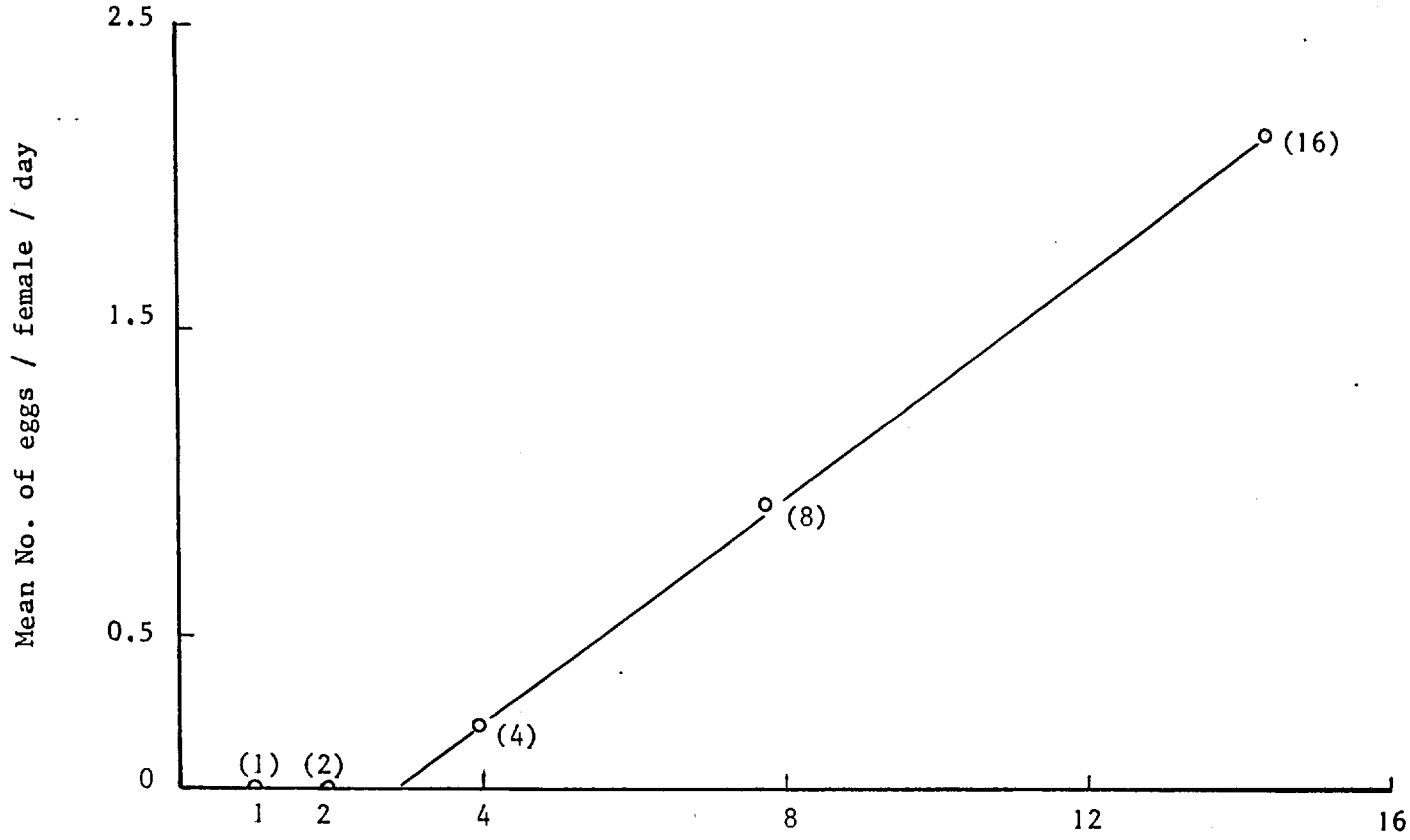


Fig. 3.4 Oviposition by P. persimilis under different levels of feeding on prey eggs

The observed longevity of adult females was 50.9 ± 3.9 days with a maximum of 72 and a minimum of 10 days (Table 3.3).

When different stages of P. persimilis were put together in a leaf disc without prey, cannibalism was observed among all the predatory stages. This was more common amongst protonymphs and deutonymphs than for adults. When starved, protonymphs and deutonymphs readily attacked eggs, larvae, and even their own stage if found to be less active. The adults, too, attacked other adults whose movement was impaired due to starvation.

Experiment B

When the protonymphs were raised under a regime of one prey egg per day, their developmental time was increased to an average of 3.41 ± 0.27 days (range of 2.5 to 5.7 days) which was double that observed when an optimum number of prey eggs were provided (Table 3.8). This effect was even observed between the regimes of one and two prey eggs provided per day, but not between that of two and three eggs per day, as shown in Table 3.9.

The average duration of deutonymph stage when fed at the rate of one prey egg per day was 6.88 ± 0.84 days with a maximum of 12 and minimum of 4 days. This is about a 3½ fold reduction in developmental rate compared with an optimal number of prey eggs upon which to feed. Fuller details of this experiment are given in Tables 3.8 and 3.9 and Figure 3.3 A and B.

Experiment C

The results are shown graphically in Figure 3.4 where the number of eggs laid per female per day is plotted against the number of prey eggs fed per day. It is seen that P. persimilis require slightly less than three T. urticae eggs per day for maintenance metabolism before any

TABLE 3.10 - Comparison of present and some reported rates of development, oviposition and longevity of *P. persimilis*

Author	Dosse (1958)			Ragusa (1965)	Begljarov (1967)		McClanahan (1968)			Laing (1968)	Takafuji & Chant (1976)	Present Studies
Prey offered				All stages of *T. urticae*			Adults of *T. urticae*			Eggs of *T. urticae*	Protonymphs of *T. pacificus*	* Eggs of *T. urticae*
Temperature	10° to 25°C	15°C	25°C	22° - 28°C	23°C	30°C	20°C	26°C	28°C	15° - 28°C (Avg. 20°C)	25°C	20°C
Developmental period in days	11.9	12.2	4.6	5 - 12	8.2	4.9			4.7	9.2 - 12.2 (Avg. 7.5)	6.87	8.14
Pre-oviposition period							2			3	1.5	3.32
Oviposition period							25			22.3	21.6	37.12
Post oviposition period										7.1	13.1	22.72
Longevity in days	37 (Avg.)			22 - 25						29.6 (Avg.)	36.4 (Avg.)	50.9
Total number of eggs/ female	60 (Avg.)			100 (max.)	104 (max.) (25°C)		78 (max.)	87 (max.)		101 - 14	79.5 (Avg.)	95 - 12
							43.8 (Avg.)	53.5 (Avg.)		53.5 (Avg.)		78.81 (Avg.)
Number of eggs/females/ day	1.6		5.2 (35°C)	4	4 (25°C)	3.6	1.75**	3.5		2.4**	3.96**	2.11**

* Fed on all stages of T. urticae for studies on longevity and oviposition

** During oviposition period only.

reproduction could occur.

The raw data of all the experiments are given in Appendix 1

3.5 Discussion

During development there is no noticeable change in the colour of the eggs, although Laing (1968) reported that the eggs changed on ageing from light to dark orange in colour. The developmental time from oviposition of the egg to mature females, at a constant temperature of 20°C, varied between 10.8 to 13.5 days with an average of 11.5 days. The corresponding value obtained by, Dosse (1958) at an oscillating temperature of 10° to 25°C was 11.9 days and Ragusa (1965) within a temperature range of 22-28°C was 5 to 12 days. Dosse (1958) also obtained a higher value of 12.2 days at 15°C. Therefore, the present results are in reasonable agreement with those already published. These results are tabulated in Table 3.10.

From the present experiments, it is evident that the rate of development of *P. persimilis* depends largely on the amount of food it receives during developmental period. It is capable of successfully completing development under low levels of diets, even at one prey egg per day, though it takes a significantly much longer time to complete development than with abundant prey (Table 3.8 & 3.9, Figure 3.3 A & B).

Laing (1968) reported in his studies that protonymphs and deutonymphs remained active throughout their respective periods. It was observed in the present studies that, in the presence of abundant prey, 98% of protonymph and 95% of deutonymph feeding occurred during the first 24 hours, and that the protonymph preferred to remain resting for an average of 0.5 days and the deutonymph 0.7 days before moulting to the next stage. This, in any case cannot be compared with the quiescent stages of *T. urticae* as the resting immature predators are capable of

movement if disturbed. The resting period may be to facilitate the complex physiological changes that take place before moulting (Wigglesworth 1965).

McClanahan (1968), Laing (1968) and Takafuji & Chant (1976) observed preoviposition periods of 2 (at 20°C), 3 (at 15° to 28°C) and 1.5 (at 25°C) respectively, while in present studies the figure was 3.3 (at 20°C) days. The corresponding oviposition periods observed by the same workers were 25.0, 22.3, 21.6 and 37.1 days. Even the post oviposition period of 22.7 days observed was very much higher than the 7.1 days observed by Laing (1968) and 13.1 days by Takafuji & Chant (1976). In the present experiment, the adults lived an average of 50.9 days and laid a total of 78.8 eggs per female in 37.1 days for an average of 2.1 eggs per female per day. At 20°C McClanahan (1968) recorded a total oviposition of 43.8 eggs per female for an average of 1.8 eggs per female per day. It is seen in Table 3.10, that at higher temperatures, the number of eggs per female per day is always higher due to shorter oviposition periods. Those values cannot be directly compared with the results of the present experiments, as most of those experiments were done either under fluctuating temperatures or at much higher constant temperatures, and also only on one of the stages of the prey as food. The present experiments were carried out at 20°C and the predators had the facility to choose their preferred prey stage as they were exposed to all stages of the prey. McClanahan (1968) observed that under same dietary conditions initial oviposition was higher at higher temperatures, but at lower temperatures they oviposited for a longer period of time. Dosse (1958) obtained a very high rate of oviposition (5.2 eggs per female per day) at 35°C. The pattern of average daily oviposition recorded by McClanahan (1968) and Takafuji & Chant (1976) resemble that obtained in the present experiment, though there are differences in other estimates of oviposition.

The relationship obtained for the reproductive rate as a function of feeding rate is linear. This is similar to the relationships obtained by several workers for number of other invertebrate predators (Beddington et al. 1976; Beddington, Free and Lawton 1976). P. persimilis is capable of oviposition at very low levels of prey consumption and require only 5.4 prey eggs over and above its maintenance requirement to lay each egg. This remarkable ability of phytoseiids to sustain oviposition at very low feeding was also reported for T. occidentalis (Chant 1961b), T. pyri (Herbert 1961) and A. hibisci (McMurtry & Scriven 1966).

The adult female predator ate eggs of T. urticae at daily averages of 11.0 during pre-oviposition, 22.2 during oviposition and 3.6 during post oviposition, consuming a total of 940.5 eggs as an adult female predator. Bravenboer and Dosse (1962) recorded an average daily consumption of 34 eggs of T. urticae during oviposition by P. persimilis. This is a very much higher value than 14.3 eggs recorded by Laing (1968) and 22.2 eggs recorded in the present studies.

No natural mortality of the immatures were observed with normal feeding under the present experimental condition. Takafuji & Chant (1976) observed no adult mortality before the females ceased to lay eggs. In the present experiment, out of 30 adult females there was 16.7% adult mortality during ovipositional period. The average of 50.9 days for the longevity of P. persimilis observed in these experiments is the longest ever recorded.

CHAPTER 4

FUNCTIONAL RESPONSE

4.1 Introduction

Solomon (1949) proposed the term "functional response" to describe the relationship between the number of prey eaten per predator and the density of prey, a relationship one would expect to be a rising function, at least over a range of prey densities. The first person to really make use of this terminology was Holling (1959a). He recognised three basic types of functional response amongst predators, which are illustrated here in Figure 4.1. The type I response is linear, at least up to a plateau and may be found in such predators as filter feeders where intake is directly proportional to prey density until the animal is satiated. The type II response rises at a decreasing rate towards an upper asymptote and was thought to be the typical form for invertebrates. Finally, the type III response is sigmoid, and this, Holling thought was due to learning in polyphagous predators, and hence most likely amongst vertebrates.

In a subsequent paper, Holling (1959b) developed a simple model for a type II response. He assumed that,

$$Na = a^1 N T_s P \qquad (4.1)$$

where Na = the number of prey killed

N = the density of prey

P = the number of predators

a^1 = a constant, the instantaneous "search-rate" per predator, and

T_s = the searching time of the predator.

If T_s is constant, a linear, type I, functional response results. However,

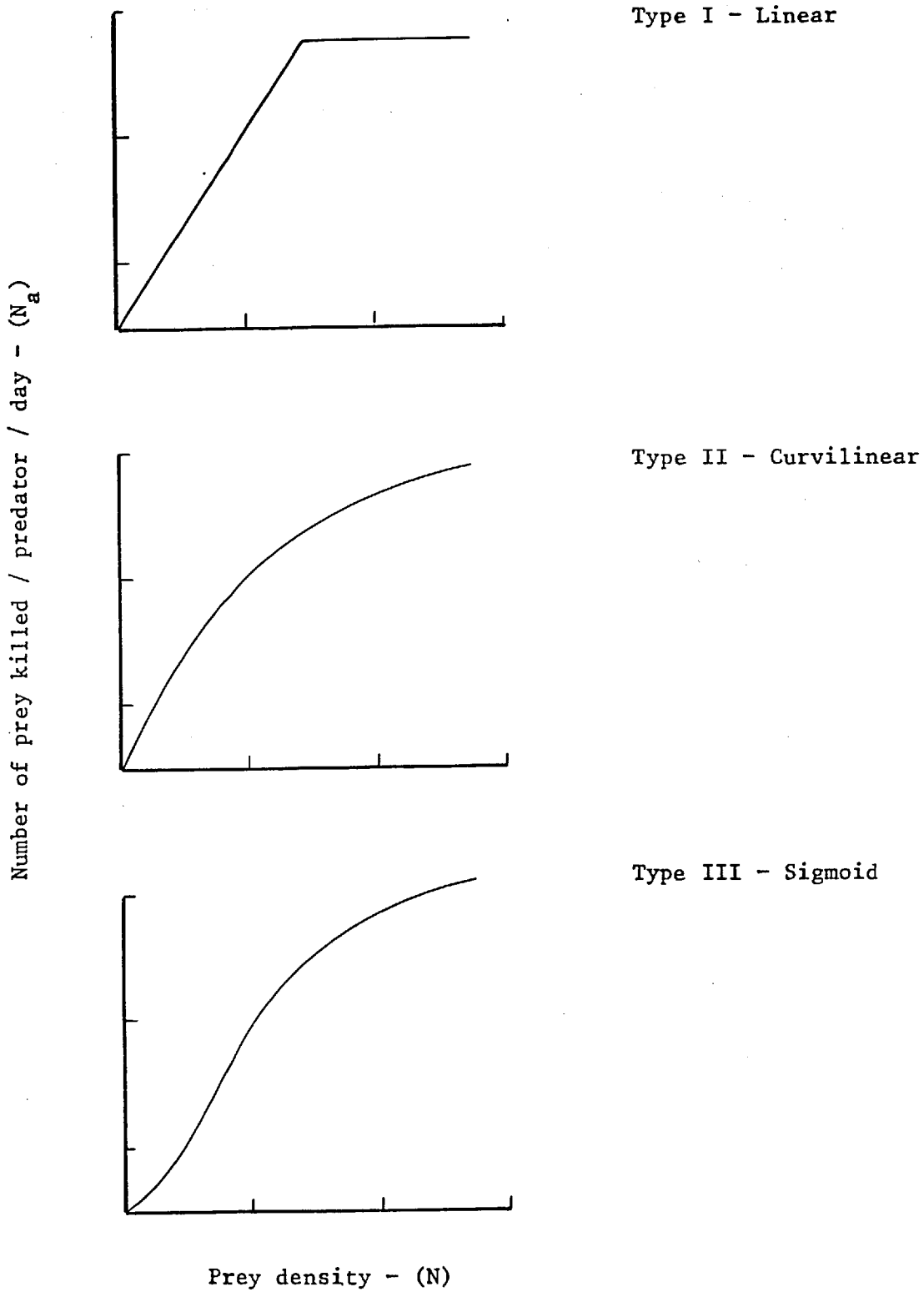


Fig. 4.1 Basic types of functional response curves distinguished by Holling

Holling assumed that T_s cannot be constant, simply because the act of killing and eating prey takes time which could otherwise be spent searching. Thus,

$$Ts = T - T_h \frac{Na}{P} \qquad (4.2)$$

where T = the total time that predator and prey are exposed to each other

T_h = a constant, the "handling time" of each prey

Substituting (4.2) into (4.1) now gives,

$$\frac{Na}{P} = a^1N \left(T - T_h \frac{Na}{P}\right)$$

or

$$\frac{Na}{P} = \frac{a^1NT}{1 + a^1T_hN} \qquad (4.3)$$

Equation (4.3), Holling called the "disc equation" since it described well the results of an experiment in which a blind-folded subject (the "predator") searched for sand-paper discs (the "prey") on a flat arena. It also gave a very good description of the experimental results of Burnett (1951, 1954), Ullyett (1949, 1950) and DeBach & Smith (1941), in which various parasitoid species were allowed to search for hosts within a cage for a fixed period of time.

The parameters a^1 and T_h were later sub-divided by Holling (1965) into 3 discrete sub-components. He considered a^1 to be a function of (i) the reactive distance of the predator, i.e. the maximum distance at which the predator will react by attacking the prey; (ii) the speed of movement of predator and prey; and (iii) the proportion of attacks that are successful: and the T_h to be a function of (iv) the time spent pursuing and subduing each prey; (v) the time spent eating each prey; and (vi) the time spent digesting each prey.

The disc equation, which was designed only as a first step towards explaining functional responses, adequately described the published data of most of the functional response experiments of parasitoids and predators. In spite of this, it was pointed out by Royama (1971) and Rogers (1972) that the disc equation did not make any allowance for the depletion of available prey during the course of predation. Therefore, it is an instantaneous equation which could be applied only for very short intervals of time, though it was used to interpret results of experiments run for much longer periods. It could also be used in situations where the predator searches completely systematically, a condition which is unlikely to occur. By assuming that the predators searched at random, Rogers (1972) corrected this defect by incorporating the disc equation into an exploitation model based on the poisson series:

$$Na = N \left[1 - \exp \left(- \frac{Ne}{N} \right) \right] \qquad (4.4)$$

where Na is the number of prey actually eaten (or hosts parasitised), in contrast to

Ne which is the number of encounters of prey assuming that they are instantly replaced (or encounters with hosts).

Because of the fundamental difference between predators and parasitoids that prey are removed as eaten but hosts remain to be subsequently re-encountered - Rogers developed separate exploitation models for the two categories:

The Random Predator Equation

$$Na = N \left[1 - \exp \left(- a^1 \ (PT - NaT_h) \right) \right] \qquad (4.5)$$

The Random Parasitoid Equation

$$Na = N \left[1 - \exp \left(\frac{- a^1 \ TP}{1 + a^1 T_h N} \right) \right] \qquad (4.6)$$

The sole difference between the two is that parasitoids will spend a time T_h handling hosts that have already been encountered.

These equations assume that for a given predator and prey, a^1 and T_h remain constant at all prey densities. It is likely, however, that the sub-components of a^1 and T_h will vary with such factors as the prey density, the predator feeding rate and the predator hunger level. These aspects have been well discussed by Hassell et al. (1976). They point out that the obvious lack of constancy of a a^1 and T_h present a paradox as the data of many functional response experiments remain satisfactorily fitted with equations which assume a^1 and T_h to be constant. This may be due to the fact that either these variations are too small to effect a change in the overall shape of the curve, or the variation of one sub-component may be masked or opposed by the variations of the other. However, there are instances where the changes in the sub-components have exerted sufficient pressure to affect markedly a^1 and T_h bringing about complex functional responses (see discussion).

A complication presented by predators more than parasitoids is that there are several developmental stages of predator, each with different searching abilities and probably different preference for prey size or prey type. Therefore, we would expect some variations in the components of functional responses within the life history of a predator where a particular instar attacks different instars of its prey or where different predatory instars attack the same instar of the prey. This could be brought about by the variations in the sizes and the behaviour of the different instars of the prey and the predator and the accompanied variations of the sub-components of a^1 and T_h. Sometimes these changes between instars may be very marked as shown by Dixon (1959), Evans (1973), Wratten (1973), Brown (1974) and Thompson (1975) and reviewed by Hassell et al. (1976).

In a realistic predator-prey situation the different prey stages (or sizes) are likely to be present in a mixture. In such a mixed prey situation the original null hypothesis is that the predator will attack each instar of the prey in the proportions predicted by the functional response on that prey alone, exactly as one would do if two or more different species were involved. This could be mathematically interpreted by an extension of the random predator equation (Rogers 1972), (or even with the disc equation (Holling, 1959b) where exploitation is unimportant), as shown by Lawton, Beddington and Bonser (1974);

$$N_{1a} = N_1 \left[1 - \exp \{ a'_1 (T - T_{h1}N_{1a} - T_{h2}N_{2a}) \} \right]$$
$$N_{2a} = N_2 \left[1 - \exp \{ a'_2 (T - T_{h2}N_{2a} - T_{h1}N_{1a}) \} \right] \qquad (4.7)$$

Where the subscripts 1 and 2 refer to prey stages or prey species.

The functional response experiments reported in this chapter have been conducted mainly with the aim of studying the variations of values of a' and T_h when different immature stages (eggs, larva, protonymphs, and deutonymphs) of T. urticae were exposed to attack by different stages (protonymphs, deutonymphs and adult females) of its predator P. persimilis. Experiments were also conducted to see the extent to which the functional responses could predict the outcome of predation when prey of two developmental stages were offered together in various proportions. Such information would be useful as stepping stones in building a more complete model for the interaction of different stages of T. urticae and P. persimilis.

4.2 Materials and methods

The prey and the predator were both placed on leaf-discs, cut out of French bean leaves, 4.5cm in diameter corresponding to an area of 16 sq.cm. As far as possible, major veins were avoided in taking the leaf-discs. On the lower surface of these discs 0.5cm squares were marked as a grid by drawing very fine lines with a pin. This arrangement facilitated quick and accurate counting of mites kept on them. These discs were then arranged

with their lower surfaces up, one on each sponge in 300ml. plastic containers, in an identical way to that described in Chapter 3 for studies on the biology of P. persimilis.

4.2.1 The prey

The functional response experiments were carried out with each of the immature stages of T. urticae. At the start of the experiment these stages were transferred with a sable-hair brush onto the leaf-discs already kept on the sponges in containers filled with water. The prey eggs were all newly laid and they were randomly placed on the leaf-discs at least two hours before the start of the experiment. This enabled any eggs damaged in transfer, which would have collapsed by then, to be replaced. The other stages - larva, protonymph and deutonymph of the prey - were also newly emerged to ensure that they remained in the active stages during the 24-hour period of the experiment without going into the quiescent stage. With experience it was not difficult to select very young ones in their respective stages. After transferring the prey onto the leaf-discs they were examined for any prey injured during the transfer, which were immediately replaced before introducing the predator. The larvae and the protonymphs used were all unsexed but deutonymphs used were all females.

4.2.2 The predator

From the cultures maintained under the same conditions as in the experiments, the larvae of P. persimilis were collected at least 12-hours before the start of the experiment and placed on clean bean leaves kept on moist cotton wool in small trays. On the following day, the protonymphs which moulted from these larvae were used in experiments soon after their emergence.

A similar procedure was carried out for standardising the deutonymphs of P. persimilis by separating from prey, well fed protonymphs of at least 1½ days old. This method of keeping the protonymphs and deutonymphs without prey on emergence was adopted, as they were known to feed soon after moulting. This helps to have them in a comparable level of hunger at the start of the

experiments. All the protonymphs and deutonymphs used in the experiments were also unsexed.

The adult females of P. persimilis were raised by introducing larvae onto bean leaves heavily infested with T. urticae, kept on moist cotton wool. When the mated adult females were 6-7 days old from their last moult, they were ready for use in the experiments. Throughout this period they were always maintained with a plentiful supply of prey so that at any given time they were regarded as in the same level of hunger. No experiments were done with any starved adult predators.

Two sets of functional response experiments were carried out with eggs, larva, protonymph and deutonymphs of T. urticae as the prey. In the first set, which was run for 24-hours, the protonymphs, the deutonymphs and the adult femals of P. persimilis were used as the predator, while in the second set of experiments lasting 8-hours only the immature stages of the predator were used. This second set of experiments was conducted since it was noticed that immature stages of P. persimilis fed mostly during the first 12-hours. An experiment of 24-hours would therefore involve a long period of satiation.

4.2.3 The procedure

The experiments were carried out in a controlled temperature room at 20 ± 0.75°C and 55-65% R.H. and with alternating 16-hour light and 8-hour dark periods. The densities of each stage of the prey used with one predator per disc were 1, 2, 4, 8, 16, 32 and 48. In addition, for the experiments where an adult female predator searched for prey eggs or larvae, prey densities of 64 and 96 were used. At the end of the experiment the number of prey killed were estimated by counting the number of shrivelled carcasses. Only in the case of the eggs, the remaining number was counted and subtracted from the original density as this was very much easier than looking for the empty egg shells. The 8-hour and 24-hour experiments were replicated 5 and 10 times, respectively.

Where the pattern or predation in a mixture of two stages of the prey with each predator stage were studied, the experiments were set up in an identical manner, except for the fact that the two prey stages under investigation were introduced in 5 combinations in the proportions, 1:4, 2:3, 1:1, 3:2 and 4:1, to make up a total of 20 in each treatment. The experiments with adult female predators were replicated 20 times while those with the predator protonymphs and deutonymphs were each replicated 10 times.

4.3 Method of analysis

The results of functional response experiments were analysed using the linear regression transformation of the random predator equation:

$$\left[\ln \left(\frac{N - Na}{N} \right) = -Ta^1 + a^1 T_h Na \right] ,$$

as described by Rogers (1972). The intercept (Ta^1) and the slope (a^1T_h), were therefore used to estimate the search-rate ($\underline{a^1}$) and the handling time ($\underline{T_h}$) respectively. The values thus obtained for $\underline{a^1}$ and $\underline{T_h}$ were then used in the random predator equation to describe the experimental results. Where the responses appeared sigmoid, successive data points from the lowest prey density were eliminated until the transformed data was significantly described.

In experiments where two prey stages were used in combination, an attempt was made to see how closely the experimental data could be described by the random predator equation which was modified to include more than one prey stage. This was done by using the computer programme in Appendix 3 (Cock 1977).

4.4 Results

In Figure 4.2 the curves A to H show the results from the 8-hour set of experiments while in Figure 4.3 the curves I to T are for 24-hour set. In estimating $\underline{a^1}$ and $\underline{T_h}$ with the linear regression transformation of the random predator equation, the lowest prey density (one) of B, C,

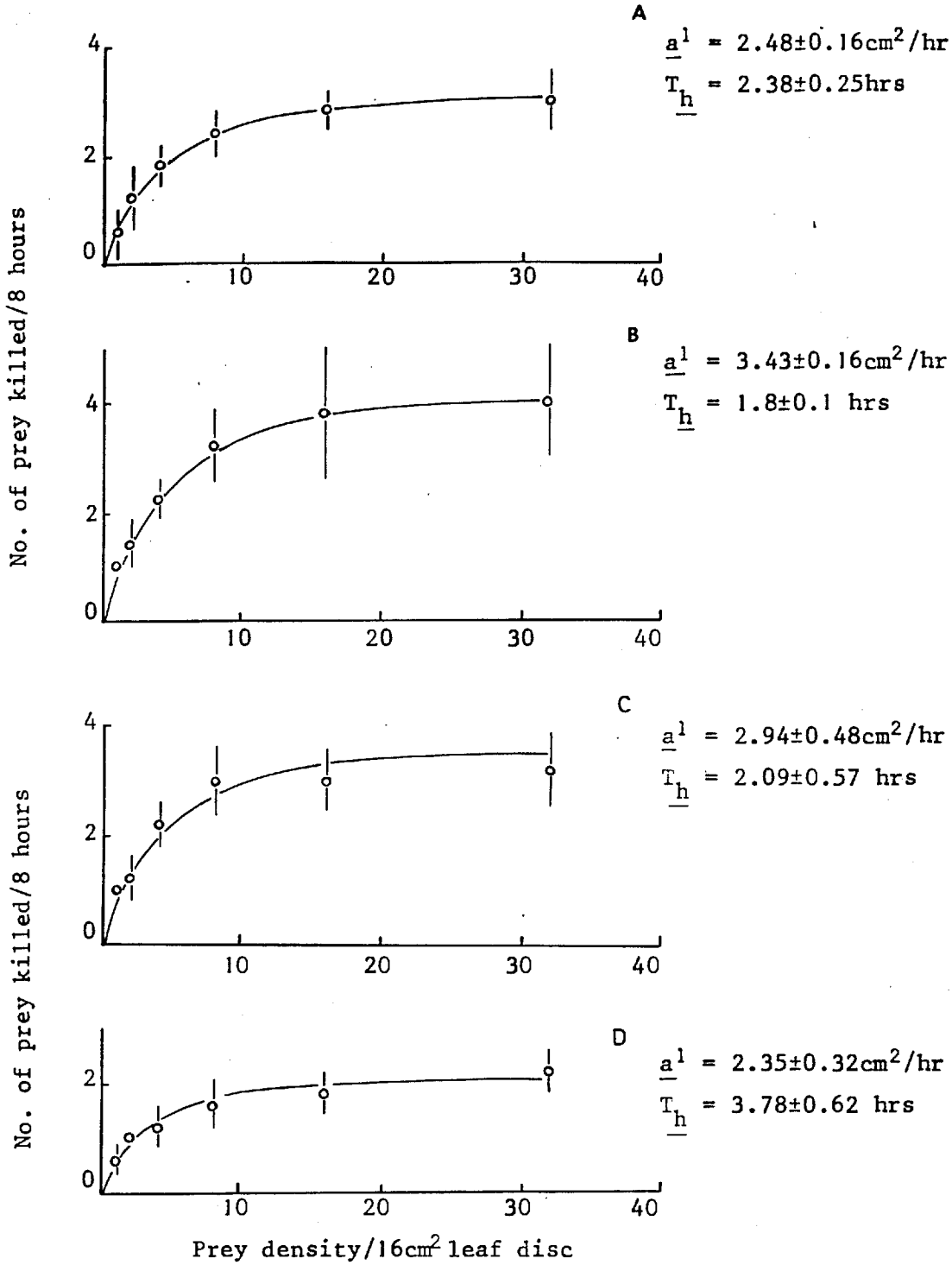


FIG. 4.2 A, B, C & D Functional response of the protonymph of P. persimilis to the density of different stages of T. urticae. 95% confidence limits shown. (Curves fitted by the 'random predator equation').

A-Eggs of T. urticae
B-Larvae of T. urticae
C-Protonymphs of T. urticae
D-Deutonymphs of T. urticae

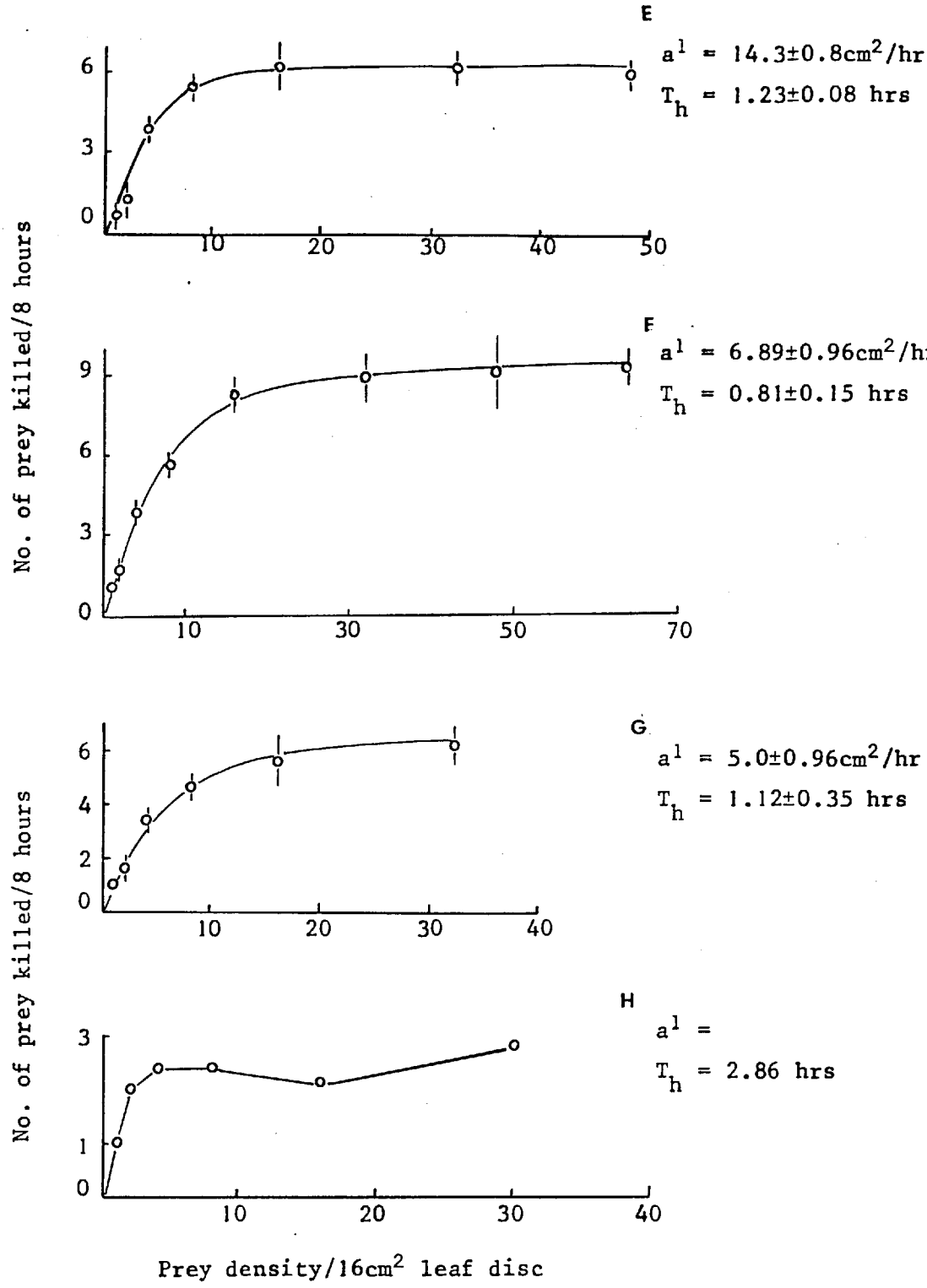


Fig. 4.2 E, F, G, & H Functional response of the deutonymph of P. persimilis to the density of different stages of T. urticae. 95% confidence limits shown. (Curves fitted by the 'random predator equation'.)

E – Eggs of T. urticae
F – Larvae of T. urticae
G – Protonymphs of T. urticae
H – Deutonymphs of T. urticae

Fig. 4.3 I, J, K & L Functional response of the protonymph of P. persimilis to the density of different stages of T. urticae. 95% confidence limits shown. (Curves fitted by the 'random predator equation').

I - Eggs of T. urticae

J - Larvae of T. urticae

K - Protonymph of T. urticae

L - Deutonymph of T. urticae

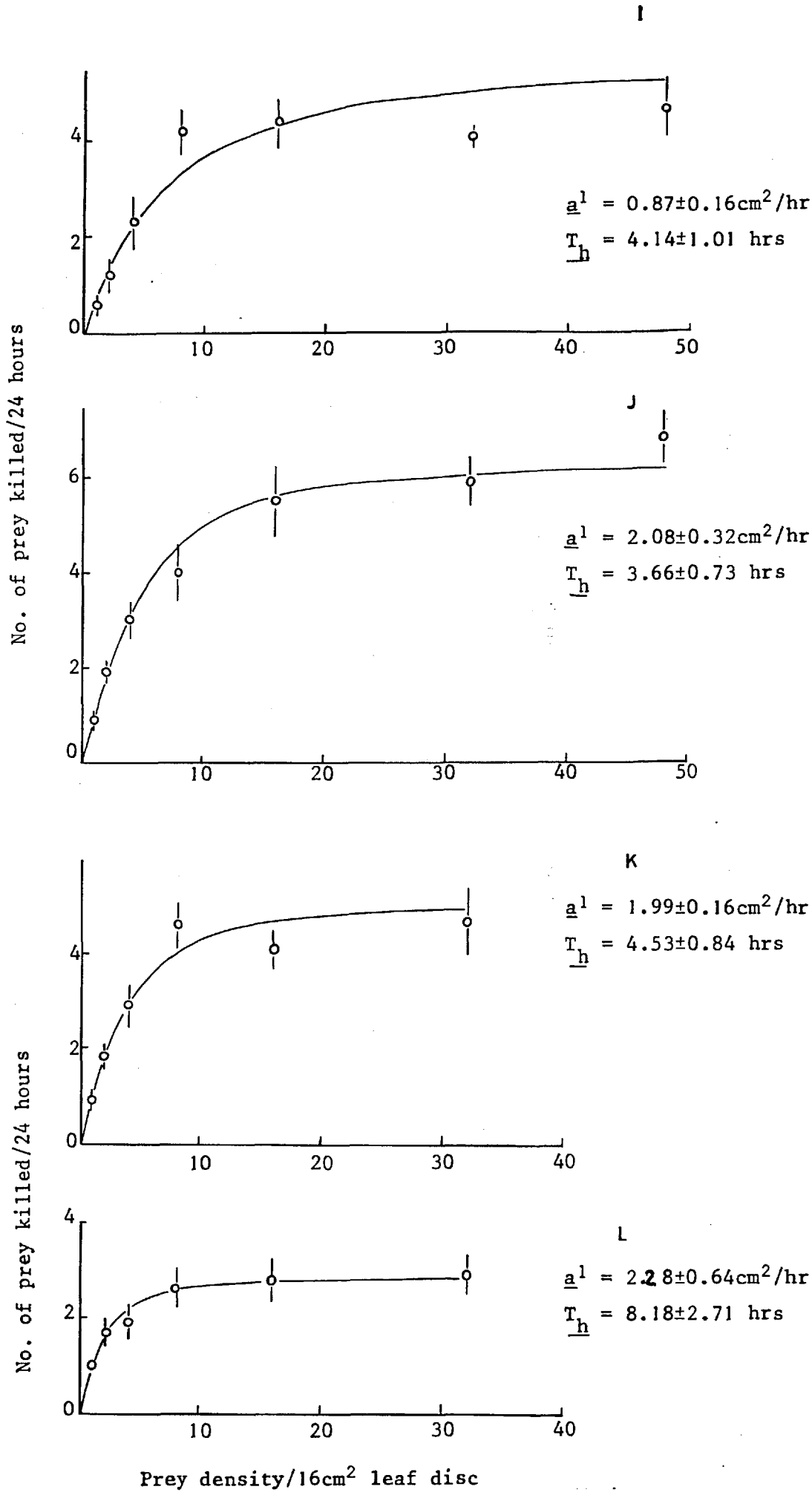

I
a^1 = 0.87±0.16cm²/hr
T_h = 4.14±1.01 hrs
J
a^1 = 2.08±0.32cm²/hr
T_h = 3.66±0.73 hrs
K
a^1 = 1.99±0.16cm²/hr
T_h = 4.53±0.84 hrs
L
a^1 = 2.28±0.64cm²/hr
T_h = 8.18±2.71 hrs
No. of prey killed/24 hours
No. of prey killed/24 hours
Prey density/16cm² leaf disc

Fig. 4.3 I, J, K & L

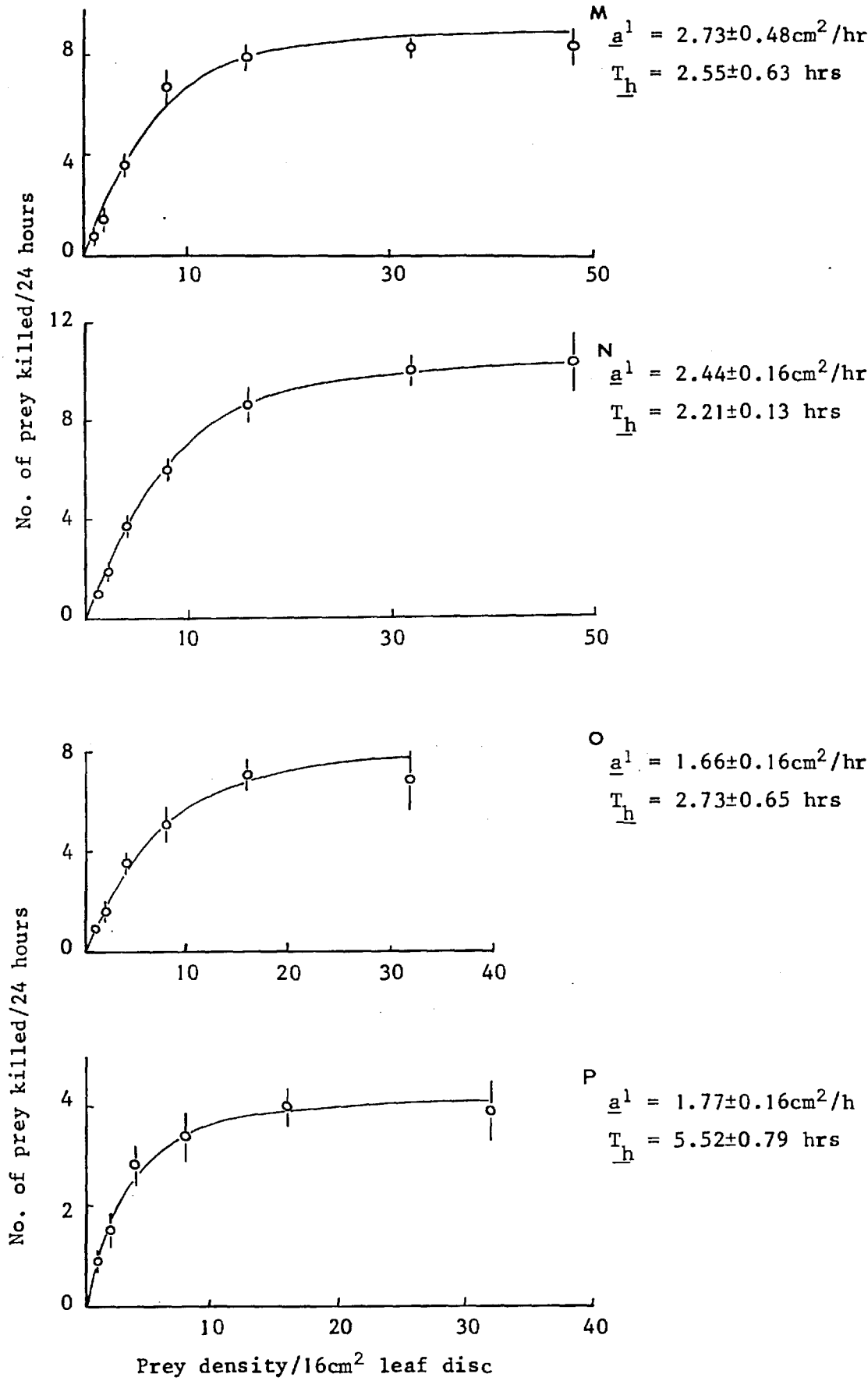


Fig. 4.3 M, N, O & P Functional response of the deutonymph of P. persimilis to the density of different stages of T. urticae. 95% confidence limits shown (Curves fitted by the 'random predator equation').

M– Eggs of T. urticae N– Larvae of T. urticae
O– Protonymphs of T. urticae P– Deutonymphs of T. urticae

Fig. 4.3 Q, R, S & T Functional response of the adult female *P. persimilis* to the density of different stages of *T. urticae*. 95% confidence limits shown. (curves fitted by the 'random predator equation').

Q - Eggs of *T. urticae*

R - Larvae of *T. urticae*

S - Protonymph of *T. urticae*

T - Deutonymph of *T. urticae*

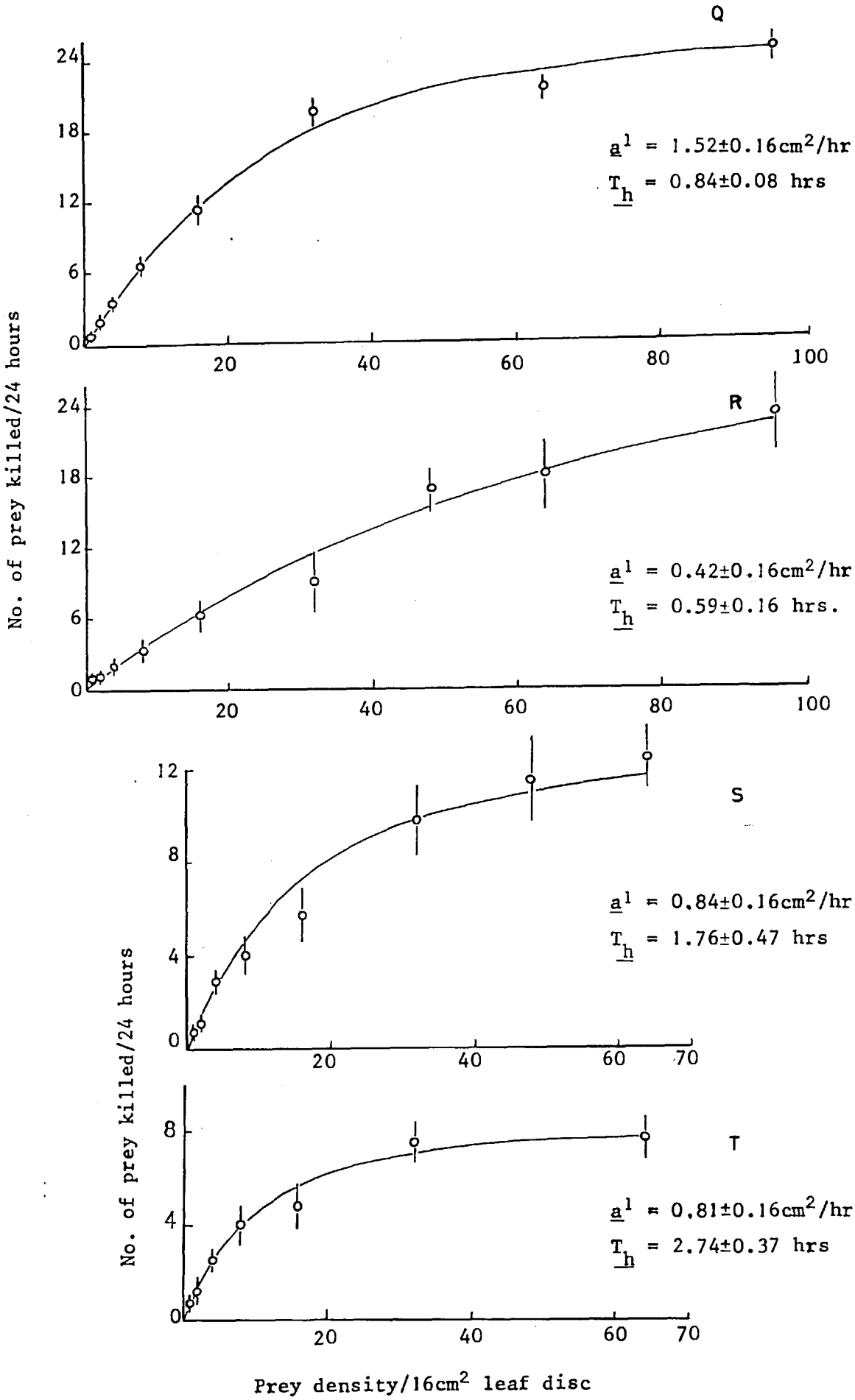

Q
a^1 = 1.52±0.16cm²/hr
T_h = 0.84±0.08 hrs
R
a^1 = 0.42±0.16cm²/hr
T_h = 0.59±0.16 hrs.
S
a^1 = 0.84±0.16cm²/hr
T_h = 1.76±0.47 hrs
T
a^1 = 0.81±0.16cm²/hr
T_h = 2.74±0.37 hrs
No. of prey killed/24 hours
No. of prey killed/24 hours
Prey density/16cm² leaf disc

Fig. 4.3 Q, R, S & T

TABLE 4.1 - Fitting of the functional responses to the random predator equation (8-hour experiments)

		PREDATOR / PREY	Coe. of reg. r	d.f.	F	PROBABILITY P
	A	Protonymph / Eggs	0.978	1, 4	91.25	<0.01
*	B	Protonymph / Larvae	0.994	1, 3	266.94	<0.01
*	C	Protonymph / Protonymphs	0.904	1, 3	13.38	<0.05
	D	Protonymph / Deutonymphs	0.951	1, 4	37.57	<0.01
	E	Deutonymph / Eggs	R E F E R T A B L E 4 . 3			
*	F	Deutonymph / Larvae	0.920	1, 5	27.48	<0.01
*	G	Deutonymph / Protonymphs	0.880	1, 3	10.338	<0.05
	H	Deutonymph / Deutonymphs	Not fitted with the random predator equation			

* Density one omitted where prey were eaten in all replicates.

TABLE 4.2 - Fitting of the functional responses to the random predator equation (24-hour experiments)

		PREDATOR / PREY	Coe. of reg. r	d.f.	F	PROBABILITY P
	I	Protonymph / Eggs	0.887	1, 5	16.689	<0.01
	J	Protonymph / Larvae	0.914	1, 5	25.24	<0.01
	K	Protonymph / Protonymphs	0.938	1, 4	29.418	<0.01
*	L	Protonymph / Deutonymphs	0.867	1, 3	9.116	<0.1
	M	Deutonymph / Eggs	R E F E R T A B L E 4 . 3			
*	N	Deutonymph / Larvae	0.993	1, 4	272.91	<0.01
	O	Deutonymph / Protonymphs	0.904	1, 4	17.95	<0.05
	P	Deutonymph / Deutonymphs	0.961	1, 4	48.00	<0.01
**	Q	Adult Females / Eggs	0.979	1, 5	120.212	<0.01
**	R	Adult Females / Larvae	0.837	1, 6	14.02	<0.01
	S	Adult Females / Proto-nymphs	0.831	1, 6	14.08	<0.01
	T	Adult Females / Deuto-nymphs	0.956	1, 5	53.797	<0.01

* Density one omitted where prey were eaten in all replicates.

** Density one omitted to get a better fit.

TABLE 4.3 - Attempts to fit the sigmoid functional responses to the random predator equation.

PREDATOR / PREY		Data points omitted		
		Nil	1	1-2
Deutonymphs / Eggs				
8-hours				
	r	0.21	0.35	0.99
E	F	0.17	0.42	198.87
	d.f.	1, 4	1, 3	1, 2
	P	>0.05n.s.	>0.05n.s.	<0.01
24-hours				
	r	0.53	0.62	0.92
	F	1.95	2.53	16.50
M	d.f.	1, 5	1, 4	1, 3
	P	>0.05n.s.	>0.05n.s.	<0.05

n.s. - not significant.

TABLE 4.4 - The values of Search-rate (a^1) ± S.E. (cm^2/hr.)

Duration	Prey / Predator	egg	larva	protonymph	deutonymph
8-hours	protonymph	2.48 ±0.16	3.43 ±0.16	2.94 ±0.48	2.35 ±0.32
	deutonymph	14.3 ±0.8	6.89 ±0.96	5.0 ±0.96	- -
24-hours	protonymph	0.87 ±0.16	2.08 ±0.32	1.99 ±0.16	2.28 ±0.64
	deutonymph	2.73 ±0.48	2.44 ±0.16	1.66 ±0.16	1.77 ±0.16
	adult females	1.52 ±0.16	0.42 ±0.16	0.84 ±0.16	0.81 ±0.16

TABLE 4.5 - The values of handling-time (T_h) ±S.E. (hrs.)

Duration	Prey / Predator	egg	larva	protonymph	deutonymph
8-hours	protonymph	2.38 ±0.25	1.8 ±0.1	2.09 ±0.57	3.78 ±0.62
	deutonymph	1.23 ±0.08	0.81 ±0.15	1.12 ±0.35	2.86
24-hours	protonymph	4.14 ±1.01	3.66 ±0.73	4.53 ±0.84	8.18 ±2.71
	deutonymph	2.55 ±0.63	2.21 ±0.13	2.73 ±0.65	5.52 ±0.79
	adult females	0.84 ±0.08	0.59 ±0.16	1.76 ±0.47	2.74 ±0.37

Fig.4.4 A to D Variations in a^1 and T_h in different stages of *P. persimilis* feeding on the same stage of the prey, *T. urticae*, (8 hour experiemnts).

Fig.4.4 E and F Variations in a^1 and T_h within the same stage of *P. persimilis* feeding on different stages of the prey, *T. urticae*, (8 hour experiments).

E - Egg; L - Larva; Pn - Protonymph;
Dn - Deutonymph; ♀ - Adult females

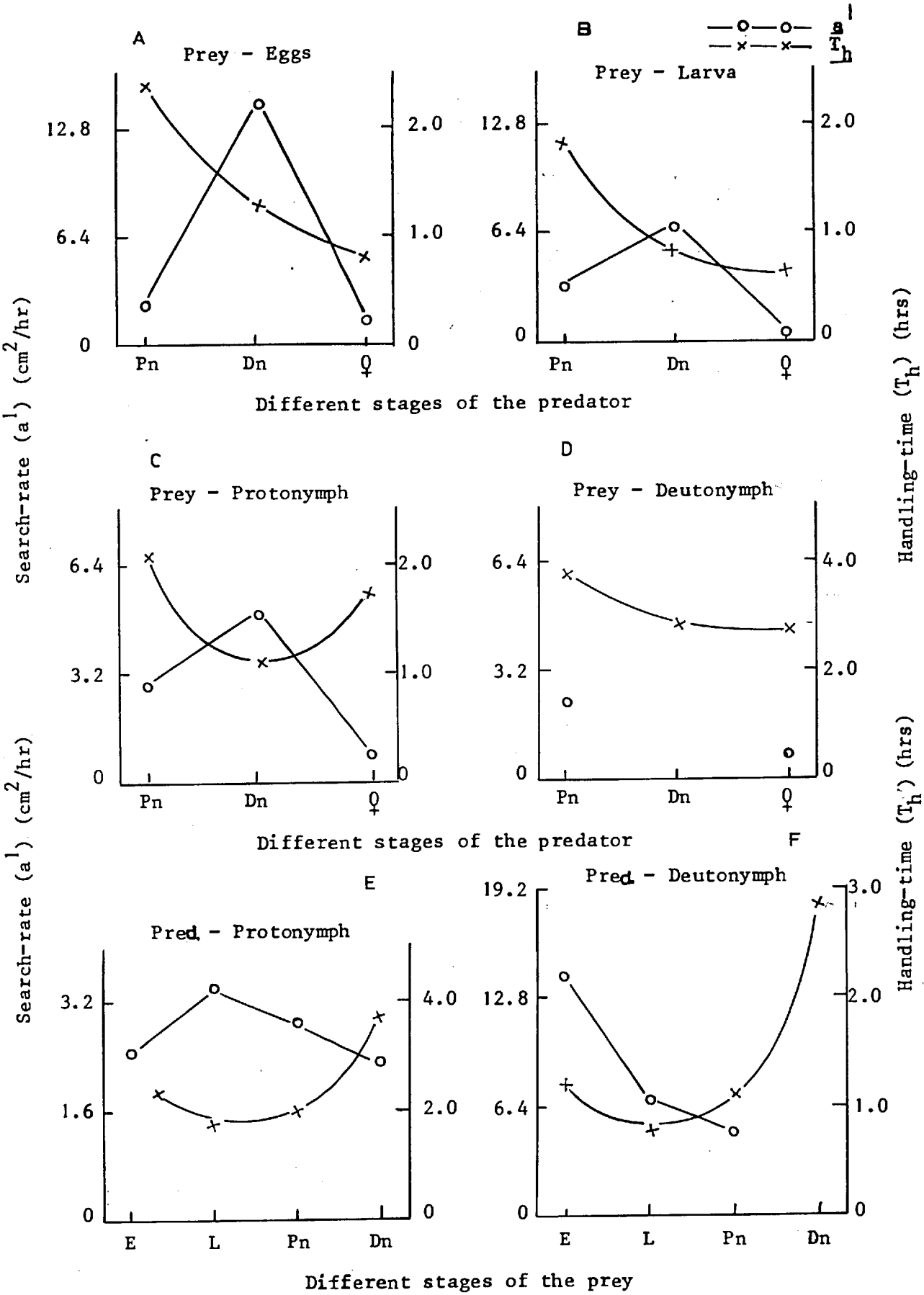
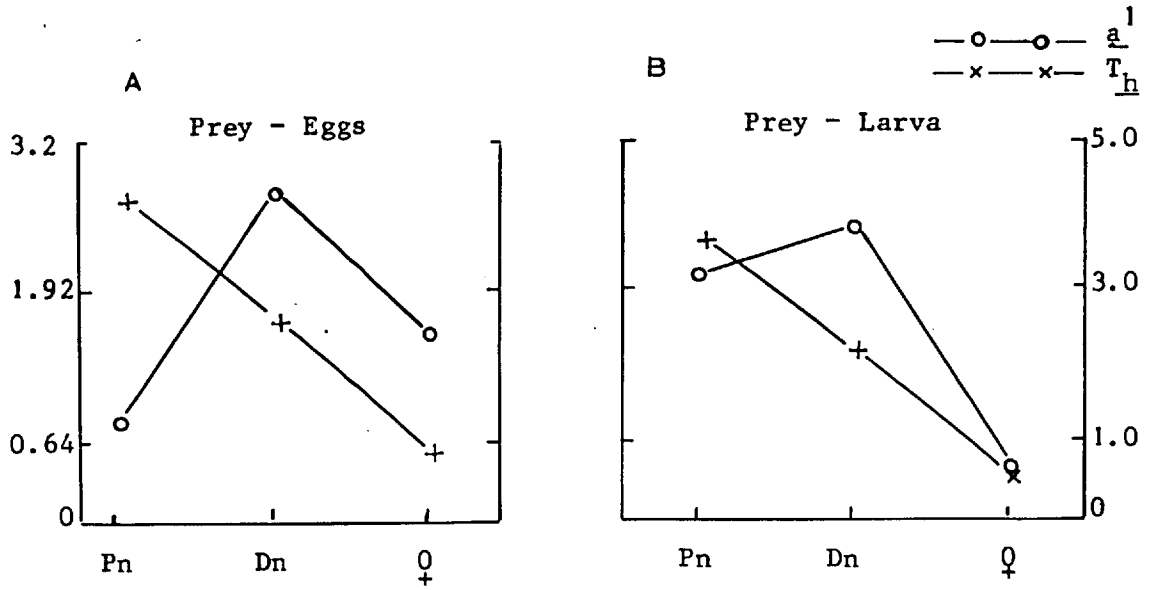

A
Prey - Eggs
B
Prey - Larva
a
T_h
12.8
6.4
0
2.0
1.0
0
Pn
Dn
♀
Different stages of the predator
Search-rate (a^1) (cm^2/hr)
Handling-time (T_h) (hrs)
C
Prey - Protonymph
D
Prey - Deutonymph
6.4
3.2
0
2.0
1.0
4.0
2.0
E
Pred. - Protonymph
F
Pred. - Deutonymph
19.2
12.8
1.6
3.0
E
L
Pn
Dn
Different stages of the prey

Fig.4.4 A to F



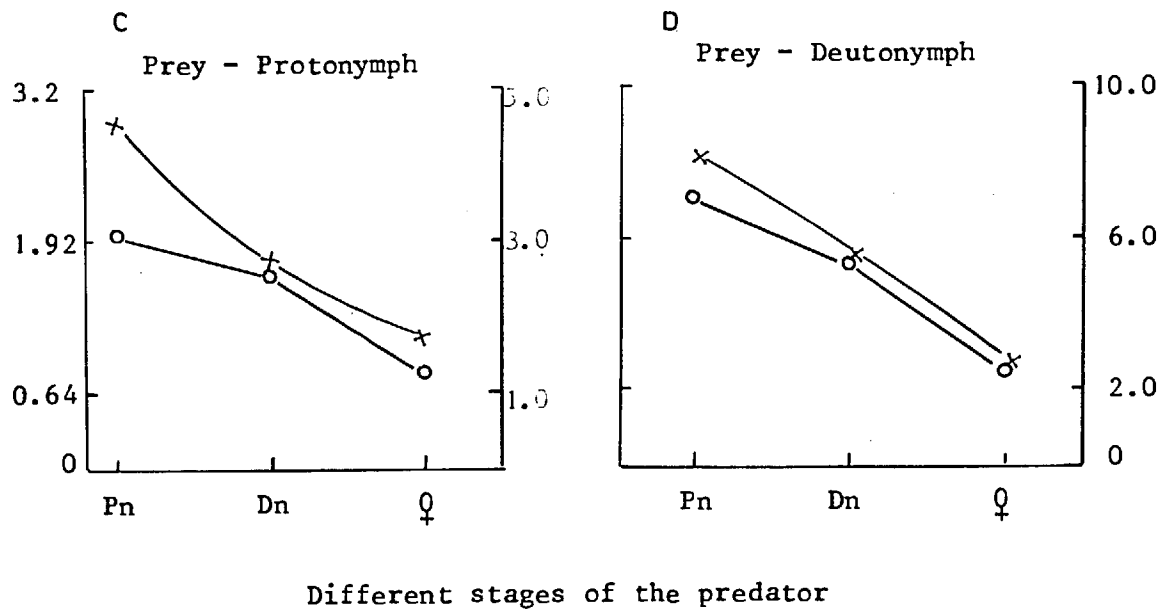


Fig.4.5 A to D Variations in a^1 and T_h in different stages of *P. persimilis* feeding on the same stage of the prey, *T. urticae* (24 hour experiments).
Pn - Protonymph; Dn - Deutonymph;
♀ - Adult females

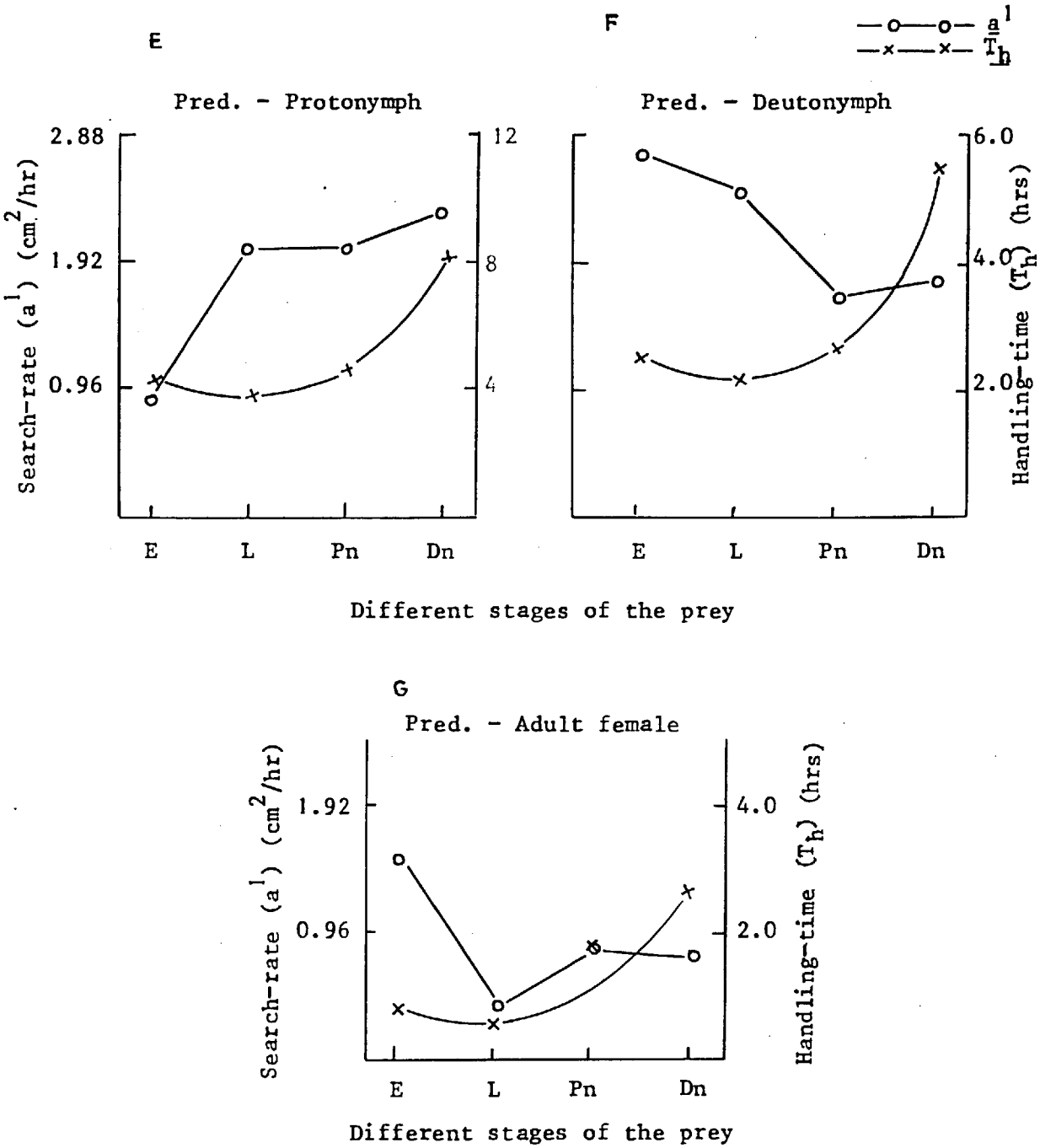


Fig.4.5 E to G Variations in a' and T_h within the same stage of *P. persimilis* feeding on different stages of the prey, *T. urticae*. (24 hour experiments)

E - Egg; L - Larva; P - Protonymph; D - Deutonymph

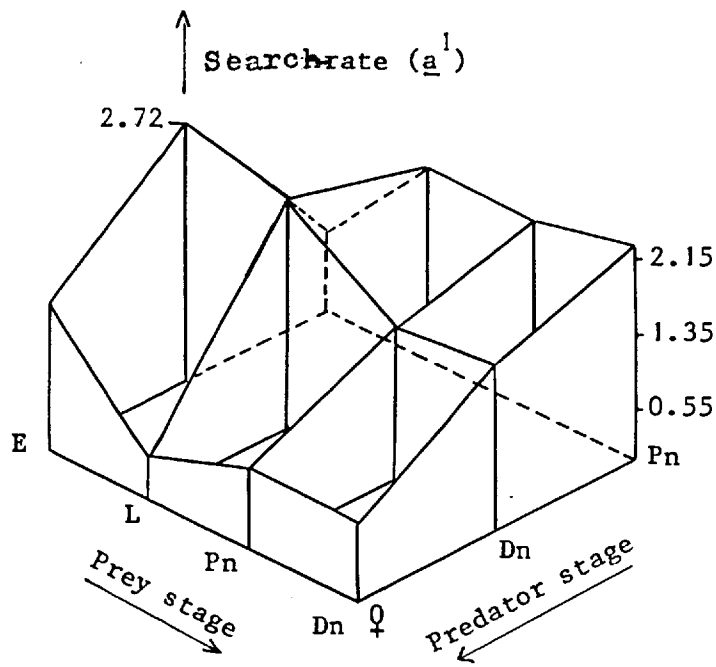


Fig.4.6 The effect prey and predator stage (size) on the search-rate. E - Egg; L - Larva; Pn - Protonymph; Dn - Deutonymph; ♀ - Adult females. (24 hour experiment)

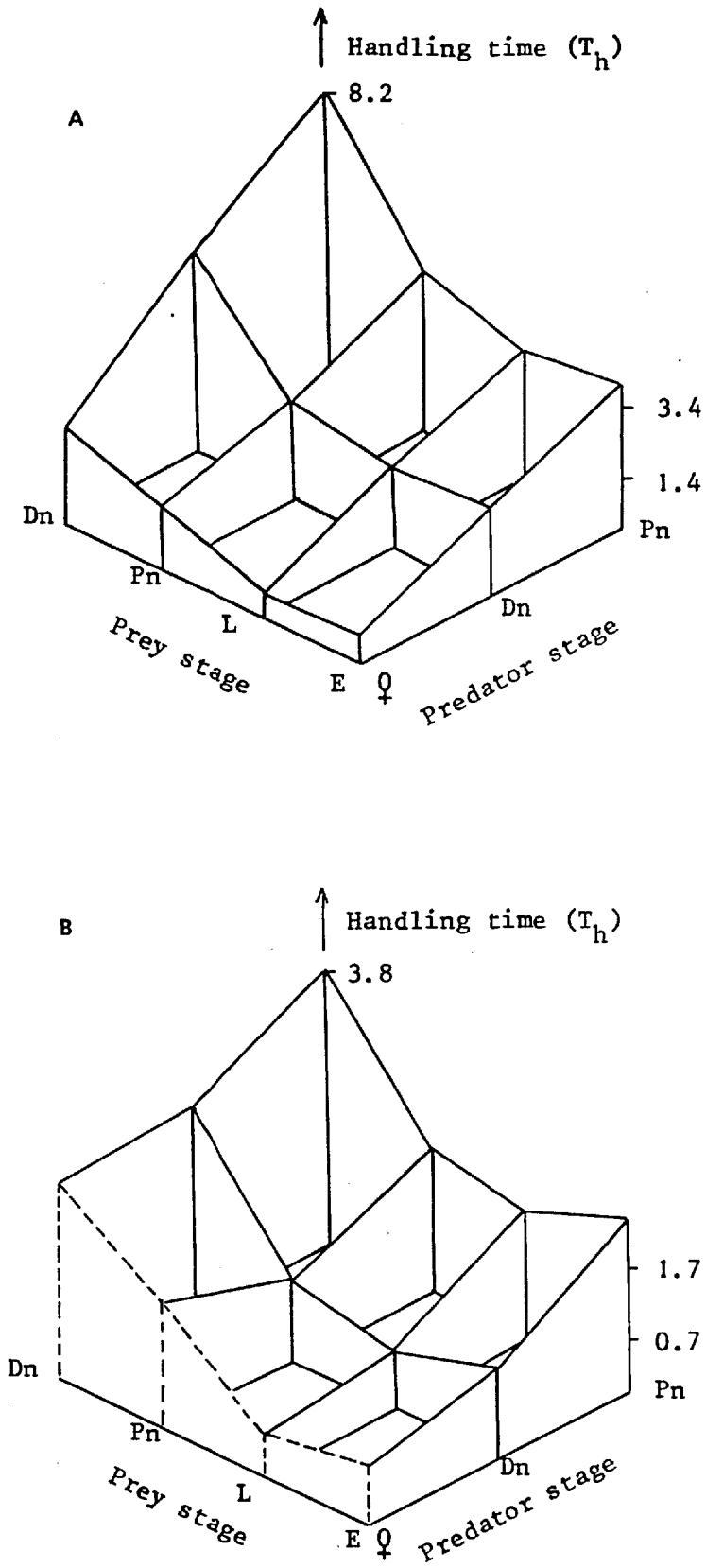


Fig. 4.7 The effect of prey and predator stage (size) on the handling-time. E - Egg; L - Larva; Pn - Protonymph; Dn - Deutonymph; ♀ - Adult females

A - 24 hour experiment

B - 8 hour experiment (broken lines indicate handling-times from 24 hour experiment).

F and G (8-hour) and L and N (24-hour) had to be omitted since there was 100% predation in all the replicates. Similarly, the lowest prey density of Q and R and the lowest two prey densities of E and M were also omitted due to the responses being somewhat sigmoid at low prey densities (Table 4.3). Only the functional response of H was not fitted with the random predator equation as there was 100% predation in the lowest two densities, above which the response had reached its upper asymptote. All the other transformed data were very well described by the linear regression; L at the 10% level, C, G, M and O at the 5% level and the rest at the 1% level (Table 4.1 and 4.2).

The values obtained for the search-rates and the handling-times from the analysis of the two sets of experiments (8 and 24-hour) are summarised in Tables 4.4 and 4.5 respectively. The same data are shown graphically in Figure 4.4 (A to F) and Figure 4.5 (A to G), in terms of the variation of $\underline{a^1}$ and $\underline{T_h}$ with changes in the predator stage (protonymph, deutonymph and adult females) and the prey stage (egg, larve, protonymph and deutonymph).

The data in Figures 4.4 and 4.5 are represented as three dimensional surfaces in Figure 4.6 (for $\underline{a^1}$) and Figure 4.7 (for $\underline{T_h}$) much as recently done by Thompson (1975) with Ischnura elegans (van der Lind) feeding on Daphnia magna (Straus). This gives a useful comprehensive picture of the pattern of variation of $\underline{a^1}$ and $\underline{T_h}$ for different predator-prey combinations. The surface for $\underline{a^1}$ from the 8-hour experiments has not been plotted due to absence of satisfactory estimates of $\underline{a^1}$ from experiment H where all prey were eaten at low prey densities (see above).

The values of $\underline{a^1}$ and $\underline{T_h}$ in Figure 4.4, and $\underline{T_h}$ in Figure 4.7B plotted for adult females are those of the 24-hour set of experiments as no experiments were done with adult females for the 8-hour period. This was done for comparison as all the three stages of the predator were

assumed to be in an active state throughout the respective periods.

The results obtained by introducing each stage of the predator to a two-prey situation are plotted as the percentage of each prey in the diet against the percentage of respective prey offered as shown in Figures 4.9 A-F. The Figures 4.9 A & B show the results for protonymph predators when introduced into prey combinations of eggs and deutonymphs (A), and larvae and deutonymphs (B).

The Figures 4.9 C & D show these results for deutonymph and E & F for adult female predators. The fitted line in each case shows the expected results predicted from the functional responses to each prey stage separately. The experimental results are shown as points with their confidence limits.

The raw data of all the experiments are given in Appendix 2.

4.5 Discussion

Previous workers who have studied the functional responses of acarine predator-prey systems have either worked with single predator and prey stages or on an incomplete range of predator and prey combinations. In the present study the functional responses of all combinations were obtained with the exception of using adult male and female prey.

The functional response curves obtained in the present study are mostly curvilinear except for the ones with predator deutonymph and prey eggs which are sigmoid and the one with predator and prey deutonymphs (8-hour) which is linear due to all prey being eaten at low densities. Pruszynski (1973) also obtained a type II functional response for adult females of *P. persimilis* feeding on female deutonymphs of *T. urticae* on a leaf-disc arena, and this agrees with the results obtained in the similar experiment reported here (Figure 4.3T). The respective values of a^1 and T_h calculated from the data of Pruszynski were 1.16 and 1.88

hours, a higher value for a^1 and a lower value for T_h than the values obtained in the present study. Takafuji & Chant (1976) working with predatory mites P. persimilis and Iphiseius degenerans Berlese, and prey mite Tetranychus pacificus McGregor reported functional response curves which could be regarded as linear, similar to the type I of Holling (1959a). They were obtained for the protonymphs, deutonymphs and adult females of the two predator species feeding on the eggs and protonymphs of the prey. This type of response in this case was attributed to the use of paper substrates and very much smaller arenas (4.0 sq. cm). On a paper substratum the prey would be restless and, therefore, could more easily bump into the predators, increasing the chances of predation. Chant (1961b) also reported a similar linear response for Typhlodromus occidentalis preying on T. telarius.

The functional responses of the deutonymph predator with prey eggs show a distinct sigmoid response in both sets of experiments (8 & 24-hours) (Figures 4.2E & 4.3M, Table 4.3). Even the functional responses of an adult female predator with eggs and larvae of prey show a tendency to be sigmoid (Figure 4.3 Q & R). Earlier it was thought that sigmoid functional responses were primarily characteristic of vertebrate predators, a feature sometimes attributed to the capacity for learning that prey are abundant (Holling 1959a). However, there is growing evidence to show that sigmoid responses are also found in invertebrate predators. Several examples are given by Hassell, Lawton & Beddington (1977), who suggested that they could be obtained if the rate of encounter is reduced by use of cryptic, relatively small or non-preferred species of prey in large experimental universes. In the present studies a condition similar to that could have operated with minute eggs and larvae of prey at very low densities.

For P. persimilis feeding on adult females of T. urticae, Mori &

TABLE 4.6 - Search-rates and handling-times of P. persimilis on protonymphs of T. pacificus (Takafuji & Chant 1976). (a^1 corrected to $cm^2/hr.$)

	Protonymph	Deutonymph	Adult
a^1	0.608	1.024	0.384
T_h	2.96 hrs.	4.00 hrs.	1.11 hrs.

TABLE 4.7 - Comparison of observed and calculated handling-times of prey eggs and larvae, by protonymph, deutonymph and adult females of P. persimilis. The observed T_h gives the time from start to end of feeding.

Predator	T_h of eggs in minutes		Obs./Cal.	T_h of larvae in minutes		Obs./Cal.
	Observed	Calculated		Observed	Calculated	
Protonymph	15.18	142.8	0.11	20.38	108.0	0.19
Deutonymph	5.6	73.9	0.076	11.8	48.6	0.24
Adult	2.21	50.16	0.04	4.19	35.7	0.12

Chant (1966a) and Takafuji & Chant (1976) obtained 'domed' shaped functional responses. The former authors attributed this to interference from prey resulting in abandonment of captures at high densities, and the latter argued that it was due to increased consumption of eggs at high prey densities. In the present series no experiments were conducted at very high prey densities so that it remains uncertain whether different stages of P. persimilis would exhibit any such deviations from a type II response.

These results all support the view expressed by Fransz (1974) that there is little uniformity in the functional responses of mite systems, and there are often deviations from the fundamental types distinguished by Holling. Indeed, from the results of the experiments reported here, it is clear that P. persimilis can exhibit all the three basic types of functional responses described by Holling (1959a), merely by varying the developmental stages of predator and prey.

4.5.1 Search-rate

The search-rate (a^1) is the product of several components. They may interact in a variety of ways making it difficult to generalise on how it will vary with predator and prey sizes. For example, for a given predator, the increase in size of prey may increase a^1 by improving prey detection or may have the opposite effect by improving the prey ability to escape. For a given size of prey the search-rate of the predator might increase with its size by improved prey perception and faster movement.

The final outcome of the interaction of such components in the present study are shown graphically in Figures 4.4 and (8-hour) and Figures 4.5 and 4.6 (24-hour). The clearest results come from the 8-hour experiment where the changes in a^1 for different predators feeding on a given prey stage follow the same pattern. Deutonymph predators have a greater searching efficiency than either protonymphs or adult females, with the females having the lowest values.

The responses of the two immature predator stages with the four immature prey stages do not show any common trend in the variation of search-rates. For protonymph and deutonymph predators, the greatest value of a^1 is when searching for larvae, and for eggs respectively.

The results for the search-rate over 24-hours present a more confused picture. They all have a much lower value due to the long periods of inactivity of the immature predators during these experiments and any tendency for satiation to occur after different times with different prey stages will tend to obscure any 'real' differences in search-rate. For this reason we now focus on 8-hour experiment in conjunction with the results of the adult predator in 24-hour experiment in seeking possible explanation for the trends observed.

It has been widely reported that the predacious phytoseiids detect their prey only by sense of touch, mostly through the 1st pair of legs (Putman 1962; Mori & Chant 1966a; McMurtry *et al.* 1970). These legs which are longer than the others have tactile setae and chemoreceptors known as trichobothria (Krantz 1970; Jackson & Ford 1973). In the case of *P. persimilis*, the adult predator (the largest) should have the biggest perceptual field out of the three predators. One would therefore, expect the adult predator to have the highest search-rate for any given size of prey. But, surprisingly we find the reverse to be true.

One or all of the following may be given as possible explanations for this unexpectedly low search-rate by the adult predators.

(1) Loss of time by adult females due to egg laying activities. Cessation of the feeding behaviour in *P. persimilis* for a short period before and after oviposition has been observed by Awan (1974).

(2) Higher search-rates of immatures may be due to their more 'aggressive nature' than the adults. Both immature stages were seen to resort to cannibalism more readily than the adult predators. This could be an important adaptation since it is known that survival and developmental rates are critically influenced by feeding rates (see review by Beddington et al. 1976).

(3) The immatures were introduced into the experiment before they have had any meal after they moulted. But the adult females were well fed before the start of the experiment.

It is important that the width of perception is not affected by hunger levels in phytoseiids (Takafuji & Chant 1976). The influence of hunger level could be complex depending on initial hunger level of the predator and the density of prey to which it is exposed. But the differences obtained in search-rates of immatures and adults of P. persimilis is too large in a 24-hour experiment to be accounted for by any hunger level of immatures (Table 4.4).

Within the four prey stages, the highest a^1 of deutonymph and adult predator (24-hour) for prey eggs must be due to the eggs being the most defenceless and stationary stage of the prey. Here every encounter with an egg could result in an attack if the predator is hungry. With larger and active prey, only a certain portion of the encounters result in an attack, the prey escaping at other times (Mori & Chant 1966a; Takafuji & Chant 1976). The lowest a^1 of the adult predators for larvae is understandable as it is the smallest of the mobile stages of the prey and it could easily escape attack due to its small size and mobility. In both sets of experiments, protonymph predators have the smallest a^1 for prey eggs and this may well be due to their small width of perception which makes them miss the eggs. It could even be due to the chemoreceptors on

the first pair of legs in the protonymph not being fully developed, which according to Jackson & Ford (1973) help P. persimilis to identify immobile prey eggs from other inert materials. Very careful observations are needed in this respect before any definite conclusions can be drawn.

When the search-rates of the three stages of P. persimilis on the protonymph of T. pacificus were calculated from the results of Takafuji & Chant (1976) almost an identical result is obtained with deutonymph and adult predator having the highest and the lowest a^1 respectively (Table 4.6). There are records of other invertebrate predators which do not have the same trend of variation of search-rates with the variations of sizes of different stages of the same prey. Evans (1973) found that third instar of Anthocoris confusus feeding on a species of Aulacorthum have a lower searching efficiency than the first two instars. This was attributed to a fall in preference for smaller prey by larger instars of the predator. Glen (1975) reported that hungry 5th instar and the adults of the capsid, Blepharidopterous angulatus (Fall.) missed the attack on a certain proportion of the young aphids they encounter. This was attributed to the presence of a 'blind spot' between the antennae as a result of greater range of perception. Thompson (1975) obtained an increase of a^1 with predator size and decline with prey size in the Ischnura - Daphnia system mentioned earlier. He thought this to be due to a decline in capture success with increased prey size, as it is not matched by an increase in the reactive distance. A detailed review of the variations of a^1 with prey and predator size in different predator-prey systems is given by Hassell et al. (1976).

4.5.2 Handling-time

Due to the nature of the sub-components of handling-time (T_h) (Holling 1965, 1966), it is possible to predict its likely changes with changes in predator and prey size. Therefore, for a given predator the

handling-time should increase with size of the prey since it will now take longer to kill, eat and digest each item.

In the present studies the variation of T_h with size of predator is shown graphically for the 8-hour experiment in Figures 4.4 A to D and 4.7B, and for the 24-hour experiment in Figures 4.5 A to D and 4.7A. In both cases it is clearly seen that T_h decreases with the size of predator. Similarly, there is a general trend for an increase in T_h as larger prey are presented to a given predator stage, with the exception of prey eggs which have a very slightly longer T_h than prey larvae. These variations of T_h with size of prey and predator are best seen in Figures 4.7 A and B. (T_h of adult female predators shown in Figures 4.4 & 4.7B are from 24-hour experiment for comparison.) The principal difference between the 8 and 24-hour experiments is that the calculated handling-time in the 24-hour set was more than twice the value of that in the 8-hour set. This follows directly from the long resting periods due to satiation during the longer experiment.

The pattern of variations of T_h in Figures 4.7 A & B is very similar with that of Thompson's (1975) Ischnura - Daphnia system. Almost all the published data in this respect show the same trend (see review by Hassell et al. 1976).

The unexpected results obtained with prey eggs need further consideration. Clearly, time consuming processes such as chasing, capturing, subduing and killing do not apply with an egg as prey. Jackson & Ford (1973) give a detailed description of how P. persimilis identify and attack prey eggs. The actual times taken by the protonymph, deutonymph and adult female predator for consuming an egg and also a larvae as observed under the binocular microscope are given in Table 4.7. It is also seen in Table 4.7 that the observed T_h is only a small fraction of the calculated T_h from functional response experiments. This is because

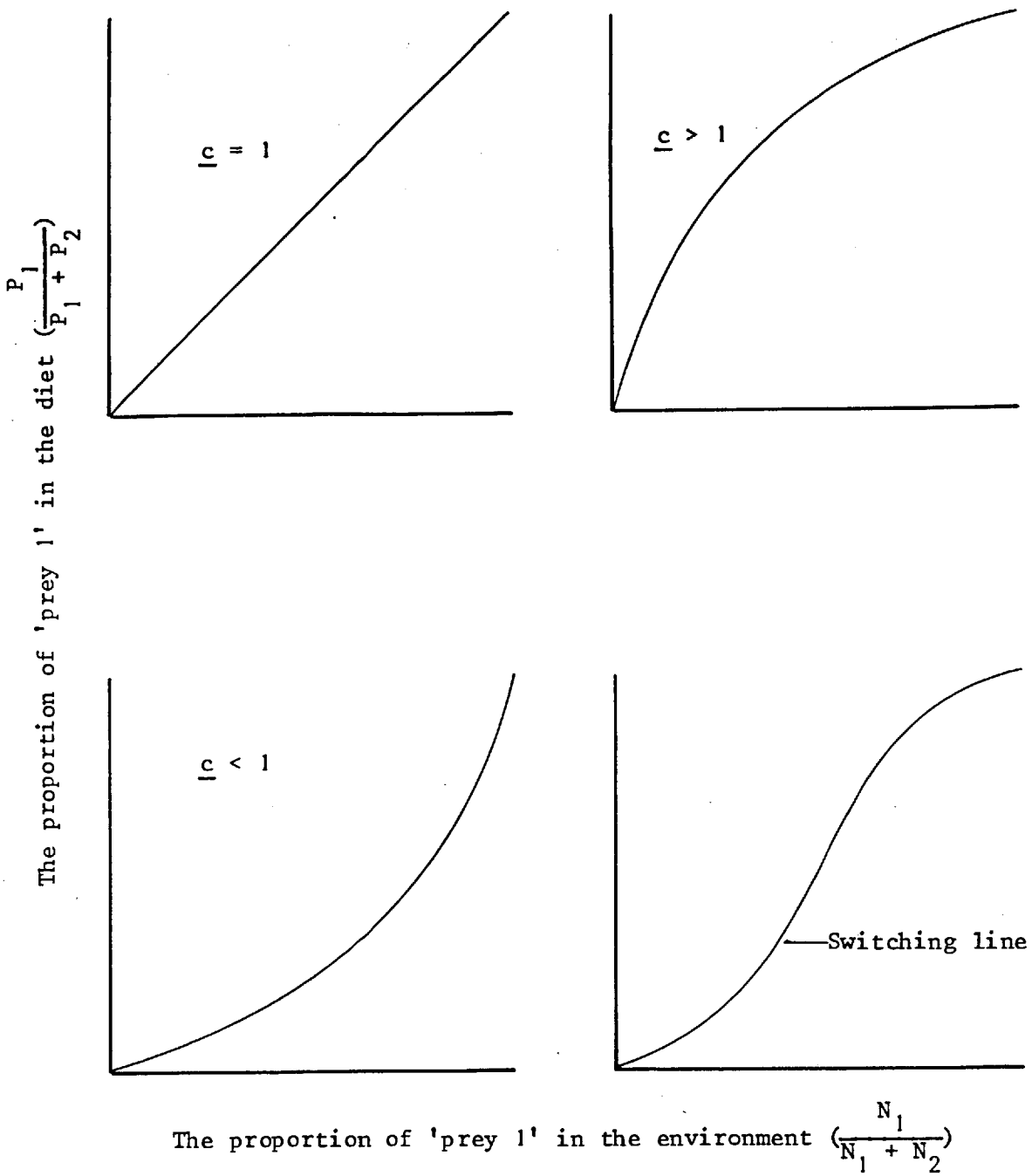


Fig. 4.8 The theoretical possibilities of attack by a predator when faced with a two prey situation

N_1 - No. of 'prey 1' in the environment
N_2 - No. of 'prey 2' in the environment
P_1 - No. of 'prey 1' in the diet
P_2 - No. of 'prey 2' in the diet
$\underline{c}$ - The value of P_1/P_2 when two prey types are equally abundant

A - No preference for any of the prey types ($\underline{c} = 1$)
B - 'Prey 1' preferred ($\underline{c} > 1$)
C - 'Prey 2' preferred ($\underline{c} < 1$)
D - Switching

calculated handling-time includes the time the predator spends in digesting the prey.

For all three stages of the predator, the proportion of the calculated handling-time spent in activities other than feeding on the prey eggs is much longer than that recorded for a larva.

4.5.3 Functional response to two-prey situation

The theoretical possibilities of attack by a predator when two-prey species are offered together were first discussed by Savage (1931), Ivlev (1961) and Murdoch (1969). The simplest null hypothesis for two-prey species is that the ratio in the diet (P_1 & P_2) is proportional to the ratio in which they were offered (N_1 & N_2).

Thus,

$$P_1 / P_2 = C \; N_1 / N_2 \text{ , and}$$

C is a constant.

The constant C has two basic components: the behaviour of the prey, which makes it more or less available, and the behaviour of the predator as shown by its preference for a prey species, "preference" being defined as a bias in favour of that species preponderant in the predator's diet.

The conventional way of expressing the results of experiments in which mixture of two-prey are presented to a predator is to plot the proportion of a paritcular prey type (eg. N_1) in the diet against the proportion of that N_1 available as shown in Figure 4.7. The effect of varying the value of C (i.e. the value of P_1/P_2 when the two-prey types are equally abundant) is shown in Figures 4.7 A-C. When there is no preference C = 1 as in Figure 4.7A; preference for N_2 leads to C < 1 (Figure 4.7C) and preference for N_1 to C > 1 (Figure 4.7B). These relationships may be regarded as null hypotheses against which the possibility of "switching" may be tested.

Murdoch (1969) defined switching as follows:

" As a prey sepcies become relatively more abundant, switching occurs if the relative amount which that species forms of the predator's diet increases disproportionately in comparison with the expected amount. The expected amount is based on the proportion that the species forms of the food supplied and on the observed diet when both prey are equally common."

In Figure 4.7D, the curve for switching is expected to intersect the expected line at $N_1/N_2 = 1$.

Ivlev (1961) stated that switching will occur in active, choosing predators (vertebrate predators), but not in more passive predators (eg. invertebrates such as coccinellids, surphids, mites etc.), which tend to eat merely what they find.

Murdoch et al. (1975) made three generalisations about preference and switching mechanisms in predators:

(1) if the average preference at equal prey densities is strong, and constant among all the individuals in the replicates then strong preference will occur and remain constant throughout all the ratios of N_1/N_2

(2) if this preference is weak at equal prey densities, but consistant as above among all the individuals in the replicates, weak preference will remain constant throughout the ratios of N_1/N_2

(3) if the preference is weak and at the same time highly variable among individuals in replicates at equal prey densities, then switching should occur.

Thus, it is seen that the above null hypothesis is based on the

preference evaluated from the numbers of prey killed when both types are offered in equal numbers. It is purely a numerical statement about the expected prey ratios eaten as the ratios presented are varied and no restrictions are set on any change in $\underline{a^1}$ and $\underline{T_h}$, but merely show as either "preference" or "switching".

In experiments, although it is ensured that the availability of prey is proportional to its density by having a homogenous environment, any differences in the sizes of prey could affect availability. Also, the outcome of predation could vary with changes in the relative availability of the prey and/or change in the search-rate of the predator, both due to the depletion of the prey in the course of an experiment.

The above drawbacks are overcome in the present method. The null hypothesis is based on the assumption that when two-prey stages are exposed to a predator the predicted responses from equation 4.7 depend on the values of $\underline{a^1}$ and $\underline{T_h}$ for the two-prey stages obtained from separate functional response experiments. Therefore, if the values of $\underline{a^1}$ does not change when the predator is faced with a mixture of prey, the results should be described by equation 4.7. Any deviations of the observed responses from the predicted responses will appear as a preference for one of the prey types.

It is important to note the condition of the predators at the start of the present experiments. The immature predators were used immediately after they had moulted and, prior to any feeding. Therefore, there was no case of conditioning for any particular stage of the prey. The adult females used in ten of the replicates in each set were taken from a general culture of prey where the predator had access to the prey stage of its choice. In another ten replicates the adult females were allowed to feed exclusively on prey eggs or larvae, depending on which combination they were to be used, at least eight days before the experi-

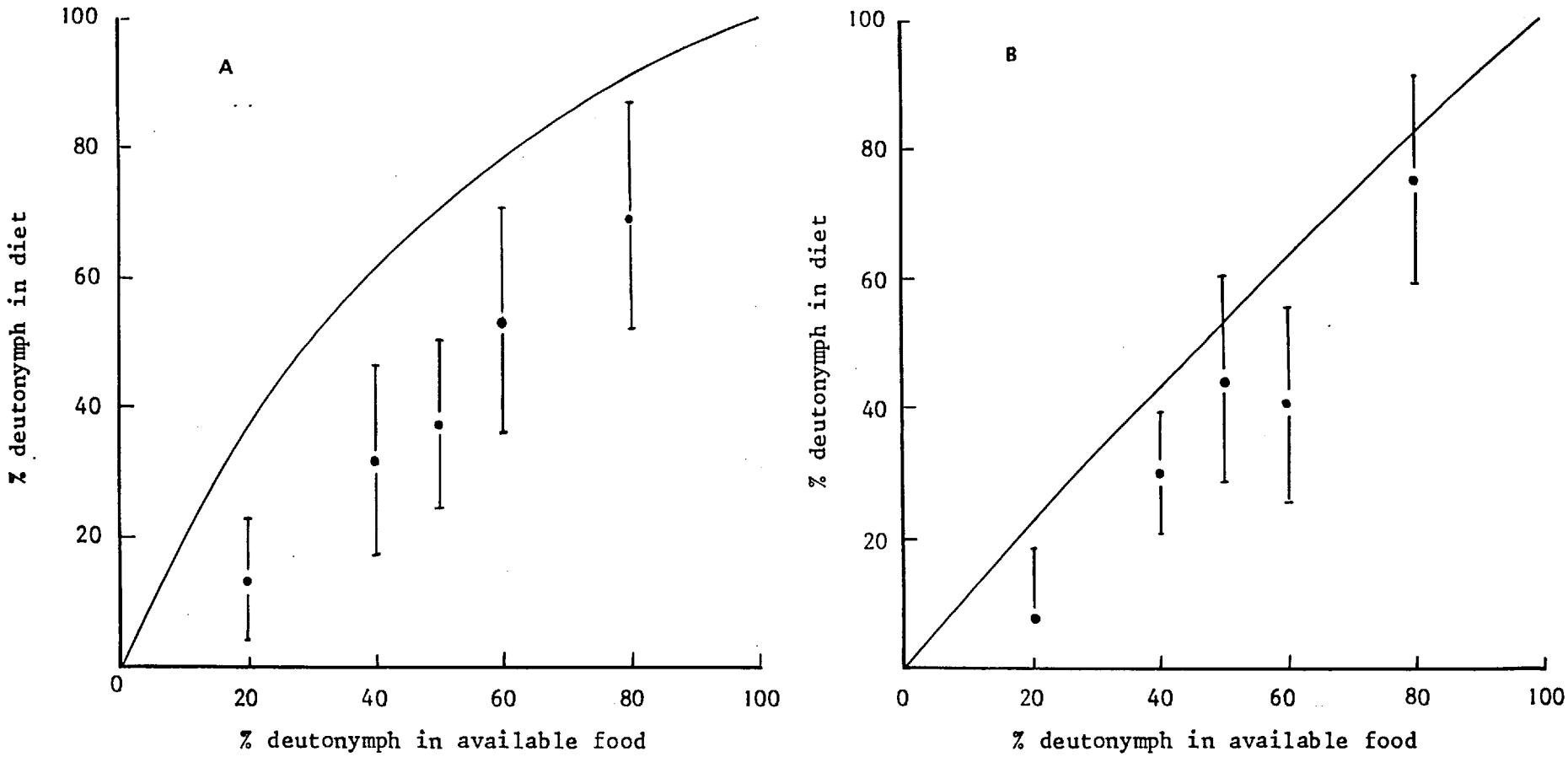


Fig.4.9 The functional response of protonymph P. persimilis when exposed to combination of densities of two prey stages. 95% confidence limits shown. (Curves fitted by the equation of Lawton et al (1974).)

A - Eggs and deutonymphs of T. urticae
B - Larvae and deutonymphs of T. urticae

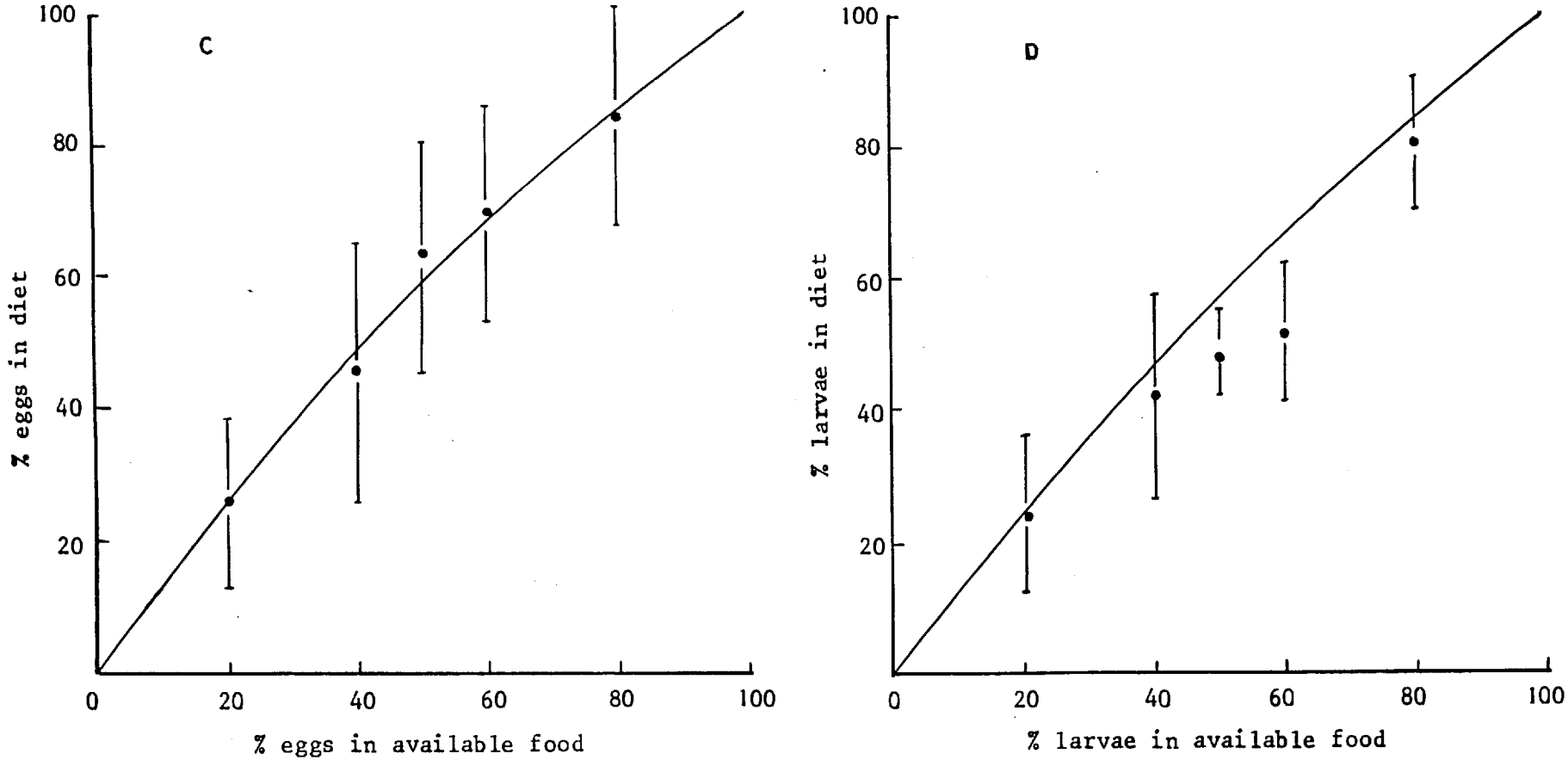


Fig.4.9 The functional response of deutonymph P. persimilis when exposed to combination of densities of two prey stages. 95% confidence limits shown. (Curves fitted by the equation of Lawton et al (1974).)

C - Eggs and deutonymphs of T. urticae
D - Larvae and deutonymphs of T. urticae

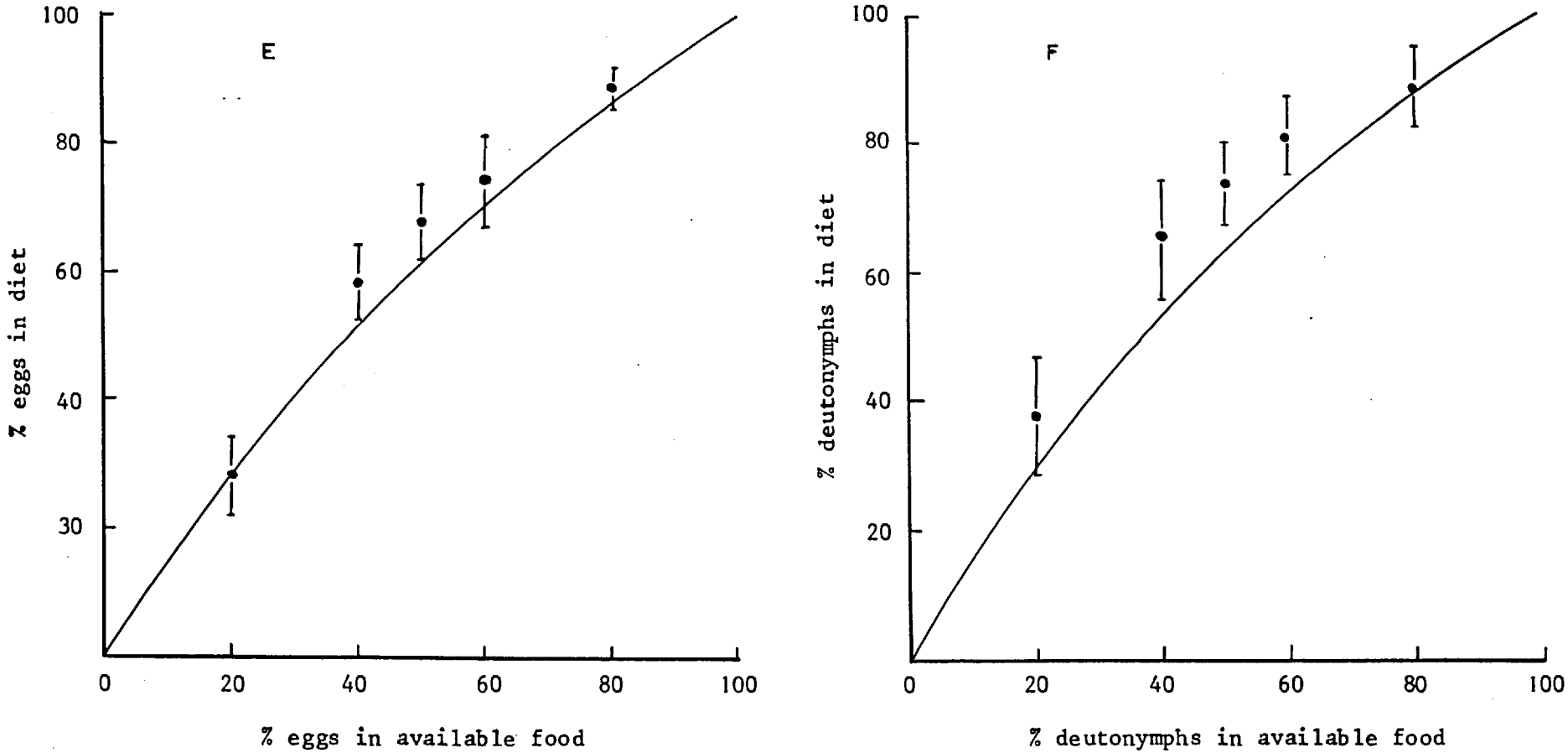


Fig.4.9 The functional response of adult female P. persimilis when exposed to combination of densities of two prey stages. 95% confidence limits shown. (Curves fitted by the equation of Lawton et al 1974).)

E - Eggs and deutonymphs of T. urticae
F - Larvae and deutonymphs of T. urticae

ment. Since there was no difference in the two sets of training the data were finally pooled together to make 20 replicates in each set of experiments. Santos (1976) also reported on unsuccessful attempts on training in the predatory mite, Zetzellia mali.

The observed results conform to the predicted responses only in the case of the deutonymph predator with eggs and deutonymph prey (Figure 4.9D). In the remainder the observed results do not conform to prediction but show a definite change in preference for one of the two-prey stages. Therefore, for the protonymph, the deutonymph (except the case mentioned above) and the adult predators, one or both the search-rates are seemingly changed in the presence of both prey compared with each one presented separately. This could happen either from the behaviour of the prey, the predator or both (Murdoch 1969; Lawton, Beddington & Bonser 1974). In no case was any sign of switching observed.

As mentioned earlier P. persimilis detect their prey by contact, mostly through the first pair of legs. Therefore, the larger the predator, the better the chances of contacting a given prey. Out of the three stages of prey considered, eggs are minute, larvae are very small and mobile, and deutonymphs are large and mobile. Deutonymph prey will therefore be the most frequently encountered prey by any stage of the predator but, due to its size, it is the most likely to escape attack, especially from smaller stage of the predator. The small larvae are difficult to detect but comparatively easier to attack than a deutonymph. Eggs are the most difficult to detect but once detected are the easiest to attack.

Once a prey is encountered in a mixture, the decision to attack is probably dependent on the palatability and 'reward rates' from the prey. For example, Burnett (1971), working with predatory mite Amblysieus fallacis (Garman) and eggs of T. urticae, found that the degree of development of the eggs can apparently influence discrimination by the adult female

predators. In this instance they preferred eggs less than 24-hours old.

Higher T_h perhaps indicates that eggs of T. urticae have a higher nutritive value than larvae. A deutonymph prey could have a high food value but the net energy return when subduing and killing is considered may well be less than that for eggs.

In the results obtained in the present study, the protonymph predators seem to have a higher preference for prey eggs (Figure 4.9A) in an egg-deytonymph prey mixture, deviating away from the predicted preference for deytonymphs. This is to be expected if the above explanation of relative profitabilities is correct. With larvae and deutonymph prey, the predators have a preference for larvae instead of deutonymphs as predicted (Figure 4.9B). However, the preference shown for larva against deutonymphs is not so great as that shown for eggs when mixed with deutonymphs. This may again reflect the relative profitabilities of the two-prey types presented.

With deutonymph predators, the results obtained for mixtures of eggs and deutonymph prey correspond well to the predicted curve from equation 4.7. This shows that there is no change in a^1 for the two-prey stages when presented in a mixture (Figure 4.9C). But with larvae and deutonymph prey, the predicted slight preference for larvae has disappeared (Figure 4.9D) and the results show no signs of any discrimination between the two-prey types. Deutonymph predators being much bigger than protonymph predators, should be able to attack and overcome deutonymph prey with relative ease.

In the case of adult female predators there is a well marked preference for prey eggs when eggs and deutonymphs are offered together (Figure 4.9E). The preference for eggs is even slightly greater than that predicted from equation 4.7. Here, too, the predator is taking in preference the comparatively more rewarding eggs rather than the deutonymphs.

However, when deutonymphs are presented with larvae, it is the deutonymphs that are preferred, and more so than predicted. The observed points lie above the predicted line indicating an increased preference (Figure 4.9F). This might result from the larvae being the least profitable of all the stages of prey considered, and perhaps because they are also relatively the least palatable.

The results reported here agree with those reported by Awan (1974) and Takafuji & Chant (1976) who also observed that all the predatory stages of P. persimilis fed preferentially on eggs of T. urticae. Similar results were reported by Burnett (1971) who studied selective feeding on various stages of T. urticae by Amblyseius fallacis.

CHAPTER 5

MUTUAL INTERFERENCE

5.1 Introduction

The presence of mutual interference between predators and parasitoids can lead to a reduction in their searching efficiency, *a* (Hassell & Varley 1969; Hassell 1976). It is likely that this results from an increase in the frequency of encounters between searching predators as their density increases, in turn leading to an increase in various time-wasting behavioural activities. Most of the information on this comes from laboratory observations on insect parasitoids (Hassell 1971a, b; Rogers 1970). For instance, Hassell (1971a) observed that encounters between the searching parasitoids, *Nemeritis canescens*, either led them to stop searching for sometime or emigrate from the area of encounter. Among predators, Kuchlein (1966) has shown the predatory mite, *Typhlodromus longipilus* Nesbitt to have an increased tendency to migrate from the experimental arena as its density is increased.

Much of the published data showing a decline in the searching efficiency of parasites as their density increases is adequately described by the simple inductive model of Hassell & Varley (1969):

$$\log a = \log Q - m \log P,$$

$$\text{or} \quad a = QP^{-m}$$

where *a* is the "area of discovery"

Q the "quest constant", the value of *a* when the parasite density *P* is one, and

m the "mutual interference constant".

Alternatively, instead of using the area of discovery the relationship

may be expressed in terms of the search-rate (a^1), either on the basis of the experimental duration (T) or the actual searching time (T_s) of the predators.

Thus,

$$\log\ a^1 = \log Q^1 - m \log P.$$

Ideally, a^1 should be calculated from

$$a^1 = \frac{1}{P(T-T_h Na)} \ln \left(\frac{N}{N-Na} \right),$$

so allowing for the reduction in T due to handling time, $T_h Na$. This, requires, however, an independent estimate of T_h such as that available from the functional response experiments in Chapter 4. Using these values, however, in the above equation, occasionally led to negative values for T_s, the time available for search. It was decided therefore, to calculate a^1 in this chapter from the simpler expression

$$a^1 = \frac{1}{PT} \log_e \frac{N}{N-Na}$$

It is not possible to describe interference relationships of all types of predators by the linear model of Hassell & Varley (1969), since several of the relationships tend to be curvilinear. Subsequent models developed by Rogers and Hassell (1974) and Beddington (1975), which take into account a period of inactivity following each encounter, predict such curvilinear relationships.

The experiments described in this chapter were conducted with the aim of determining the nature of the interference relationship, either linear or curvilinear, for the different predatory stages, protonymph, deutonymph, and adult females of *P. persimilis*. Two series of experiments were carried out:

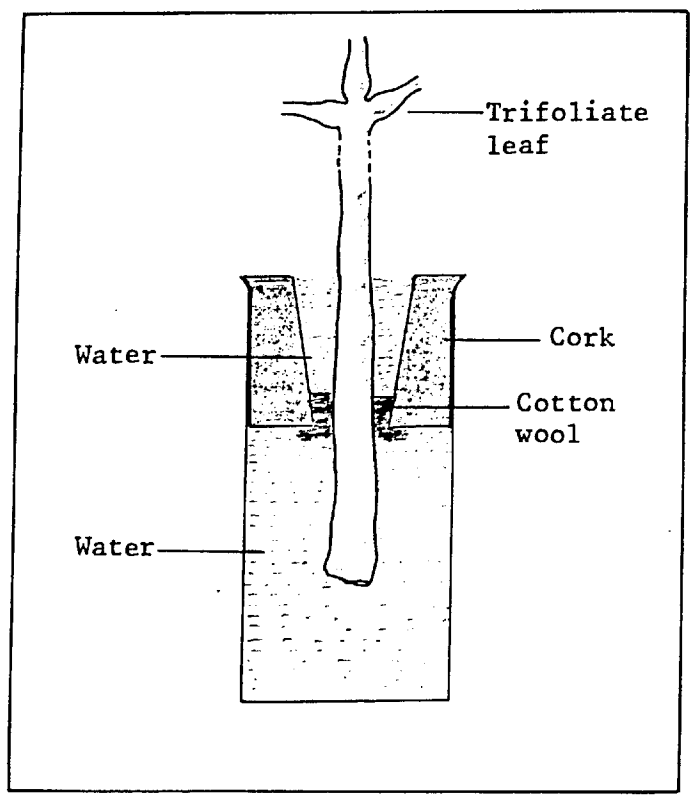


Fig. 5.1 Method used to study the mutual interference between individuals of P. persimilis on a trifoliate bean leaf

Series I, on a 32 sq.cm bean leaf-disc kept on a moist sponge, and Series II, on a trifoliate bean leaf.

5.2 Materials and methods

Series I

The materials, the methods and the environmental conditions used in this series of experiments were just the same as those described in Chapter 4 for the functional response experiment, except that exactly double the size of bean leaf-discs were used (i.e. 32 cm^2).

The experiments were carried out with young unsexed larvae and young female deutonymphs of T. urticae as the prey, and unsexed protonymphs and deutonymphs and adult females of P. persimilis as the predators. Both prey and predators were taken from cultures raised under the conditions described in Chapter 3. The predators were standardised in the same way as described for the functional response experiments.

The density of prey used in all the experiments was 150. The prey were counted and placed on the leaf-discs with a soft sable hair brush and then examined carefully for any injured which were replaced before introducing the predators. The collection of protonymphs, deutonymphs and female predators was done in an identical way to that for functional response experiments. The protonymphs and deutonymphs were unfed and the adult females which were 6-7 days old from their last moult were well fed at the start of the experiment. The prey on the leaf-discs were exposed to each of the different densities (1, 2, 4, 8 and 16 and in some 32), of each stage of the predator for 24-hours. At the end of the experiment the dried carcasses of the prey were counted to estimate the number of prey killed. The experiments were replicated five times.

Another set of experiment with the protonymph of P. persimilis and larvae of T. urticae were conducted for an eight-hour period and was repli-

cated only four times.

Series II

This experiment was conducted on a trifoliate bean leaf held in a glass specimen tube as shown in Figure 5.1. The leaf was cut, with about 15 cm of stem, under water to prevent wilting of the leaflets. The three leaflets were then trimmed, each to an area of 32 cm^2 per surface. The stem of the leaf was then passed through a conical hole made in the centre of a cork which fitted tightly into the specimen tube, 2.4 cm diameter and 7.5 cm high, filled with water. This arrangement ensured a reservoir of water around the stem which acted as a barrier against the emigration of predators. The prey were placed on the under surface of one of the three leaflets, around the petiole of which a collar of wet cotton wool was kept to prevent them dispersing prior to settling down. Only the female deutonymphs of T. urticae and adult female P. persimilis were used in this experiment. The density of prey used was 150 and the series of densities of predators used were 1, 2, 4, 8, 16 and 32. At the end of the experiment (i.e. 24-hours after the introduction of the predators) the leaflets and the stem were cut and dead and live prey were counted under a binocular microscope. The experiments were conducted under the same conditions as in the previous experiments and were replicated five times.

5.3 Method of analysis

For each set of experiments the search-rate (a^1) was plotted against the predator density (P) on the X axis, both on logarithmic scale. The points were fitted to a linear regression by the least square method, giving the slope (m) and intercept on Y (Q^1).

5.4 Results

The results are summarised in Table 5.1 and Figures 5.2 and 5.3. The linear relationships of log a^1 to log P are significantly described at the 1% level only in experiments 5, 6 and 7 (Table 5.1).

In the experiment where three leaflets were used, it was observed that

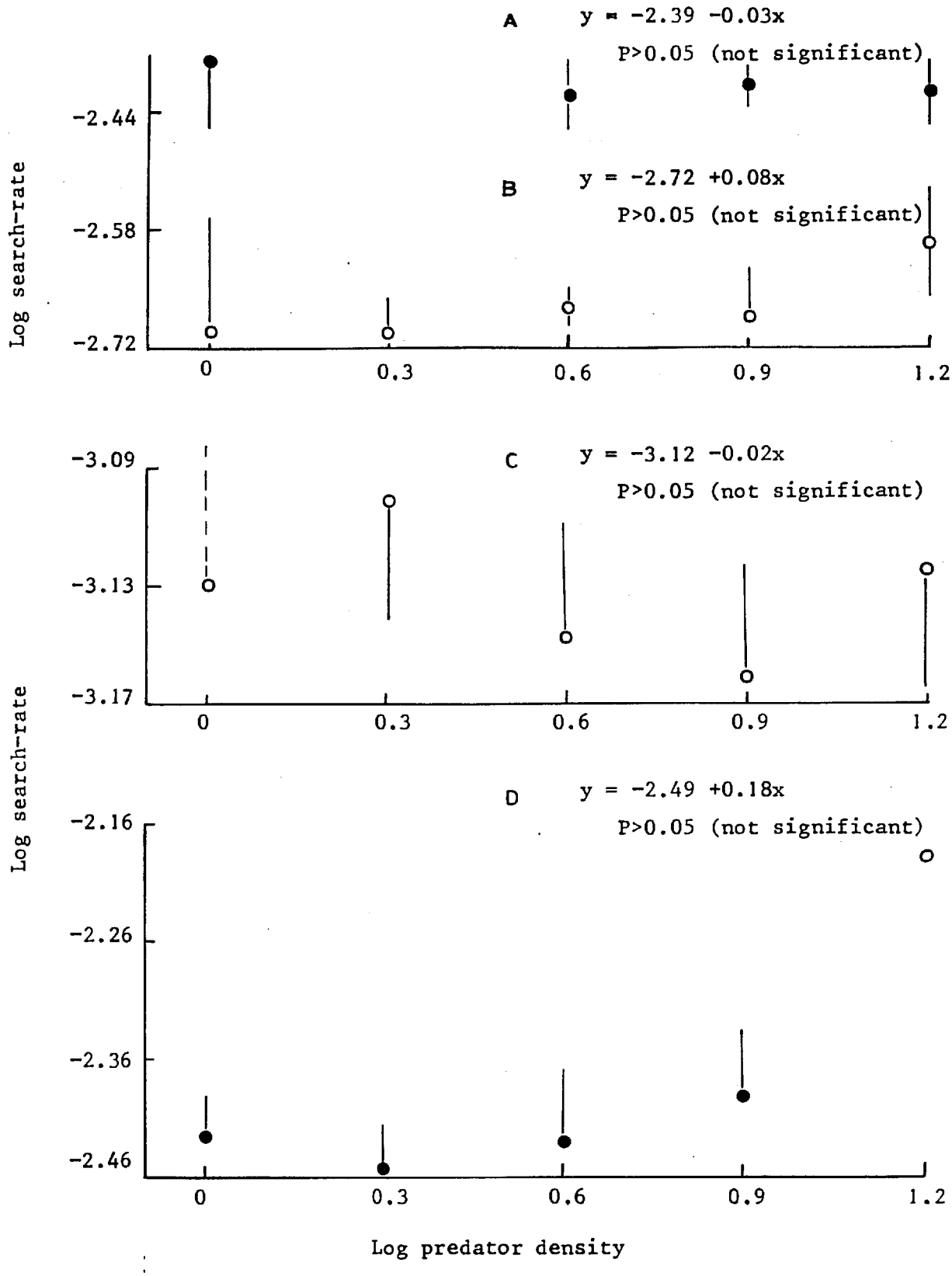


Fig. 5.2 A, B, C & D Relationships between log search-rate (a^1) and log predator density. (95% confidence limits shown). All the experiments conducted on 32cm^2 bean leaf discs.

A—Protonymphs of P. persimilis with larvae of T. urticae (8 hour experiment)
B—Protonymphs of P. persimilis with larvae of T. urticae (24 hour experiment)
C—Protonymphs of P. persimilis with female deutonymphs of T. urticae (24 hour experiment)
D—Deutonymphs of P. persimilis with larvae of T. urticae (24 hour experiment)

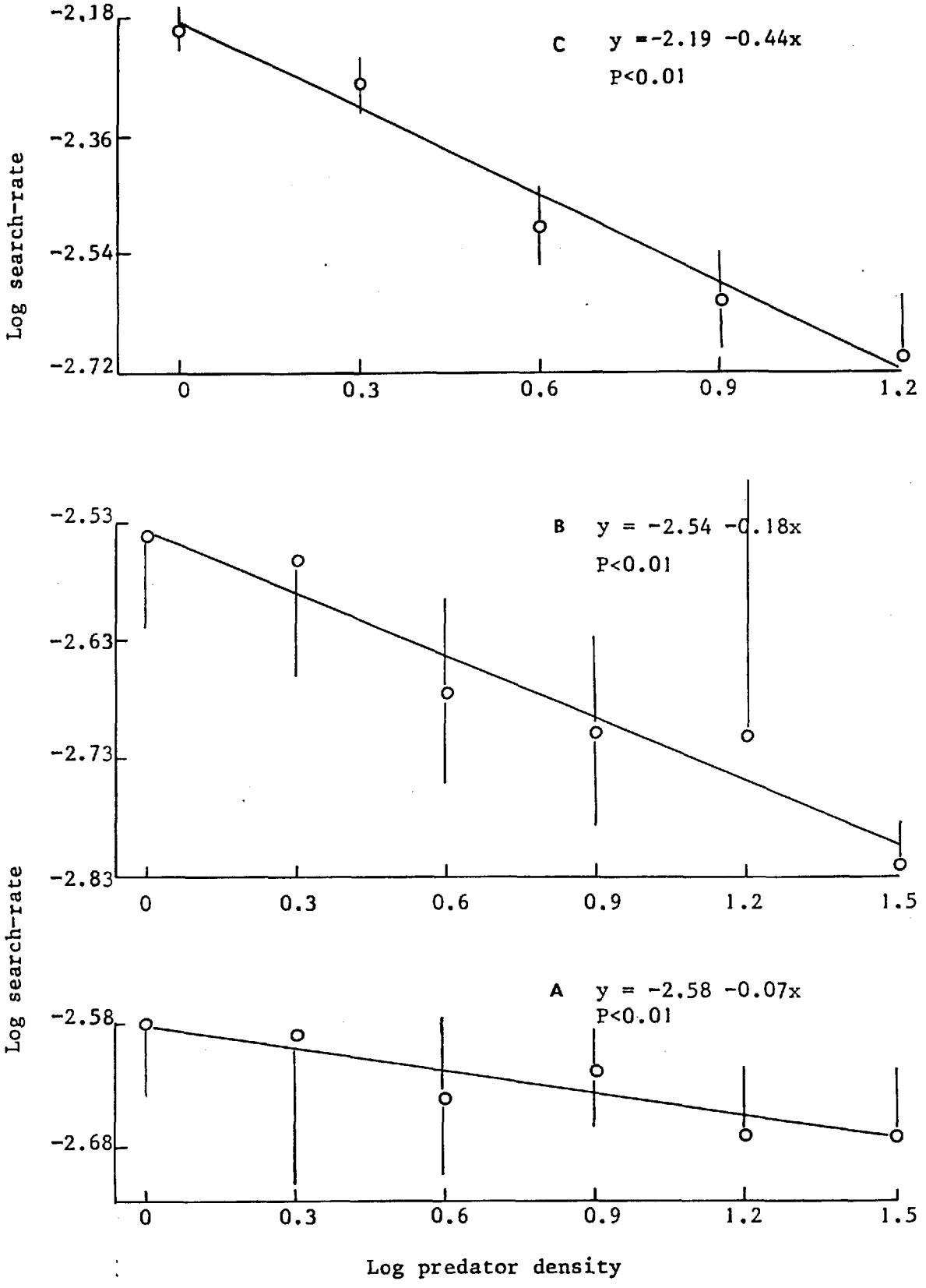


Fig. 5.3 A, B & C Relationships between log search-rate (a^1) and log predator density. (95% confidence limits shown.)

A– Adult females of P. persimilis with female deutonymphs of T. urticae on 32cm^2 bean leaf discs

B– Adult females of P. persimilis on a trifoliate bean leaf with only one leaflet containing female deutonymphs of T. urticae. Each leaflet was trimmed to 32cm^2 per surface

C– Adult females of P. persimilis with larvae of T. urticae on 32cm^2 bean leaf discs.

All the experiments conducted for 24 hours

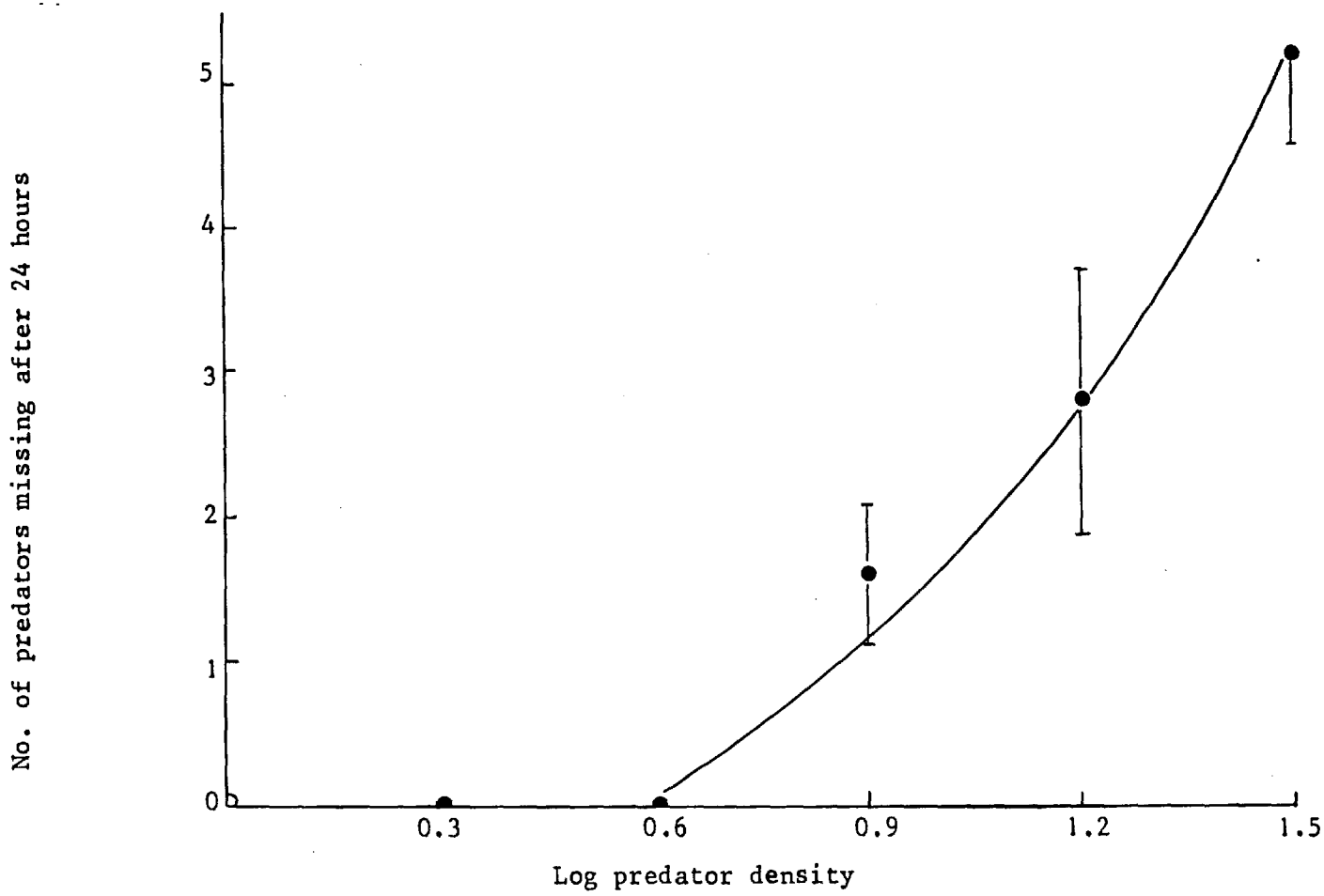


Fig. 5.4 Number of predators missing at the end of 24 hours from three 32cm^2 bean leaflets with only one containing 150 prey (±S.E. of 5 replicates shown.) (Fitted by eye.)

TABLE 5.1 - Summary of the results of the experiments on mutual interference.

Expt. No.	Expt. System	Stage of predator and densities	Stage of prey and densities	log Q^1 ($32cm^2/hr.$)	m	No. of replicates	F Value	Probability	Experimental duration
1	32 sq.cm bean leaf disc	Protonymph (1, 2, 4, 8 and 16)	Larva (150)	-2.388	-0.029	4	2.834	>0.05 n.s.	8-hours
2	32 sq.cm bean leaf disc	Protonymph (1, 2, 4, 8 and 16)	Larva (150)	-2.718	0.075	5	6.007	>0.05 n.s.	24-hours
3	32 sq.cm bean leaf disc	Protonymph (1, 2, 4 8 and 16)	Female deutonymph (150)	-3.124	-0.015	4	0.365	>0.05	24-hours
4	32 sq.cm bean leaf disc	Deutonymph (1, 2, 4, 8 and 16)	Larva (150)	-2.487	0.178	4	4.81	>0.05 n.s.	24-hours
5	32 sq.cm bean leaf disc	Adult Female (1, 2, 4, 8 and 16)	Larva (150)	-2.187	-0.443	5	119.4	<0.01	24-hours
6	32 sq.cm bean leaf disc	Adult female (1, 2, 4, 8, 16 and 32	Female deutonymph (150)	-2.538	-0.178	6	55.189	<0.01	24-hours
7	Three 32 sq.cm bean leaves	Adult female (1, 2, 4, 8, 16 and 32	Female deutonymph (150)	-2.581	-0.067	5	25.478	<0.01	24-hours

there was a progressive increase in the number of predators missing at the end of the experiment from the density eight onwards (Figure 5.4). Except for one or two replicates the prey were found to have remained on the under surface of the same leaflet onto which they were originally placed.

5.5 Discussion

There was no significant relationships between log a^1 and log P for the immature stages of the predator (protonymphs and deutonymphs) (Table 5.1 and Figures 5.2 A, B, C and D). It appears, therefore, that the behaviour of the immature stages of *P. persimilis* is not affected by the presence of other individuals of the same stage.

In all the three experiments with adult female predators, log a^1 and log P showed an inverse linear relationship, all significant at the 1% level (Figures 5.3 A, B and C). None of the relationships showed any tendency to be curvilinear. It seems, therefore, that unlike the immature stages, adult females of *P. persimilis* tend to show mutual interference as their densities increase.

When the mutual interference constants of the two experimental systems were compared, both with deutonymph prey, m in the three leaflet experiment gave a lower value ($m = 0.067$) than that on the leaf-discs ($m = 0.178$). The likely explanation for this is that the three leaflet system presented six times the surface area for the same number of predators and therefore must have considerably reduced the frequency of mutual encounters.

As shown in Figure 5.4, using the three leaflet system resulted in some of the predators emigrating from the leaflets, particularly at the higher predator densities. At the same time the predators at those higher densities were seen to move around all over the three leaflets, whereas with densities 1, 2 and 4, the predators all remained on the infested

leaf, almost from the start of the experiment. A likely explanation for this behaviour is that, the initial aggregation of the predators at high densities on the infested leaf, led to an increased frequency of encounters, so inducing them to disperse. These observations are in accord with those made by Kuchlein (1966) on the predatory mite, Typhlodromus longipilus, described above. Akinlosotu (1973) also observed a similar tendency to disperse following interference in Diaeretiella rapae McIntosh a braconid parasite of cabbage aphids (Brevicoryne brassicae L.)

Under conditions of very low prey densities, two starved immatures or even two adult females of P. persimilis could be seen sharing the same prey, especially when the prey was of a larger size. Therefore, any experiments done with starved predators and run for very short period of time could tend to show no interference even between adult P. perimilis. Such were the results obtained by Yao (1976 - pers. comm.) in his experiments with adult P. persimilis and males of T. urticae. The series of experiments reported here were run with well fed adult females and for a period of 24-hours.

The presence of mutual interference between parasitoids was directly observed by Hassell (1971a), Rogers (1970), Akinlosotu (1973) and Chua (1975). Hassell (1971a) working with Nemeritis canescens the parasitoids of larvae of the almond moth Ephestia cautella (Walk.), listed a number of possible behavioural changes following encounters between the parasitoids: either one or both parasitoids may

(i) fly off the container,

(ii) walk off the container,

(iii) if probing for hosts, cease to do so and start cleaning, walking or resting on the container, or

(iv) show no obvious change in behaviour.

Similar behavioural changes were observed for the same parasite by Rogers (1970) when it encountered an already parasitised host.

The mutual interference between adult females of P. persimilis reported in this chapter probably resulted more from the predators trying to emigrate following encounters than by any other behavioural changes. Detail observations are necessary in this respect before drawing any definite conclusions on the behavioural mechanism underlying interference.

CHAPTER 6

THE RESPONSE TO PREY DISTRIBUTION

6.1 Introduction

It is a common observation that the distribution of phytophagous species is not uniform on or between their host plants, but have a clumped spatial distribution resulting from certain areas or units being preferred for food or shelter. Although most of the methematical models for predator-prey interactions assume predators to search randomly for their prey, this is likely to be the exception rather than the rule. Many predators tend to spend more time in areas of high, rather than low, prey density, resulting in some degree of aggregation (Hassell 1966, 1968, 1971 a, b; Hassell & Rogers 1972; Hassell & May 1973, 1974). Several behaviours may be involved. There may, for instance, be some long range attraction of predators to a volatile chemical substance whose concentration is a function of prey density per unit area (eg. Ullyett 1953; Wood *et al*. 1968; Mitchell & Mau 1971; Sternlicht 1973; Wood 1973). Aggregation of predators also could occur by predators remaining for longer periods of time where their reward rate is higher. This, for example could be achieved by increased turning behaviour or reduced speed of movement after successfully capturing a prey which lead them to spend more time in the vicinity where a prey was found (Fleschner 1950; Dixon 1959; Murdie & Hassell 1973; Evans 1973). Hassell & May (1973) and Hassell *et al*. (1976) give a review of these factors leading to aggregation in various predators and parasitiods. Despite the widespread occurrence of such aggregative behaviour it has been included in only a few predator-prey models (Royama 1971; Hassell & Rogers 1972; Hassell & May 1973, 1974).

One outcome of the aggregative behaviour of the predators is to lead to an increased rate of contacts between predators, which could in turn

result in interference. Under natural conditions, the likely result is some density dependent dispersal which may increase the overall efficiency of the average predator. The selective value is therefore one of counteracting the tendency to over-exploit high prey density areas that results from aggregative behaviour. Within a laboratory experiment, however, where opportunity for dispersal is limited, the net result is more likely to be one of reduced efficiency, detected as an interference relationship. A classic example showing the inter-relationship between aggregation and interference comes from the work of Hassell (1971a) on Nemeritis canescens, a parasite of Ephestia cautella.

The methods, both direct and indirect, used by a number of workers to evaluate aggregative responses of predators are discussed by Hassell & May (1974). In direct methods, the time spent per predator per unit area, or the number of predators searching at one time per unit area is plotted against different prey densities. In the latter method a series of simple counts are made in which the number of predators per unit area at a given time is recorded, and from which the average density or the proportion of total predators at different prey densities is obtained (Goss-Custard 1970, 1977; Hassell 1971a; Smith & Dawkins 1971; Noyes 1974). As an indirect method, the evidence of percentage predation in different prey areas could be compared (Hassell 1968, 1971a).

Hassell & May (1974) suggested that the aggregative response has an idealised form in which the predators do not distinguish between patches which contain very high prey densities, nor those which contain very low prey densities, but that patches of intermediate density are the subjects of marked discrimination. Therefore, if the time spent per patch by a predator, or predator density per unit area is plotted against the prey density a sigmoid response would be obtained. A model developed by Murdoch & Oaten (1975) also showed this response to be slightly sigmoid. The published examples of aggregative responses are considered as lying

on different parts of this ideal response (see review by Hassell et al. 1976). The only published example of a complete sigmoid response comes from the field observations on the distribution of red-shanks on a sea shore (Goss-Custard 1970).

The experiments reported in this chapter are conducted with the aim of studying the aggregative responses of different densities of P. persimilis to an uneven spatial distribution of its prey, T. urticae, and also to determine the extent of any interference resulting from this aggregation.

6.2 Materials and methods

The experimental design consisted of five bean leaflets, each trimmed to 32 sq.cm per surface, radially arranged, as far as possible on the same horizontal plane. To obtain this arrangement, two trifoliate bean leaves with 15 cm of stem were tied together with a fine thread. The design of the rest of the experiment and the method of introducing the prey were identical with the series II experiment described in the preceeding chapter.

Series I

One of the five bean leaves, randomly selected was infested on the under surface with 150 female deutonymphs of T. urticae. The adult female predators of P. persimilis used in the experiments were taken from a well fed culture and they were all in the ovipositional stage. The predators (either 1, 2, 4, 8 or 16 per experiment) were then relaesed onto the "stem" of the leaf cluster and so were allowed to find their own way onto the leaves. After an hour had elapsed, the leaves were then examined every hour and the presence of predators on different leaves was scored. The records were kept successively for the first eight hours and then for the last three hours in a twenty-four hour experiment, at the end of which the

leaflets were cut and examined under a binocular microscope for dead and live prey. The experiment was replicated five times.

Series II

The experimental universe was the same as that used in series I. In this case, however, the five leaflets were randomly infested with five different densities (0, 20, 40, 80 and 160) of femles deutonymphs of T. urticae. The same range of predator densities (1 to 16) was employed which again were introduced onto the stem of the leaf cluster. The experiment was replicated five times with the same observations and records made as previously.

All experiments were conducted in a controlled temperature room at 20°C, 55-65% R.H., and a 16-hour light regime.

6.3 Method of analysis

Series I

(a) The percentage predators seen on the infested leaf at each hour is plotted against each of the first eight hours.

(b) The average of the percentage of predators seen on the infested leaf during the first eight hours and also during the last three hours of the 24-hour experiment are plotted against different predator densities.

(c) The log. search-rate (a^1) per predator is plotted against the log. predator density (cf. Chapter 5).

Series II

(d) The average of the percentage of predators seen in each of the prey densities (0, 20, 40, 80 and 160) during the

first seven hours and last four hours of the 24-hour experiment are plotted against different prey densities.

(e) The percentage distribution of the predators at the 24th hour is plotted against the different prey densities.

(f) The search-rate per predator for each predator density was separately calculated on the basis of average number of predators found in each prey patch during the experimental period and the number of prey killed in each of them. Then the log mean of these values (a^1) where,

$$a^1 = \frac{1}{4} \sum_{i=1}^{4} \frac{1}{P_i T} \log_e \frac{Ni}{N_i - NA_i} \qquad (6.1)$$

(Ni is the density of prey and N_{Ai} is the number of prey killed in patch i) is plotted against log predator density (cf. Chapter 5).

(g) The proportion of total predators (βi) calculated on the basis of the average number of predators found in each prey patch, is plotted against the proportion of total prey in each of the corresponding prey patches.

The observed data is described using a model derived by Hassell & May (1973).

$$\beta_i = C\alpha_i^{\mu} \qquad (6.2)$$

(or $\log \beta_i = \log C + \mu \log \alpha_i$)

where, β_i and α_i are the proportion of total predators and prey found in ith unit area, respectively, C a normalisation constant such that the β_i values sum to

unity, and $\underline{\mu}$ the "Predator aggregation index" describing the distribution of predators relative to the prey. The values of $\underline{\mu}$ can vary from 0 to α. Thus when, $\mu = 0$, the same number of predators are found in all prey patches; $\mu = 1$, the same proportion of total predator and prey are found per unit area; and $\mu > 1$ or α, there is a differential aggregation of predators in highest prey areas.

6.4 Results

The results of the experiments where only a single prey density is used are presented graphically in the Figures 6.1, 6.2, 6.3 and 6.4. In Figure 6.1 (A, B, C, D & E) this hourly distribution of the predators on the infested leaf for the firt successive eight hours are shown as a percentage of the total number of predators released on the leaves. Figure 6.2 A & B show the average percentage distribution of the predators during the first eight hours and the last three hours of the experiment, respectively. The extent of aggregation of the predators in the 8th and 24th hour are shown in Figure 6.3 A & B, respectively. In Figure 6.2 and Figure 6.3 the aggregative responses show a decline in the proportion of predators on the infested leaf as the total number of predators released increases in density. The curves are fitted by a linear regression.

The log search-rate of predators at different predator densities shows some indication of a negative linear relationship to log predator densities ($P<0.1$) as shown in Figure 6.6A, where it is described by the linear interference model of Hassell & Varley (1969).

Figures 6.4, 6.5 and 6.6B give the results of the experiments conducted with five bean leaves infested with five different densities of the prey. Figure 6.4 shows the pattern of distribution of each of the five different densities (1, 2, 4, 8 & 16) of the predator, expressed as a percentage of the total density, among the five different densities of

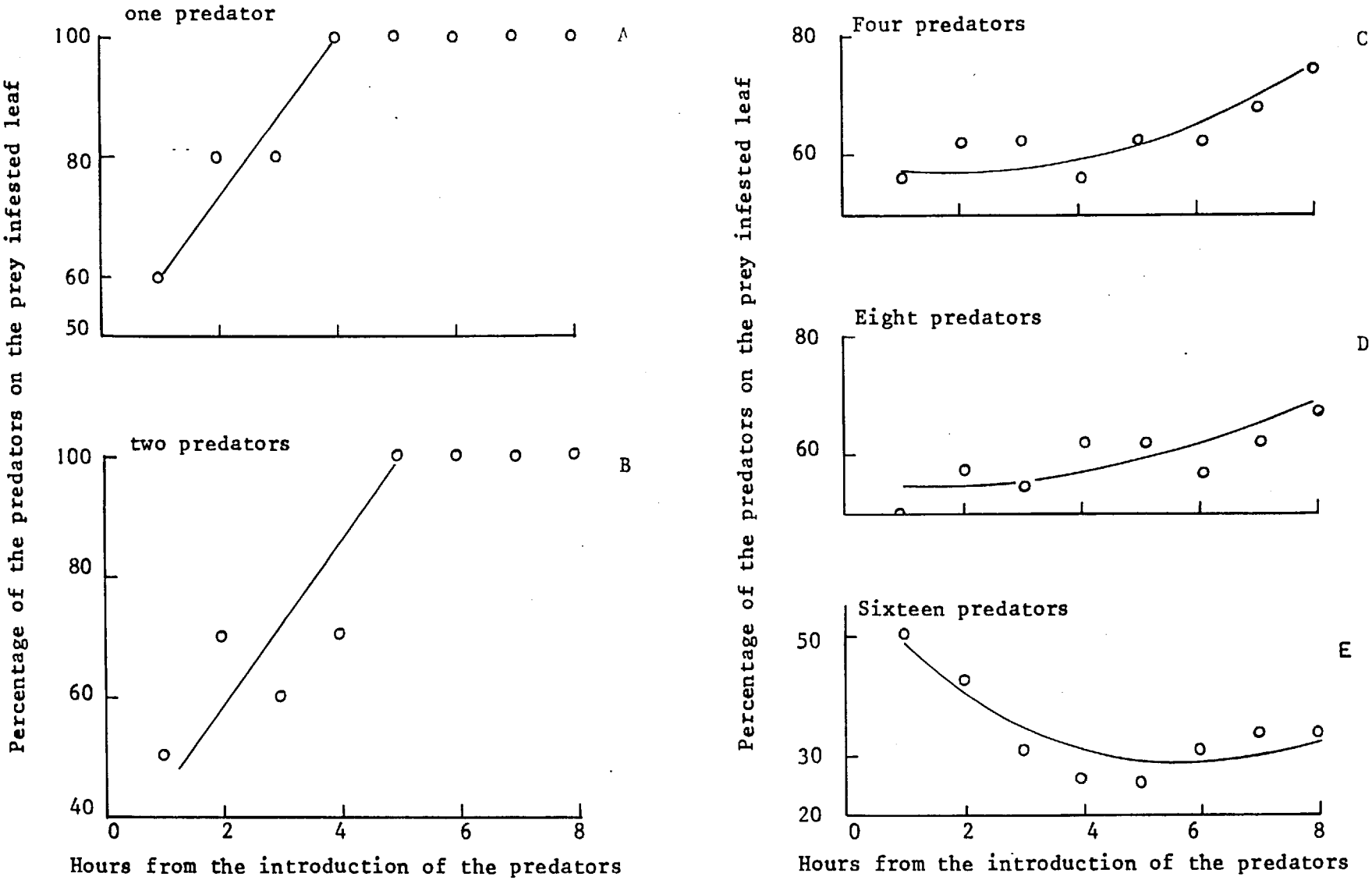


Fig.6.1 The behavioural responses of P. persimilis to its prey, T. urticae: Aggregation of the predators on the prey infested leaf during the first 8 hours. (Curves fitted by eye.)

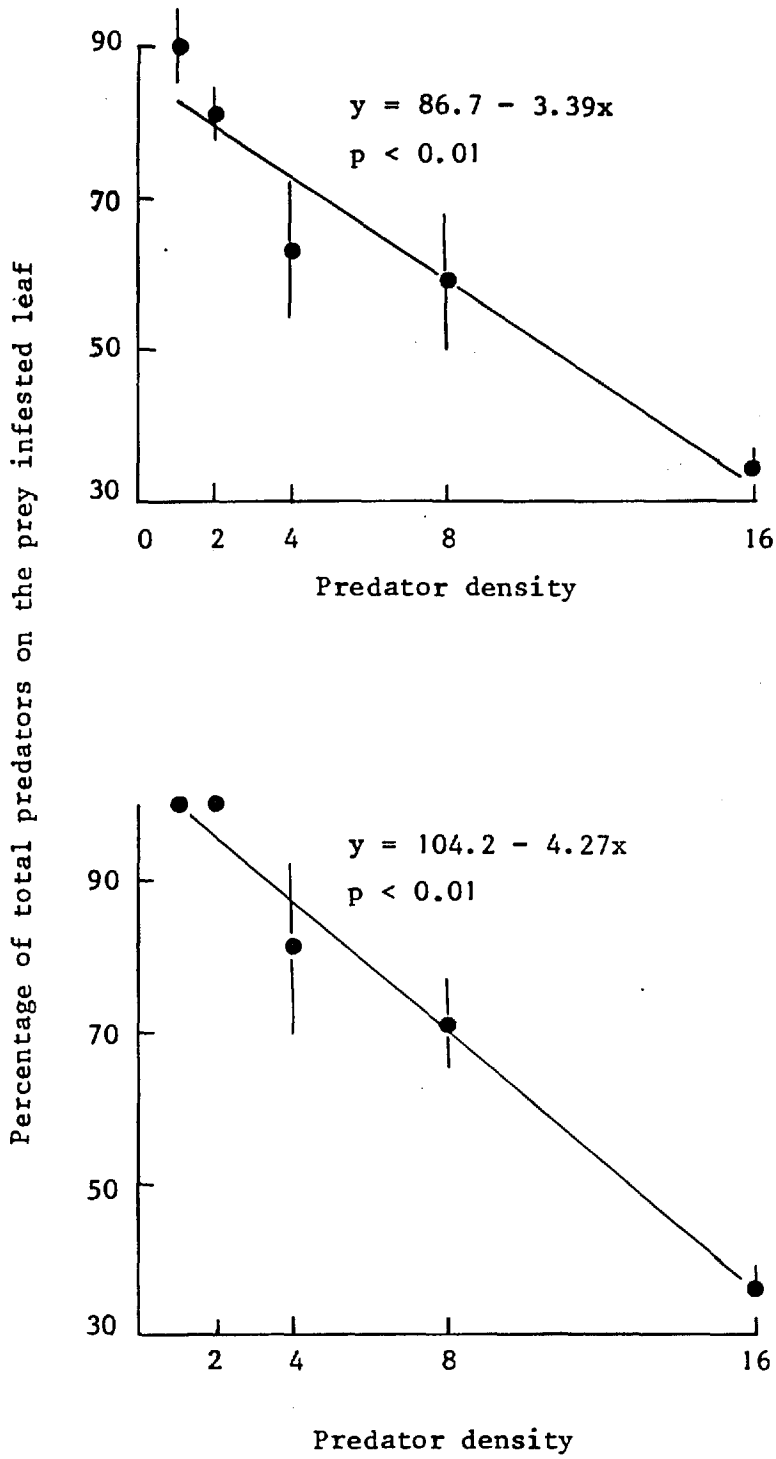


Fig.6.2 The behavioural responses of P. persimilis to its prey, T. urticae: Aggregation of the predators on the prey infested leaf. S.E. of 5 replicates shown. (Fitted by a linear regression.)

A— Average aggregation of first 8 hours.

B— Average aggregation of 22nd, 23rd and 24th hours.

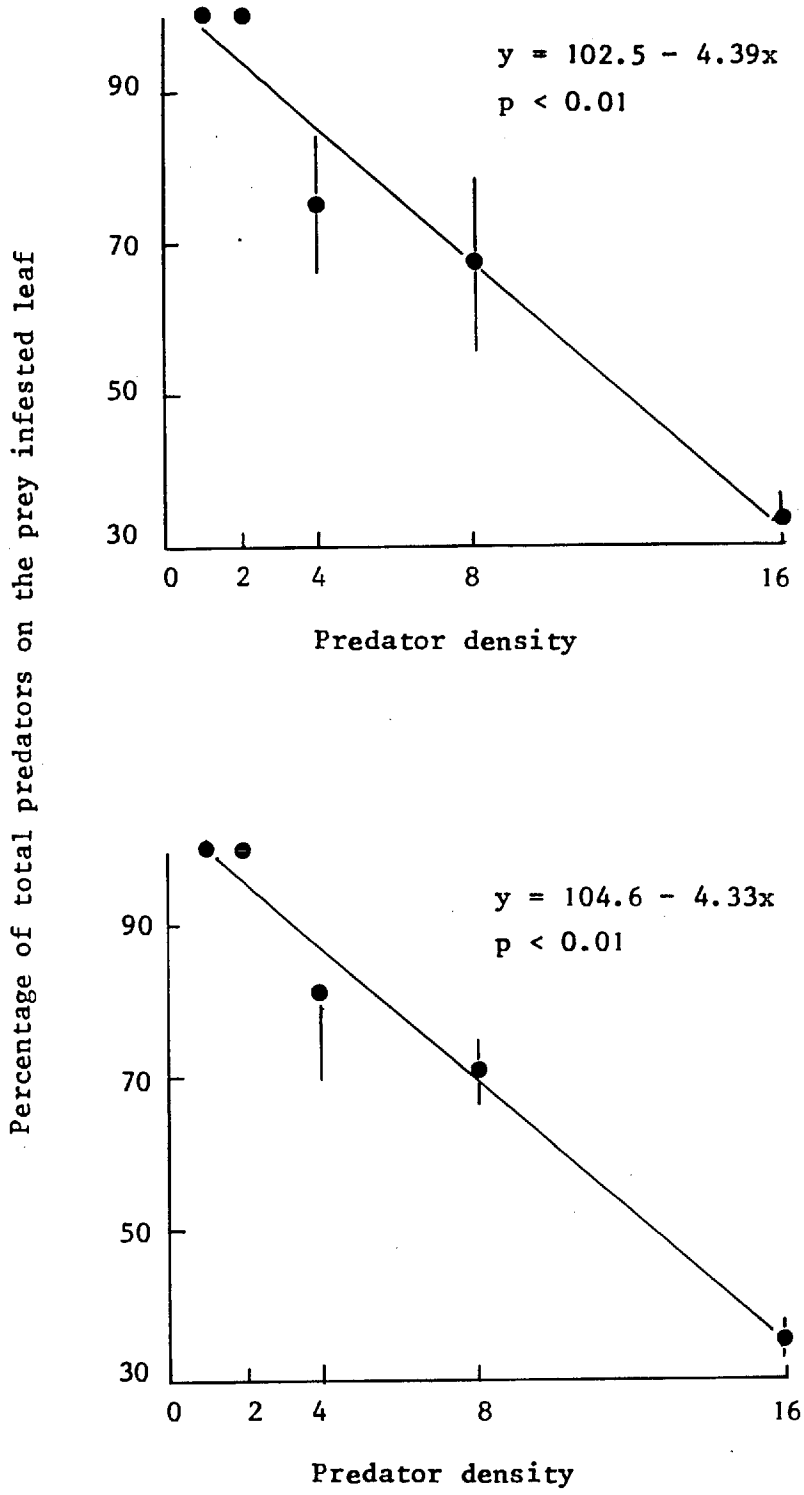


Fig.6.3 The behavioural responses of P. persimilis to its prey, T. urticae: Aggregation of the predators on the prey infested leaf. S.E. of 5 replicates shown. (Fitted by a linear regression.)

A — Aggregation during the 8th hour

B — Aggregation during the 24th hour

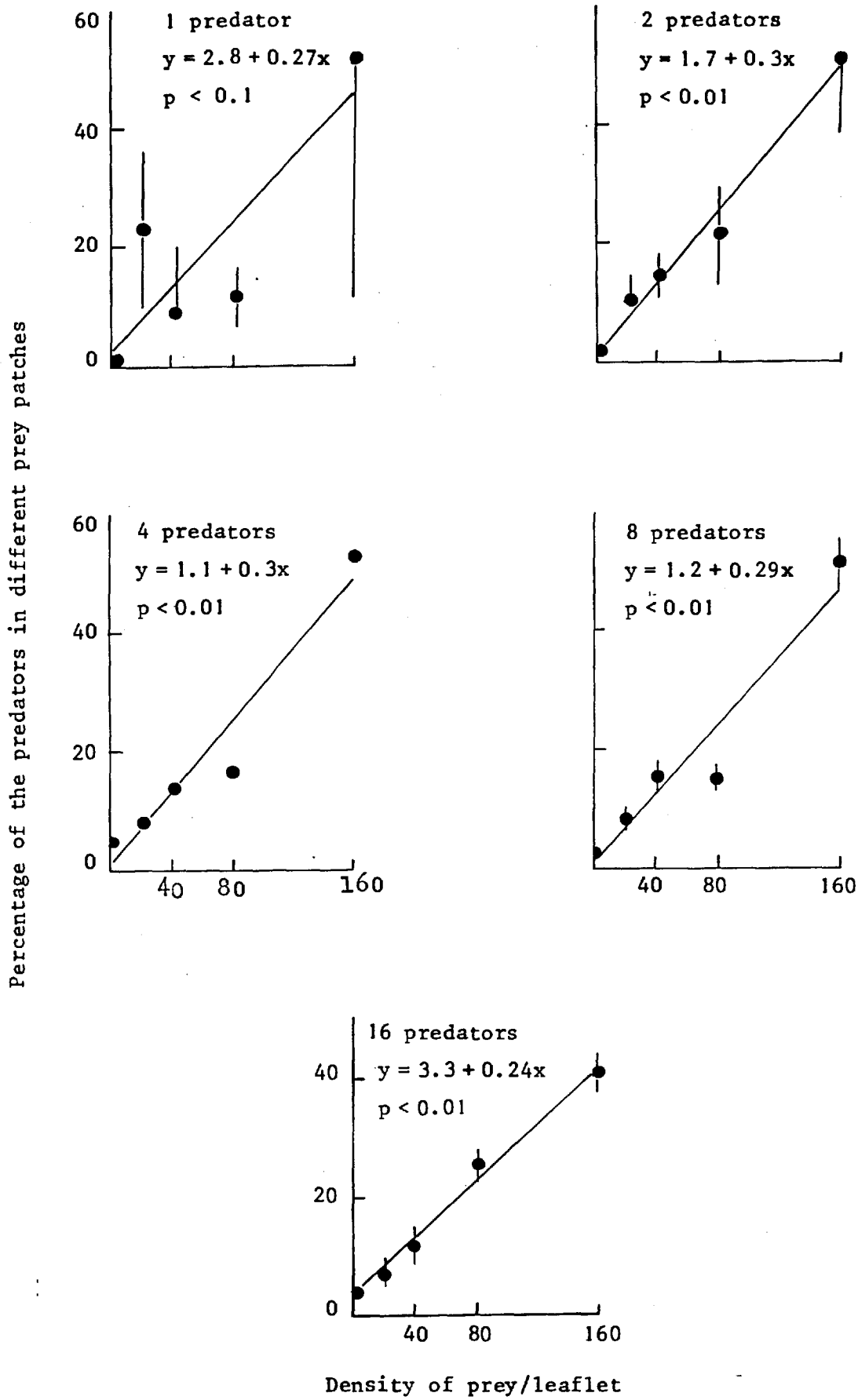


Fig.6.4A The behavioural responses of P. persimilis to an uneven distribution of its prey, T. urticae. Average of first 7 hours. S.E. of 5 replicates shown. (Curves fitted by a linear regression.)

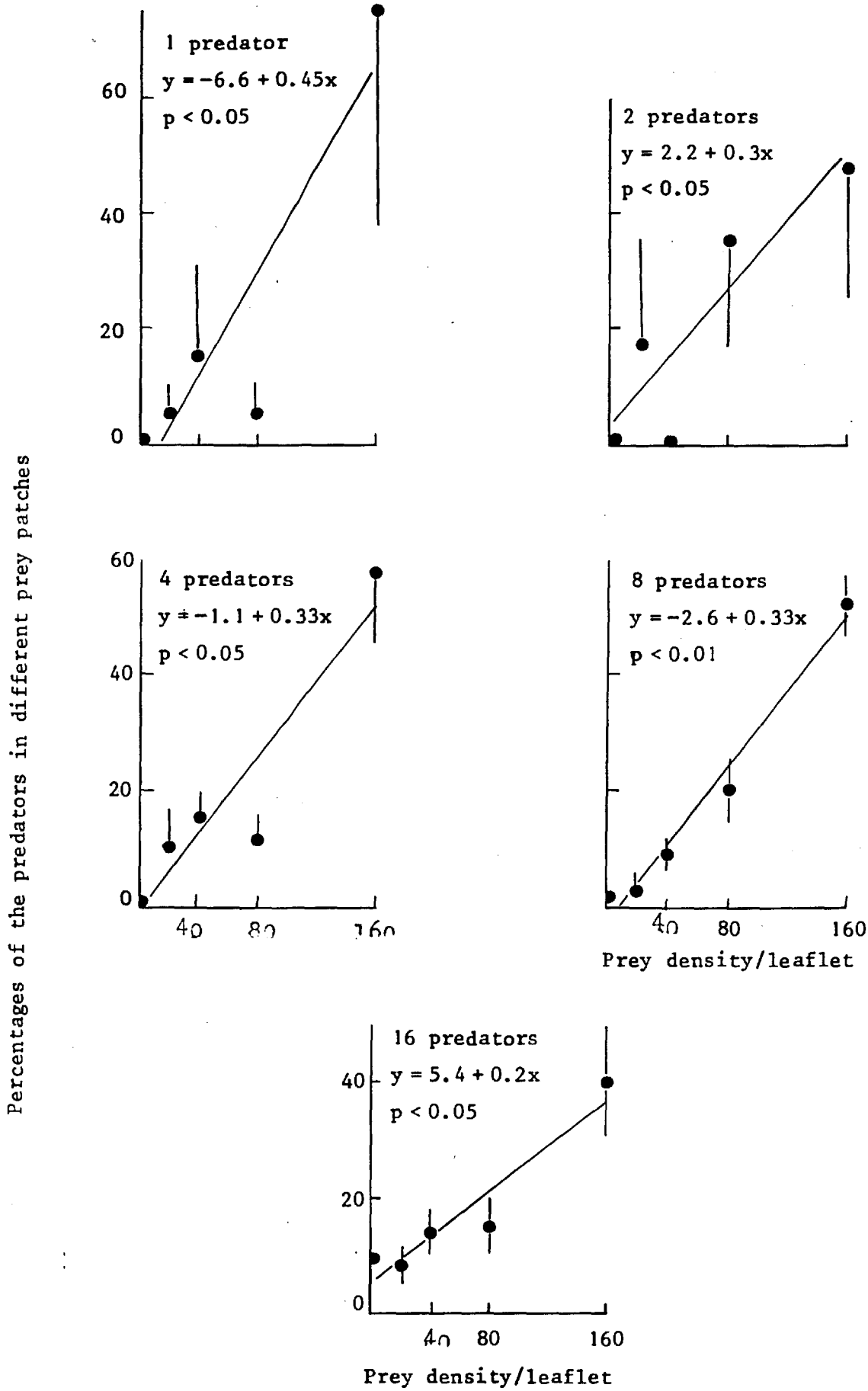


Fig.6.4B The behavioural responses of P. persimilis to an uneven distribution of its prey, T. urticae. Average of 21, 22, 23rd and 24th hours. S.E. of 5 replicates shown. (Curves fitted by a linear regression.)

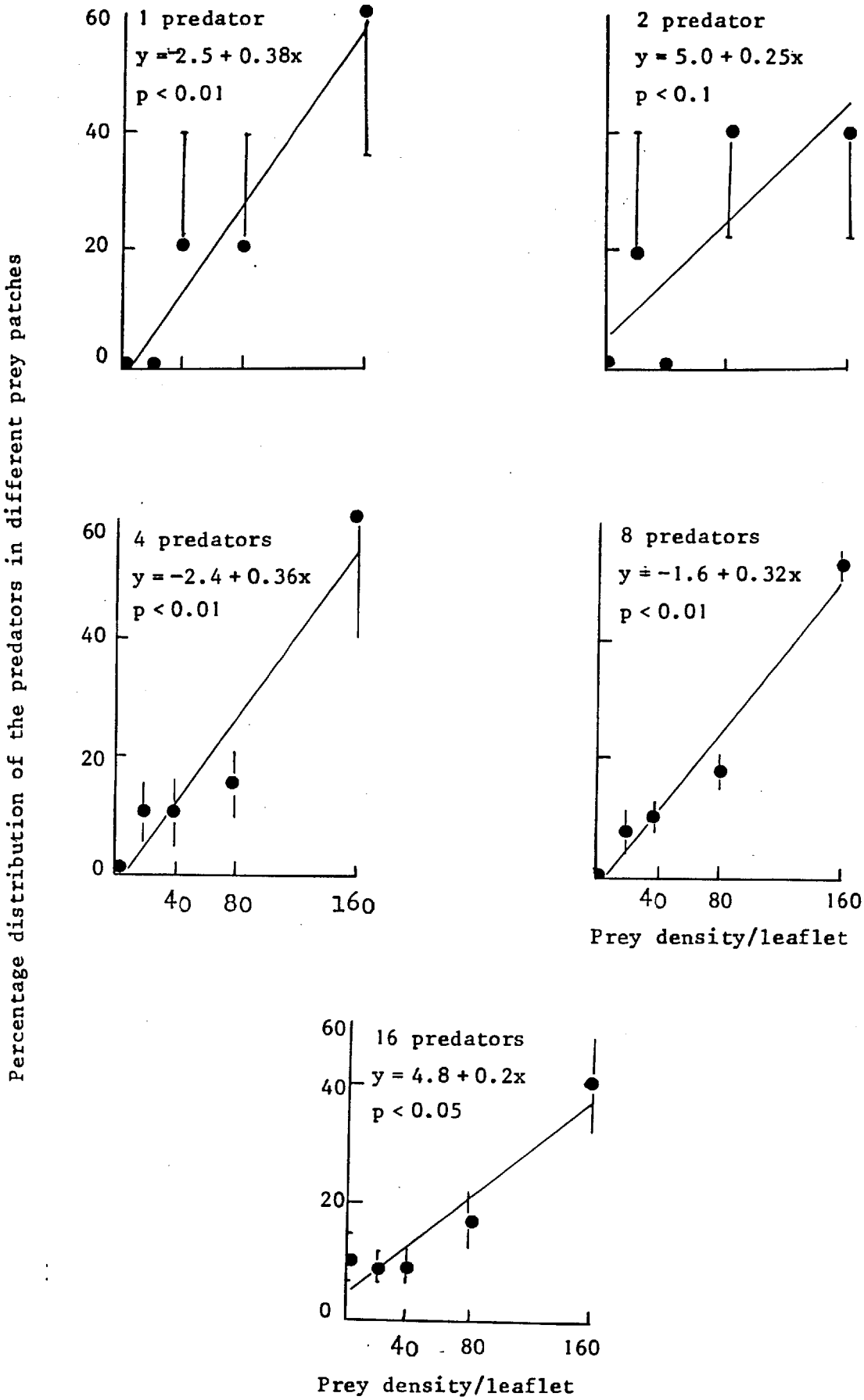


Fig.6.4C The behavioural responses of P. persimilis to an uneven distribution of its prey, T. urticae, during the 24th hour. S.E. of 5 replicates shown. (Curves fitted by a linear regression.)

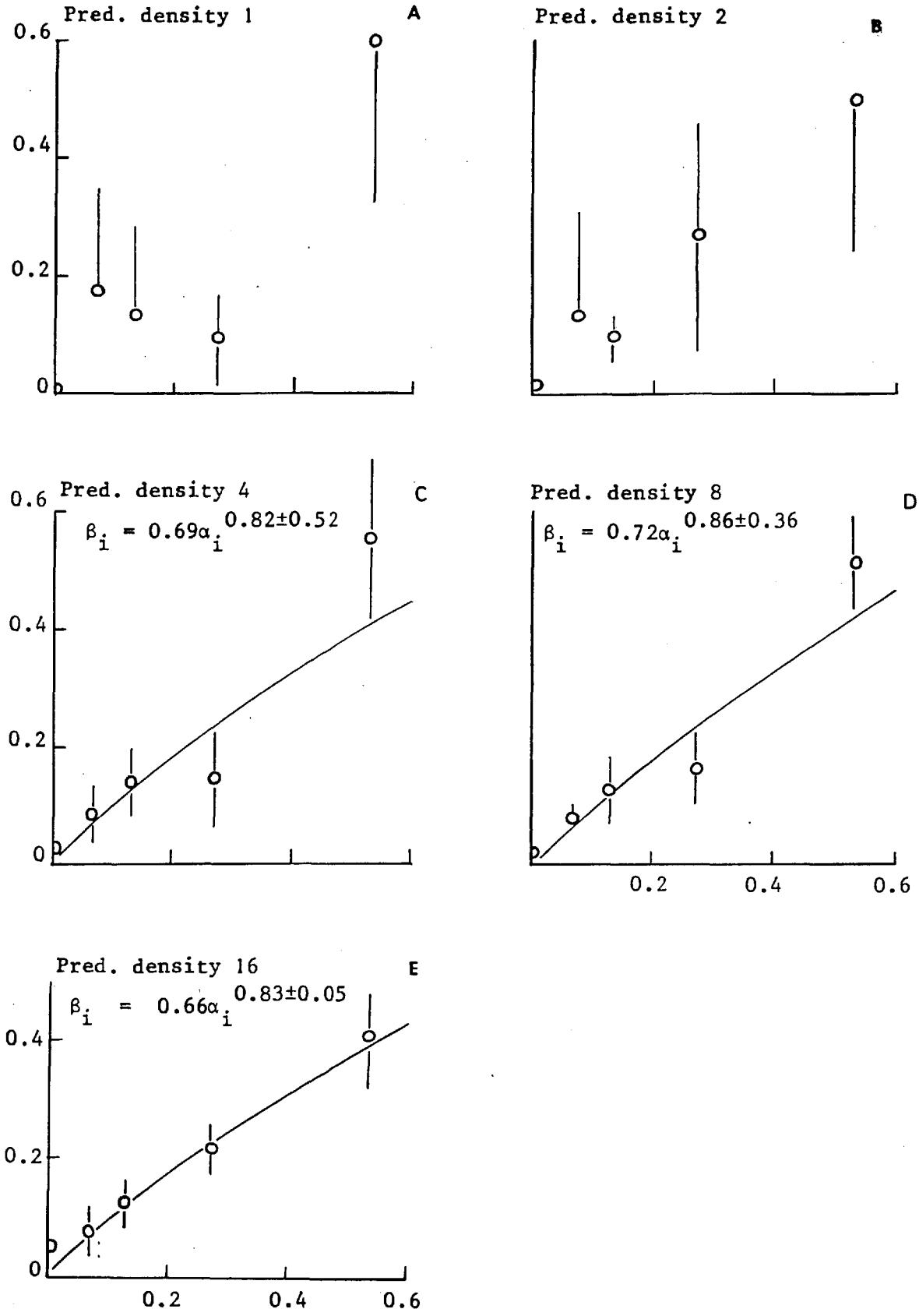


Fig. 6.5 The relationship between the proportion of female P. persimilis (β_i) and the proportion of female deutonymphs of T. urticae (α_i) per unit area. The curves fitted by the equation $\beta_i = c\alpha_i^{\mu}$. (95% confidence limits shown.)

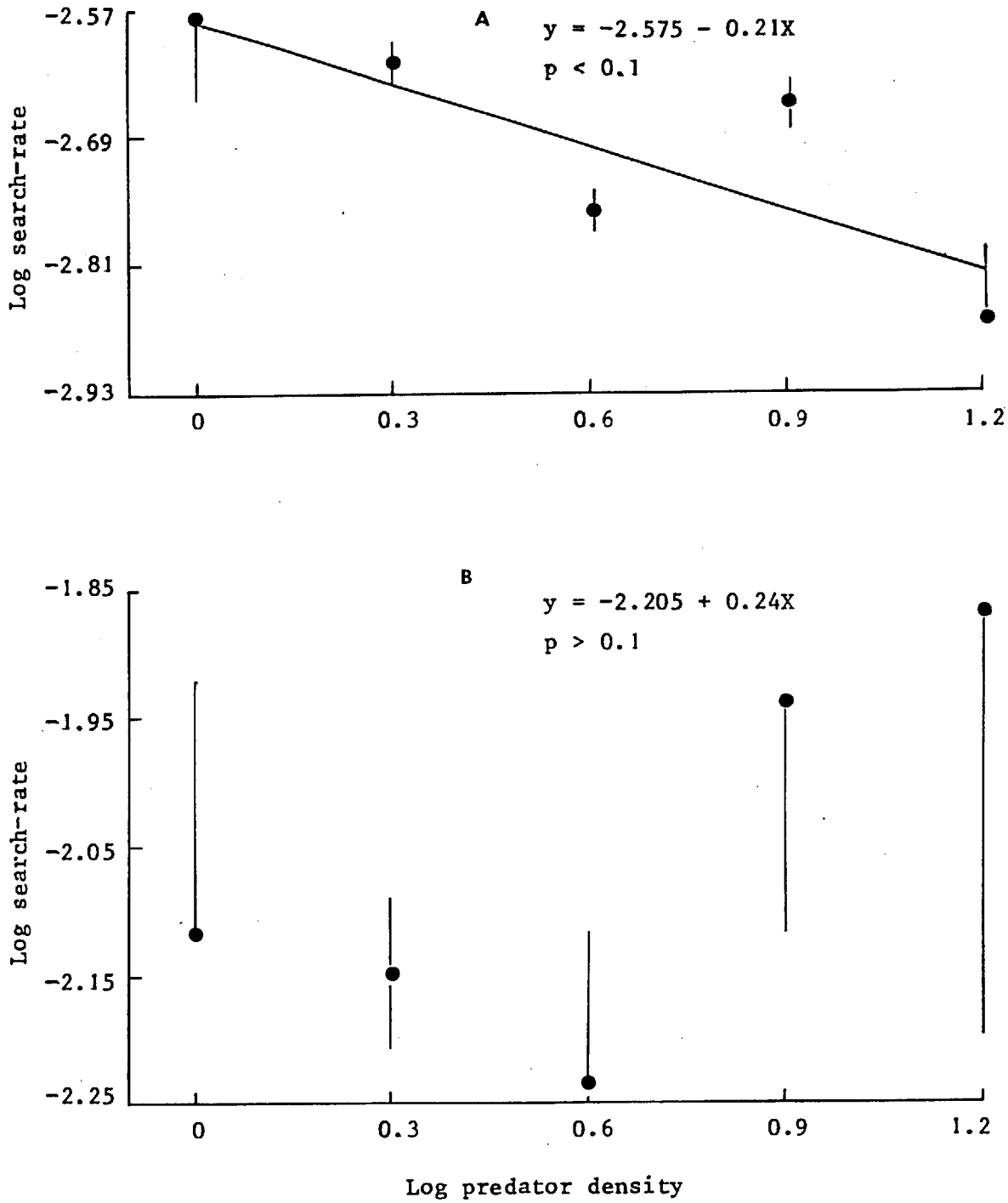


Fig.6.6 Relationships between log search-rate and log predator density. 95% confidence limits shown.

A— P. persimilis searching on five 32 cm^2 bean leaflets with only one leaflet infested with 150 deutonymphs of T. urticae. Data from series I experiments.

B— P. persimilis searching on five 32 cm^2 bean leaflets with an uneven distribution of prey (0, 20, 40, 80 and 160 deutonymphs of T. urticae). Data from series II experiments.

TABLE 6.1 Comparison of number of predators missing at the end of 24-hours in the two experimental series.

Density of predators	1	2	4	8	16
Number of predators missing in series I	0	0	0.5 ± 0.5 S.E.	1.0 ± 0.32 S.E.	6.4 ± 0.93 S.E.
Number of predators missing in series II	0	0	0	0	1.4 ± 0.6 S.E.

TABLE 6.2 Fitting the data to the model, $\beta_i = C\alpha_i^{\mu}$

Pred. Density	Coe. of Regression	Slope (μ)	Intercept (log C)	F values	Probability
1	0.538	0.51 ± 1.1	-0.36	0.815	n.s.
2	0.887	0.78 ± 0.56	-0.15	7.401	n.s.
4	0.908	0.82 ± 0.52	-0.16	9.418	n.s.
8	0.956	0.86 ± 0.36	-0.14	21.24	<0.05
16	0.999	0.83 ± 0.05	-0.17	1058.61	<0.01

the prey; Figure 6.4A gives the average percentage distribution of the predators for the first successive seven hours, Figure 6.4B for the last four hours, and Figure 6.4C shows the distribution of the predators at the 24th hour. All curves are fitted by a linear regression. In each of the densities 4, 8 & 16, the total percentage of predators on the leaves do not add up to 100% as some of the predators were found on the stem rather than the leaves. At the same time a few predators were missing at the end of the experiment (Table 6.1).

The Figures 6.5 A, B, C, D & E show the values of β_i plotted against α_i, with 95% confidence limits. It is seen in Table 6.2 that as the predator density increased the significance of fit to the equation 6.2 also increased (i.e. the best fit to the equation is observed at highest predator density of 16). In the predator densities one and two the observed data is not fitted to the equation due to high variability within the replicates. The predator aggregative indices obtained in the predator densities 4, 8 & 16 (Table 6.2) are close to the condition where $\mu = 1$.

When the mean search-rate from all the prey patches is plotted against the predator densities, both on log scales, no significant linear relationship is obtained.

The raw data is given in Appendix 5

6.5 Discussion

The results of the experiments, where only one out of the five leaves was infested with prey (Series I), indicate the ability of P. persimilis to aggregate on leaves where the prey are found (Figure 6.1 A to E). This is most marked with predator densities of one and two where all the predators were found on the infested leaf within five to six hours from the start of the experiment (Figure 6.1 A & B).

A similar conclusion is apparent from the Series II experiments.

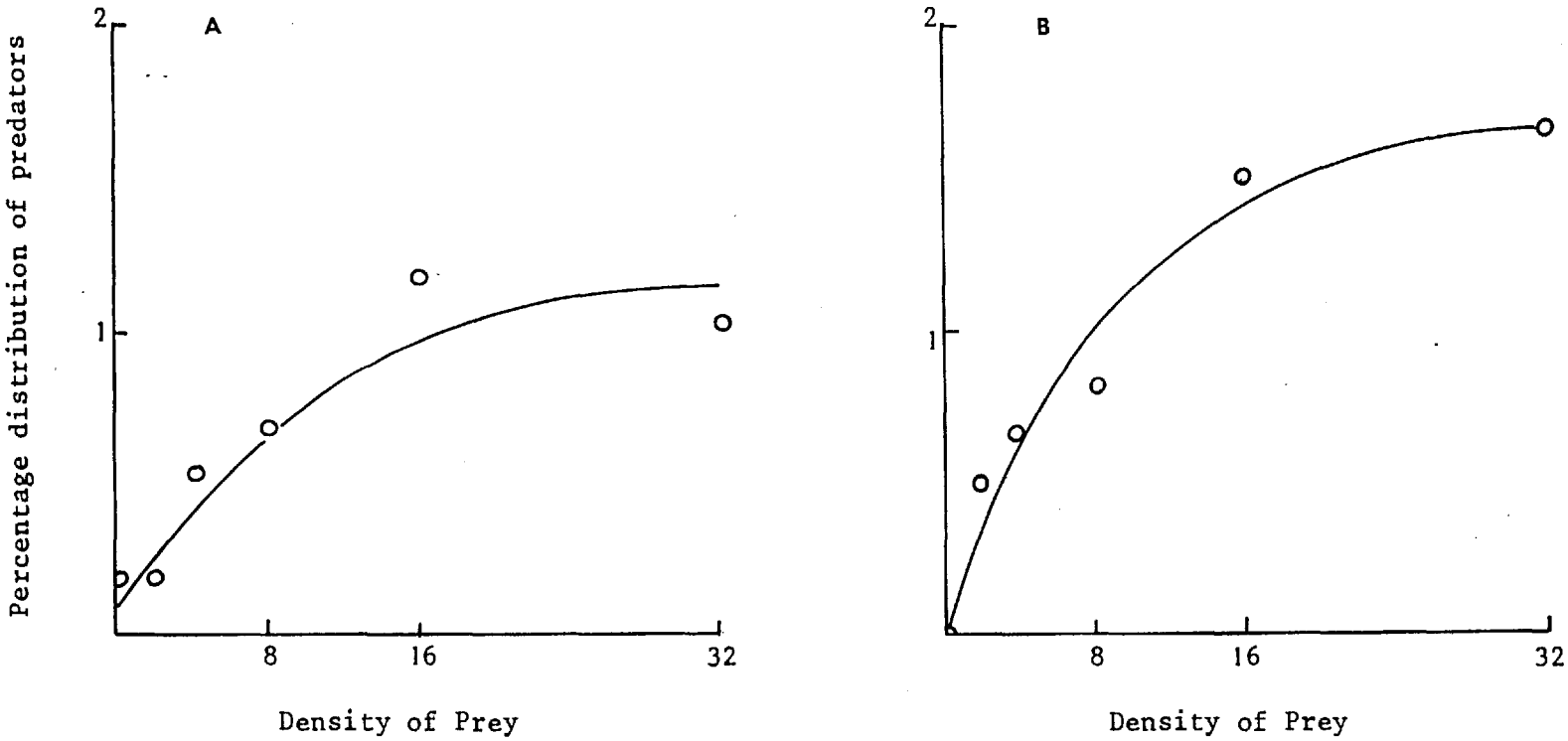


Fig. 6.7 Response of adult females of P. persimilis to spatial variation of prey density (Fitted by eye) (From Takafuji & Chant (1976)).

A - After 24 hours

B - After 48 hours

The average percentage of predators during the first seven hours and last four hours, and also the 24th hour of the experiment show a clear tendency for aggregation in areas of high rather than in lower prey densities (Figure 6.4 A, B & C). The results described by the model of Hassell & May (1973) indicate that there is a proportionate distribution of predators relative to that of prey.

This aggregative response in P. persimilis may well be due to a behavioural response resulting from direct physical contact with the prey since this predator is not known to detect prey by visual or any long range olfactory stimuli.

These results confirm the observations by Chant (1961a) and Takafuji & Chant (1976) on the aggregative behaviour of P. persimilis in relation to the density of its prey. The responses observed by Takafuji & Chant (1976) at the end of 24th and 48th hour in a similar experiment, were both convex and are illustrated here in Figures 6.7 A & B. This may have been due to the smaller experimental arena used (8 sq.cm) per leaf surface and the likely presence of the eggs of adult females of T. pacificus which was used as prey. Both these factors would have contributed to a higher number of prey per unit area. However, not all predatory mites show aggregative responses: there are reports of two species, Amblyseius potentillae (Garman) (McMurtry & Van de Vrie 1973) and Iphiseius degenerans Takafuji & Chant (1976), which distribute themselves independently of prey distribution.

In the experiment with only one infested leaf, during the first eight hours of observation, the predator densities four and eight showed increasing aggregative responses (Figures 6.1 C & D) while in the predator density 16 (Figure 6.1E) there is a gradual decline in the percentage of predators on the infested leaf. Beyond the 8th hour the distribution seems to have remained uniform throughout the experimental period as shown by the data recorded for the last three hours of the experiment (Figure

6.2B). This and the results shown in Figures 6.2A & B and 6.3 A & B, and Table 6.1 suggest the presence of some interference which tends to increase the dispersal of the predators from the highest density leaves. Kucklein (1966) also observed similar emigration of the predator T. longipilus from the experimental arena at high densities due to interference. The results also suggest that about 5 to 6 predators per leaf of 32 sq.cm containing 150 deutonymph prey can be regarded as the equilibrium number of predators, since the same number are found on the infested leaf after 24-hours when the initial predator density was 8 or 16. When the results of Takafuji & Chant (1976) are extrapolated to the same leaf area (i.e. x 4), the number of adult P. persimilis found on a similar prey density (i.e. 128) at the end of 24 and 48 hours, falls within the same range (i.e. 4-6 predators).

The presence of mutual interference which caused predators to leave the infested leaf, is supported by the suggestion, albeit not statistically significant, of a decline in the searching efficiency found in the experiment with one infested leaf (Figure 6.6A). On the other hand no interference was observed where the prey were distributed over five leaflets (Figure 6.6.B). This is probably due to the wider distribution of the predators thus minimising the number of mutual encounters. Due to the lesser interference between predators in this experiment the number of predators missing is much less than in the Series I (Table 6.1).

CHAPTER 7

POPULATION INTERACTION OF *P. persimilis* AND *T. urticae*

7.1 Introduction

Since the discovery of *P. persimilis* by Dosse (1958) as an important predator of red spider mite, many workers have studied population interactions of these two species both in glasshouses and in the field (Bravenboer & Dosse 1962; Hussey *et al.* 1965; Mori & Moriyama 1970; Gould & Light 1971; Boys & Burbutis 1972; Simmonds 1972; Mori 1975; Takafuji & Chant 1976). Most of these studies have been primarily concerned with the practicality of using these species with or without integration of other methods for control of red spider mites in commercial crops. Thus, Hussey *et al.* (1965) developed a theoretical scheme for the practical control of *T. urticae* by *P. persimilis* on glasshouse grown cucumbers. They (Gould *et al.* 1969) also reported large scale commercial control of *T. urticae* on three acres of glasshouse grown cucumbers.

There have also been promising results in the use of this species for control of *T. urticae* under outdoor conditions (Smith *et al.* 1963; Oatman 1965; and Oatman *et al.* 1966, 1967 & 1968).

In the present series of experiments the population trends of four different combinations of the two mites are studies in a simple laboratory ecosystem and compared with a control experiment in which predators were absent.

7.2 Materials and methods

The experimental system consisted of ten bean plants, each in a small plastic pot (6 cm. diameter & 8 cm high), kept on a 30 cm square

hardboard on 5 cm pegs at the four corners to form a platform. The plants which were three to four weeks old were prepared for the experiments by pruning each to only one trifoliate leaf having about 45 sq.cm leaflets. The plants of similar heights were arranged in a circle on the platform so that the leaves only just touched each other, in order to allow free movement of mites among the plants. The whole arrangement was kept in a shallow tray with about 2 cm of water to act as a barrier against the migration of predators. The water in the tray was maintained at that level throughout the experimental period. A few drops of a detergent were added to the water to lower the surface tension as starved predators were capable of floating on water acorss to the edges of the tray. The plants in the pots were watered every other day, but no fertilisers were applied as the potting mixture used was found to be quite adequate to support the plant with only one leaf.

At the start of the experiment two teneral females of T. urticae were introduced to each leaflet (ie. 6 per plant) and the plants kept apart for about three days until the mites were established on each plant. During this period the plants were examined for the mites and any missing were replaced. The plants were finally arranged after three days as mentioned above.

The different combinations of the prey and predatory mites tested were as follows:

(1) Introduction of one predator one week after the infestation with the prey mites,

(2) Introduction of two predators one week after the infestation with prey mites,

(3) Introduction of one predator two weeks after the infestation with prey mites,

(4) Introduction of two predators two weeks after the infestation with prey mites,

(5) Control - no predators were introduced.

The first count of the prey mites was made at the time of introduction of predators in each treatment. From thence onwards the counts were made on a single plant randomly selected from each treatment on every 6th day (except in the treatment with two predators introduced after one week, where it was counted every three days). The leaves of this plant were cut and all the different stages of the prey and predators were counted under a binocular microscope. When the densities of mites became high they were lightly anaesthetised with ether, and a transparent cellulose acetate sheet (8 cm x 12 cm) with a marked 0.5 cm square grid was used to facilitate quick counting. After counting, the leaves were placed on a fresh plant and returned to the experiment. This was done to prevent progressive reduction of the populations due to sampling. The counts were continued until all the mites disappeared or they started to fall off the plants in large numbers. During the course of the experiment the new leaves that appeared were nipped off. The experiments were conducted in a controlled temperature room at 20°C, 55-65% relative humidity and 16 hours light regime. The control experiment with no predators was replicated three times and the other four times.

7.3 Results

The results of the replicates are given in Tables 7.1 to 7.5 and shown graphically in Figures 7.1 to 7.5. The results of introducing one and two predators per plant at one week are shown in Figures 7.1 and 7.2, and at two weeks in Figures 7.3 and 7.4, respectively. Figure 7.3B show the result of only one replicate, where one predator per plant was introduced at two weeks in which the prey escaped predation, and multiplied to fall off the plants in large numbers on 38th day. Similar results were

TABLE 7.1 - Population interaction of prey and predator with one predator introduced one week after infestation (Avg. of 4 reps.)

Days after infestation with prey	Prey			Predator		
	eggs	active stages	all stages	eggs	active stages	all stages
0		06	06			
7	254	31	285	Introduction of Pred.		
13	165	187	351	12	05	17
19	455	155	610	17	11	28
25	786	67	853	63	51	114
31	16	22	38	28	39	67
37				00	08	08
43				00	01	01
49						

TABLE 7.2 - Population interaction of prey and predator with two predators introduced one week after infestation (Avg. of 4 reps.)

Days after infestation with prey	Prey			Predator		
	eggs	active stages	all stages	eggs	active stages	all stages
0		06	06			
7	242	35	277	Introduction of Pred.		
10	134	138	272	22	14	36
13	46	63	109	10	22	32
16	02	05	07	03	08	11
19					02	02

TABLE 7.3A - Population interaction of prey and predator with one predator introduced two weeks arter infestation (Avg. of 3 reps.)

Days after infestation with prey	Prey			Predator		
	eggs	active stages	all stages	eggs	active stages	all stages
0		06	06			
14	170	315	485	Introduction of Pred.		
20	1456	347	1803	09	03	12
26	2835	983	3818	21	15	36
32	4163	3645	7808	73	92	165
38	364	1496	1860	172	117	289
44	09	30	39	53	456	509
50	0	0	0	0	20	20
56				0	02	02

TABLE 7.3B - Population interaction of prey and predator with one predator introduced two weeks after infestation. (One rep. only)

Days after infestation with prey	Prey			Predator		
	eggs	active stages	all stages	eggs	active stages	all stages
0		06	06			
14	381	226	607	Introduction of Pred.		
20	1169	306	1475	03	09	12
26	4022	1018	5040	65	12	77
32	4286	3283	7569	84	20	104
38	1108	4195	5303	203	56	259
43	Started to fall off					

TABLE 7.4 - Population interaction of prey and predator with two predators introduced two weeks after infestation (Avg. of 4 reps.)

Days after infestation with prey	Prey			Predator		
	eggs	active stages	all stages	eggs	active stages	all stages
0	0	06	06			
14	148	322	470	Introduction of Pred.		
20	1174	347	1521	19	12	31
26	3368	421	3789	48	36	84
32	2340	1361	3701	220	185	405
38	76	173	249	200	247	447
44				00	73	73
50				00	04	04

TABLE 7.5 - Populations of prey in the absence of the predator (Avg. of 3 reps.)

Days after infestation with prey	Prey			Predator		
	eggs	active stages	all stages	eggs	active stages	all stages
0		06	06			
14	212	369	581			
20	2089	437	2526			
26	3055	1226	4281			
29	4564	2519	7083			
32*	4294	3712	8006			

* one replicate only

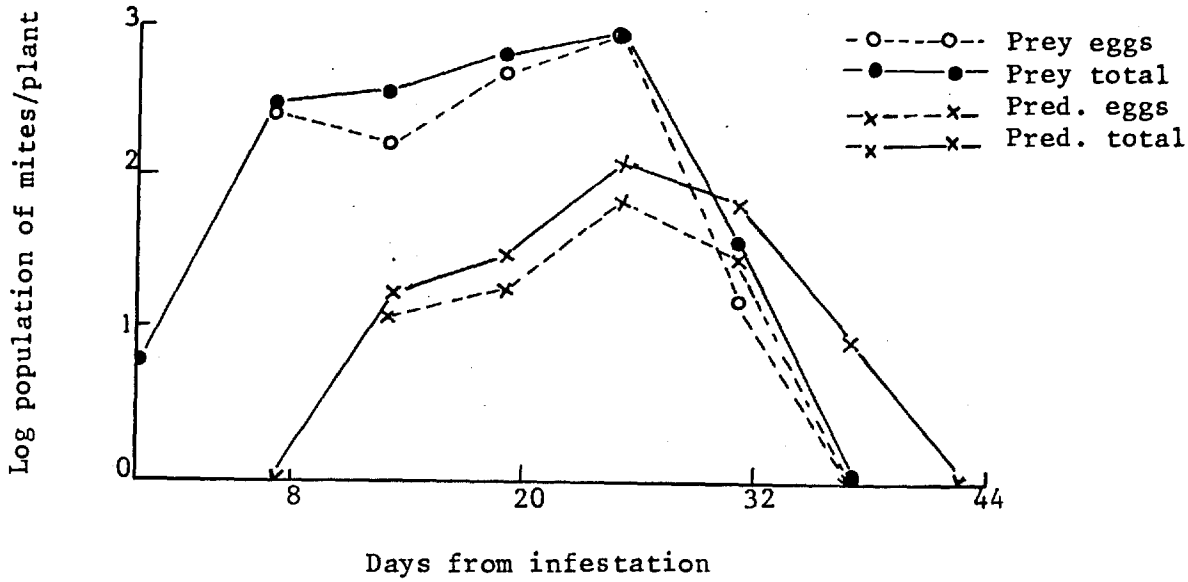


Fig. 7.1 Changes in predator (P.persimilis) and prey (T. urticae) populations. One predator introduced one week after infestation with prey. (Average of 4 replicates).

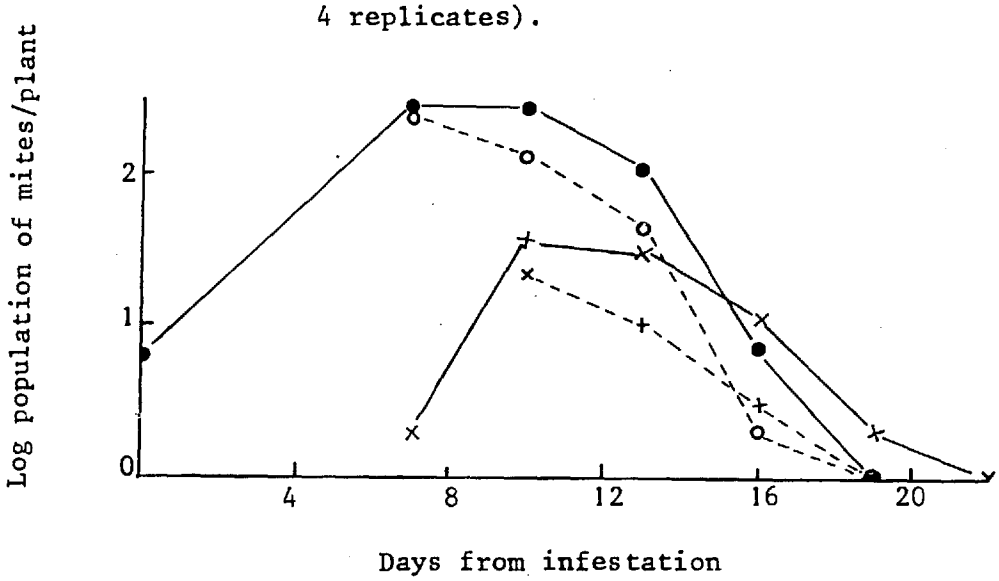


Fig. 7.2 Changes in predator (P. persimilis) and prey (T. urticae) populations. Two predators introduced one week after infestation with prey. (Average of 4 replicates).

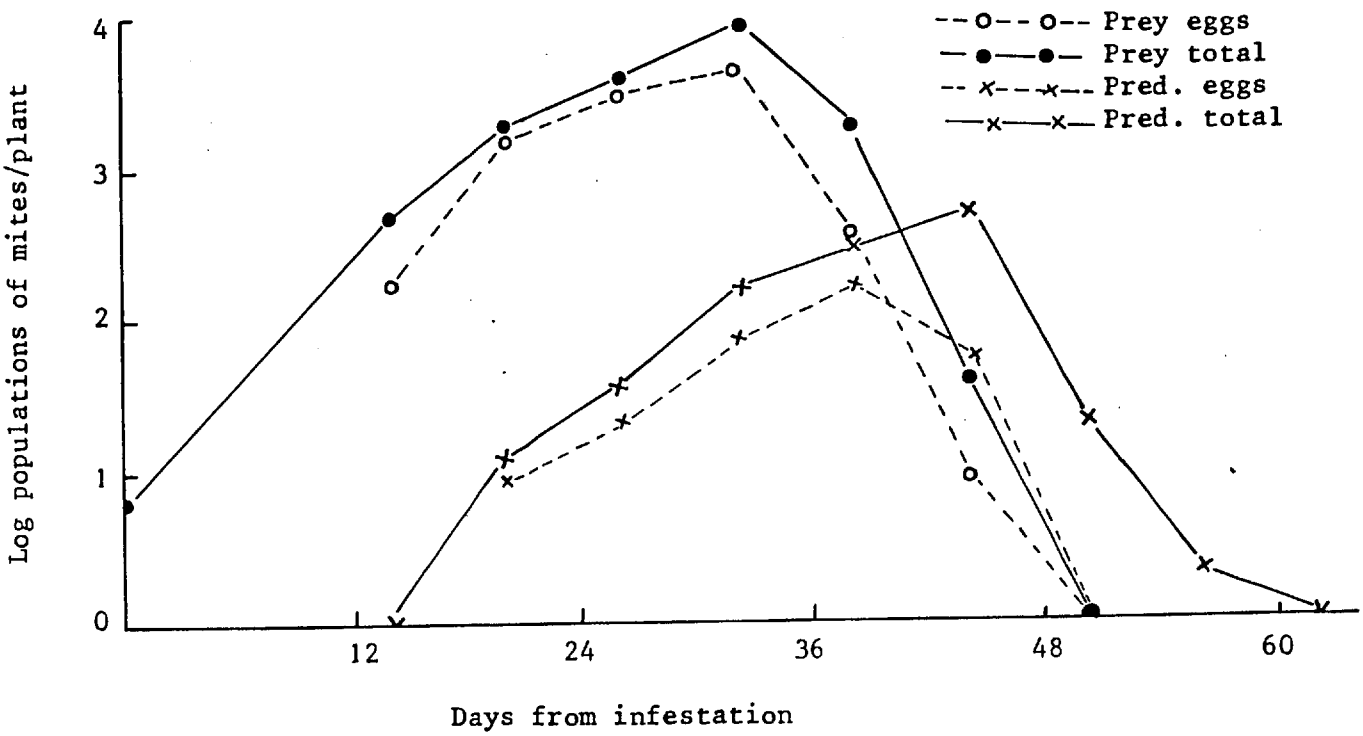


Fig. 7.3A Changes in predator (P. persimilis) and prey (T. urticae) populations. One predator introduced two weeks after infestation with prey. (Average of 3 replicates).

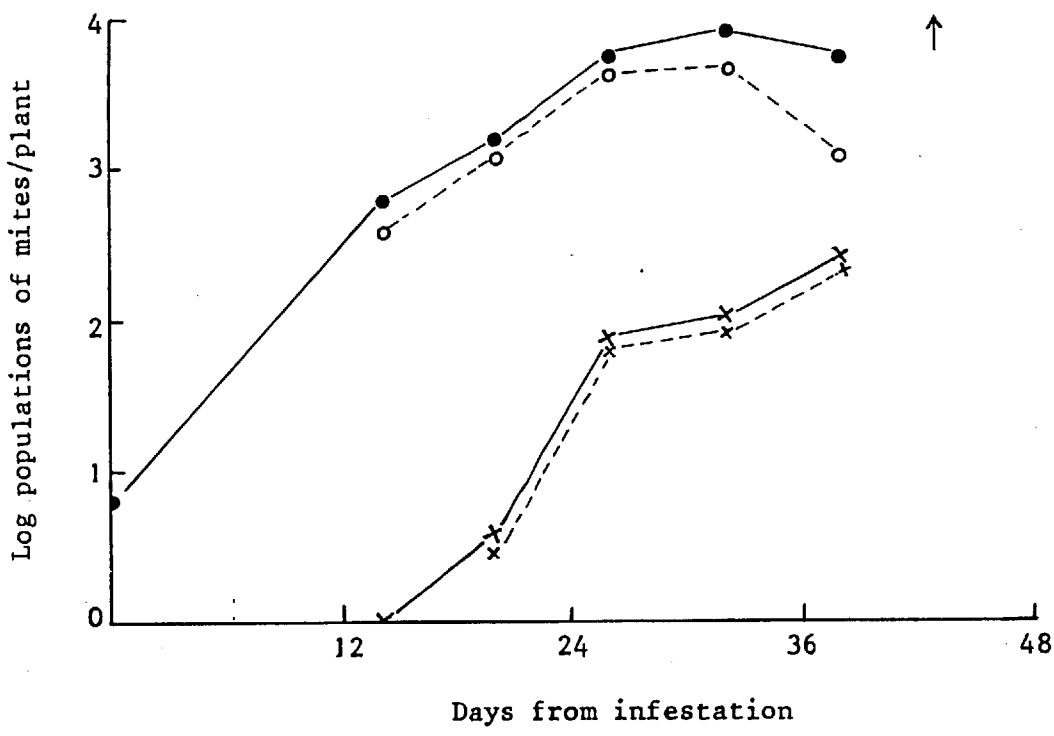


Fig. 7.3B Changes in predator (P. persimilis) and prey (T. urticae) populations. One predator introduced two weeks after infestation with prey. (One replicate).

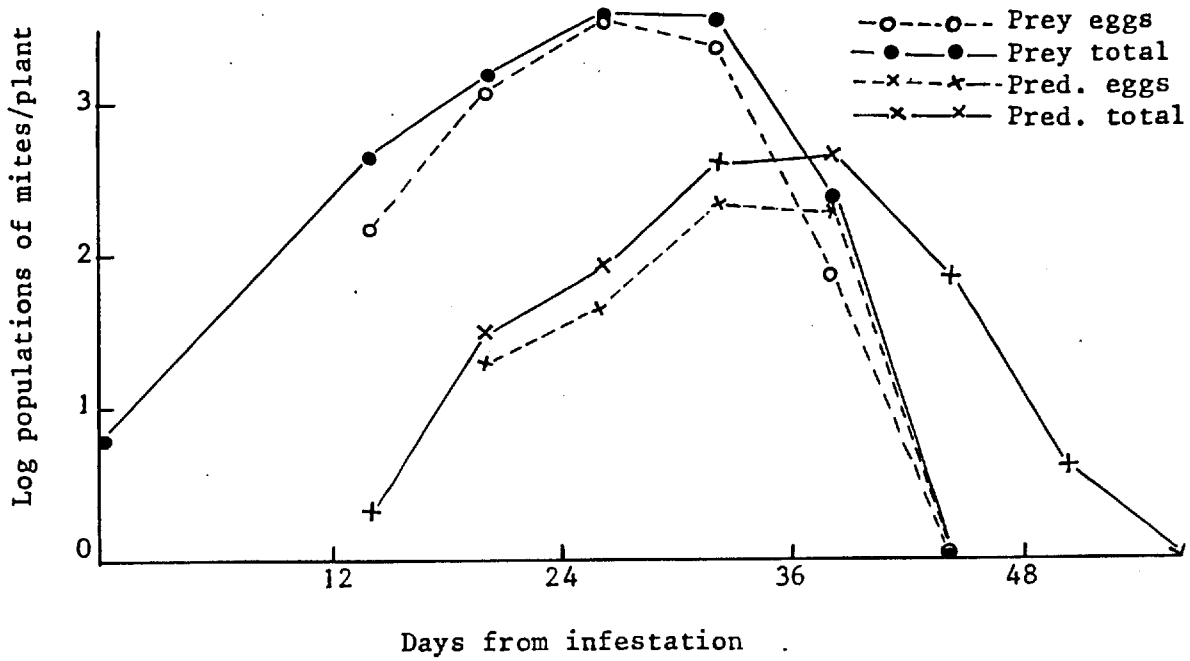


Fig. 7.4 Changes in predator (P. persimilis) and prey (T. urticae) populations. Two predators introduced two weeks after infestation with prey. (Average of 4 replicates).

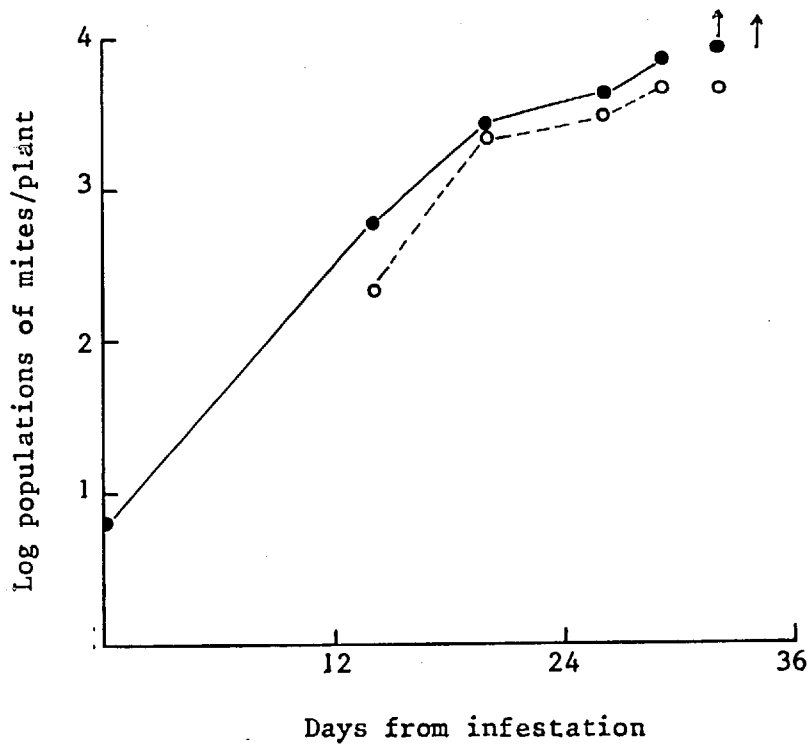


Fig. 7.5 Changes in populations of prey (T. urticae). No predators introduced. (Average of replicates).

obtained in the experiments where no predators were introduced onto the infested plants as shown in Figure 7.5. This occurred on 32nd day after infestation in two of the replicates and on the 34th day on the 3rd replicate. The vertical arrows marked on Figures 7.3B and 7.5 indicates the points at which this occurred. The falling off of the mites happened when the leaves showed severe mite damage and no longer could support large populations.

In the treatment shown in Figure 7.1 the prey and predator populations reached their peaks simultaneously. In Figure 7.2 the prey populations did not increase after the introduction of the predators but remained almost the same until the predator population reached its peak, and from thence onwards both populations declined. In the other two treatments (Figures 7.3 & 7.4) the predator populations reached their peaks with a time lag relative to the prey populations.

With two predators added per plant after one week, the prey were completely eliminated within ten days of introducing the predators (Figure 7.2). With one predator at one week and two predators at two weeks, the prey were eliminated between 24 to 30 days (Figures 7.1 & 7.4), whereas with one predator at two weeks, it took between 30 to 36 days (Figure 7.3A).

As seen from all the figures, the total populations of both prey and predator were largely comprised of eggs.

The predators survived for 6 to 12 days in all the treatments after eliminating the prey and cannibalism was observed on a few occasions during this period. The prey never re-appeared in any of the treatments even after three weeks, indicating that all the prey were eliminated before the predators themselves disappeared.

In the experiments where the predators were introduced at one week the maximum damage, observed on the leaves as bleached patches, was less than 25%, and that too was only on the under surfaces. In the experiments

with predators added two weeks after infestation, an initial predator density of one led to all the leaves becoming very badly damaged and covered with dense webbing, whereas with an initial predator density of two, the damage was about 80%, but seen on both sides of the leaves. In both these treatments the prey started to move onto the upper surfaces between 26 to 30 days after infestation. The predators and their eggs were seen on the upper surfaces only after the prey moved onto that side.

7.4 Discussion

The form of the interaction of P. persimilis and T. urticae are similar to those observed by Chant (1961a), Laing & Huffaker (1969), Mori (1975), and Takafuji & Chant (1976). The present experiments show that P. persimilis is capable of reducing populations of T. urticae, and even eliminating it entirely. This is due to a very much faster developmental rate of the predator compared to its prey and also a high rate of prey consumption. It is seen that the increase of predator populations depends mainly on the populations of the prey (Tables 7.1 to 7.4). Therefore, the predator quickly multiplied to great numbers at high prey densities (a rapid numerical response), and then subsequently brought about a quick suppression of the prey population, an increased overall predation rate. The time delay between peaks seen in Figure 7.3 & 7.4 was simply a result of the delay in introducing the predator, thus allowing the prey to built-up to an average population of 475 per plant. At one week after infestation, this population was only about 280 per plant (Tables 7.1 & 7.2). Once the predator numbers had increased, however, there was an equally rapid reduction in the prey population.

Subsequently, the predators started leaving the plants since quite a number of predators were seen on the pots and on the platform on which the pots were kept. This behaviour of P. persimilis, dispersing at low prey densities, was also observed by Takafuji & Chant (1976). However,

the initial decline in the predator populations, after reaching their peak, was due to a reduced rate of oviposition at the low prey densities. It was shown by Pruszynski (1973) and Takafuji & Chant (1976) that the rate of oviposition in P. persimilis is dependent on prey density.

Due to high voraciousness and good searching ability P. persimilis was not able to regulate the prey at low levels, but eliminated it completely. As it is not capable of feeding on non-prey food it inevitably was also eliminated after the disappearance of the prey. Although Chant (1961a) observed P. persimilis to feed occassionally on young thrips, it was not able to thrive on thrips which were seen on the leaves of the present experiment. Therefore, it is likely that the predator disappeared from the prey-free plants due to emigration cannibalism and death following starvation.

There is little difference in the period taken by P. persimilis to control the prey in three of the treatments despite the differences in the initial predator-prey populations (Tables 7.1, 7.3A and 7.4). Such were the results obtained by Mori (1975) with the same predator and prey. The "escape" of the prey in one of the replicates with one predator added at two weeks (Figure 7.3B) may have been due to the higher population of prey (607) at two weeks compared with those of the three corresponding replicates (453, 471 & 532) (Refer Appendix 6). The poor nutritional condition of mite-damaged leaves, especially in the two weeks treatment, would have retarded the multiplication T. urticae (Hamstead & Gould 1957; Henneberry 1962a, b & 1963; Rodriguez et al. 1970). It is therefore difficult in a small ecosystem to get a true evaluation of the effect of the predator with initially very high prey densities.

Several collapsed eggs of P. persimilis were observed throughout the experiments. Similar observations were made by Laing & Huffaker (1969) who attributed it to cannibalism by another predator, Metaseiulus occidentalis (Nesbitt), which was present. In the present experiments the collapsed

eggs could not have been due to cannibalism as they were seen even with abundant prey. Therefore, a possible explanation resides in the low hatchability of eggs due to inbreeding in the stock cultures, since they were maintained for more than two years without introduction of new stocks. It has been shown experimentally by Poe and Enns (1970) that there was more than 50% reduction in fertility of eggs of P. persimilis due to inbreeding within one year.

The present studies were carried out in a small ecosystem weighted in favour of the predator. It showed the ability of P. persimilis to increase rapidly and the effects of its prey consumption and mobility. The studies of Huffaker (1958), Huffaker et al. (1963) and Laing & Huffaker (1969) have shown that the larger the ecosystem the greater the insurance against extinction of prey, and/or predator after one or two small oscillations. Takafuji & Chant (1976) were able to show few damped oscillations in the population interaction of P. persimilis and T. urticae in an ecosystem of bean plants, each with six leaves. In some of the replicates there was a resurgence of prey after the predator disappeared. Therefore, they doubted the ability of P. persimilis to completely eliminate the prey in a larger ecosystem before itself dying out of starvation. The work of Chant (1961a) Bravenboer & Dosse (1962), Hussey & Parr (1965) and Mori (1975) have, however, shown the ability of P. persimilis to eliminate completely its prey even from complex glasshouse systems.

CHAPTER 8

GENERAL DISCUSSION

In studying some aspects of the biology of P. persimilis, the average observed developmental period of 11.5 days agrees well with the observations of other workers. This rate of development is particularly sensitive to the availability of food. The mites can complete their development even at very low levels of feeding, although the developmental period is now greatly extended. An important observation made in the present studies is that in the presence of abundant prey more than 95% of the feeding by protonymphs and deutonymphs occurred during the first 24 hours of the instar. This was followed by an average resting period of 0.5 days (protonymph) and 0.7 days (deutonymph) prior to moulting into the next stage. This is a feature that has not been reported in the literature. Laing (1968) reported mites to be active throughout their immature predatory stages. Similarly, the oviposition and post oviposition periods of adult female P. persimilis with abundant prey, resulted in a much higher longevity (average of 50.9 days) than so far reported. The reproductive rate of this species has a linear relationship to the feeding rate, as also found in several other invertebrates. At the same time, like most other phytoseiids, it is capable of sustaining oviposition at very low levels of feeding.

Functional responses of all the three predatory stages of P. persimilis to the density of the four immature stages of T. urticae were studied over a period of 24 hours. The experiments were repeated with only immature predators for 8 hours to eliminate the effects of their long resting periods. The majority of the responses were found to be typical type II curves. However, the functional responses of deutonymph

predators with prey eggs were found to be sigmoid in both 8 and 24 hour experiments, while the functional response of the same predator with deutonymph prey was linear in the eight hour experiment. Even the functional response of adult females with prey eggs and larvae showed a tendency to be sigmoid. The predatory stages of P. persimilis have shown linear functional responses also with eggs and protonymphs of the prey mite, T. pacificus (Takafuji and Chant 1976).

The presence of sigmoid functional responses with smaller prey stages support the suggestion of Hassell et al (1977) that smaller or non-preferred species of prey in large experimental arenas also could lead to sigmoid responses. This also adds to the existing evidence that sigmoid functional responses are not confined only to the vertebrate predators. Thus, the present experiments show P. persimilis to exhibit all the three basic types of functional responses as a result of changes in sizes of prey and predator.

The functional response data has been described by the random predator equation (Rogers 1972) in order to examine variation of search rate, a^1, and handling time, T_h, with the changes in the sizes of prey and predator. The most obvious result from the two sets of experiments is that the longer resting period in the 24 hour experiments lead to larger values of T_h and smaller values of a^1. It is interesting to note that a^1 of adult predators searching for any stage of the prey takes the lowest value of any of the three predatory stages. This may well be due to the loss of time from oviposition activities or due to lower hunger levels of the adult females compared to the immatures which were unfed prior to the experiments. On the other hand, the higher value of a^1 of immatures may be due to their more 'aggressive nature' which could be regarded as an adaptation for their survival. Similar results have been reported for other invertebrates where immature stages have a higher a^1 than that for

adults. The lowest a^1 for protonymphs searching for prey eggs, perhaps results from their smaller width of perception and under-developed chemoreceptors on their first pair of legs.

The trends of variation of the handling time of P. persimilis searching for the different immature stages of the prey is similar to those recorded for other predators, where the value of T_h increased with increase of prey size and decrease of predator size. Surprisingly, the predators searching for prey eggs, which are the smallest prey used, show a higher value of T_h than that for larval prey. This trend was observed in both the 8 hour and the 24 hour experiments. No explanation for this behaviour is apparent. Further studies on the value of food ingested, digestibility and food value of eggs and larvae are needed before making any definite conclusions.

The functional response results were also used to predict the prey consumption when faced with a combination of two prey stages at the same time: eggs with deutonymphs and larvae with deutonymphs. Only the data of deutonymph predators feeding on the combination of eggs with deutonymph prey was adequately described by the equation derived by Lawton et al (1974), which is a modification of the random predator equation to include two prey situation. In all the other predator-prey combinations the data deviated from the expected, the predator showing an altered preference for one of the prey stages. This clearly indicates a change in the search-rates or perhaps handling times for one or both of the prey stages when found together. It is likely that this resulted from the relative profitability and palatability of the two prey stages. It is observed from these data that all the predatory stages preferred to feed on eggs than on any other stage tested. No switching was observed in any of these experiments.

Increasing the density of immature predators did not lead to any effect on their search-rates, and thus showing no signs of any mutual interference. The adult female P. persimilis, however, did show mutual interference as a decline in their search-rates. Not unexpectedly, a smaller leaf disc arena showed a higher value for the mutual interference constant than on a trifoliate leaf. This difference probably results from the trifoliate leaf having more surface area for predators to move about thus reducing the frequency of contact between searching individuals. None of the relationships of log a^1 to log predator density showed any tendency to be curvilinear. Some tendency was observed at higher predator densities, for the predators to migrate out of the prey-infested leaf, and some predators were found to be missing at the end of the experiments. Similar observations where mite showed a tendency to migrate after mutual encounters have been reported by Kuchlein (1966) for the predatory mite T. longipilus. There are also several records of such behaviour from insect parasitoids.

The behavioural response of adult female P. persimilis to an uneven distribution of prey resulted in marked aggregative responses. In the presence of a single prey patch amidst non-prey areas, significantly higher number of predators were always found in the prey patch than elsewhere. When different densities of predators were exposed to uneven distribution of prey, the predators distributed themselves among the prey patches in relation to the prey distribution. These aggregative responses were adequately described by the model of Hassell and May (1973). There were more predators missing at the end of 24 hours in the single prey patch experiment than within the multi-patch experiment. This probably resulted from more encounters occurring in the single prey patch due to the initial aggregation, thus leading to greater tendency for dispersal. This behaviour of aggregation and subsequent dispersal due to interference

has the advantage that it prevents the over exploitation of prey and thus increase the efficiency of the predators.

The population interaction of P. persimilis and T. urticae studied was typical of those observed by Chant (1961a), Mori (1975), and Takafuji and Chant (1976). Despite the large differences in most of the initial predator–prey populations in different treatments, P. persimilis was able to completely eliminate the prey between five to six weeks. This ability of P. persimilis rests on its rapid numerical response in the presence of abundant prey, high voraciousness and efficient stratergy. Due to the prey specificity of the predator, it too was eliminated 10 to 12 days after disappearance of the prey. It was observed that when the population of prey was declining, the predator found to move off the plant in an attempt to emigrate.

In the present study, P. persimilis has been shown to exhibit both aggregative responses and mutual interference, characteristics which Hassell and Rogers (1972) considered important to the stability of predator–prey (or host–parasite) interactions. Unfortunately, the combined effect of these could not be properly evaluated here, the ecosystem being very small and barriers preventing the movement of the predators.

In a larger, more heterogenous environment, as expected under natural conditions, these features of aggregation and so subsequent dispersal due to interference may well be crucial components in evaluating the predator's searching performance.

SUMMARY

(1) Life history studies of P. persimilis showed that its rate of development depends on the availability of food, but the mite is capable of development even at very low levels of feeding.

(2) The immature predators have a long non-feeding resting period prior to moulting into the next stage.

(3) The different predatory stages of P. persimilis generally have type II functional responses to different immature stages of T. urticae. In cases where the prey stages are much smaller, there is a tendency for functional response to be sigmoid. A linear (type I) response was also observed with deutonymph predator and deutonymph prey in the 8 hour experiment.

(4) There is little uniformity in the variation of search-rates of different stages of the predator for different stages of the prey. The adult female predators show the lowest value of a^1 of all three predatory stages when searching for any stage of the prey.

(5) The handling-times vary uniformly with the size of prey and predator. The value of T_h for prey eggs was always found to be higher than that for larval prey.

(6) In mixed prey situations of eggs and deutonymphs, all the predatory stages showed a definite preference for prey eggs. Only the above prey combinations with the deutonymph predator fitted the equation of Lawton et al (1974) for a two prey situation.

(7) Immature predatory stages of P. persimilis do not show any mutual interference. However, the adult females do show such interference both in the presence of larval and deutonymph prey.

(8) When faced with a series of different prey densities, P. persimilis show aggregative responses: a higher proportion of the predators were always seen in the high rather than in the lower prey density areas.

(9) When predators aggregate in a single prey patch there is some indication of mutual interference as shown by a decline in the search-rate, and also by a decline in the proportion of predators on the infested leaf.

(10) Population interaction of P. persimilis and T. urticae showed the ability of the predator to multiply rapidly in the presence of prey and subsequently to eliminate it completely. Due to the prey specificity of the predator it was not able to survive in the absence of the prey.

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* Original paper not seen by author.

APPENDIX 1

THE RAW DATA OBTAINED FROM EXPERIMENTS ON THE BIOLOGY OF P. PERSIMILIS

TABLE 1·1 Duration of the different stages (in days)

Egg	Larva	Protonymph		Deutonymph		Pre-ovi-position	Ovi-position	Post-ovi position
		Rest before moulting	Total Period	Rest before moulting	Total Period			
3.38	1.08	0.42	1.75	–	2.0	3.2	36	32
3.38	1.13	0.79	1.79	1.0	2.0	3.0	39	33
3.42	1.08	0.67	1.67	0.75	2.0	3.5	36	14
3.38	1.0	0.46	1.58	0.58	2.0	4.5	36	
3.35	1.04	–	–	–	–	–		
–	–	–	–	–	–	–		
3.5	–	–	–	–	–	–		
*3.25	1.04	0.53	1.67	0.58	2.04	–		
3.33	1.17	–	–	–	–	–		
*3.32	1.13	0.54	1.58	0.63	1.96	–		
3.33	1.0	0.5	1.56	0.33	1.94			
3.29	1.17	0.75	1.77	–	1.9	3.0	44	
3.29	1.17	0.5	1.52	–	1.92	4.1	40	19
3.33	1.0	0.5	1.56	0.5	1.94	3.0	41	
3.29	–	–	–	–	–	–		
3.29	1.13	0.42	1.67	–	1.94	3.2	6	44
3.35	1.0	–	1.60	–	1.9	3.0	40	12
3.29	1.06	–	1.85	0.71	1.88	–	34	21
3.35	1.1	–	1.77	–	1.94	4.0	40	6
3.54	–	–	–	–	–	–		
3.54	–	–	–	–	–	–		
3.56	–	–	–	–	–	–		
3.79	1.06	–	1.83	–	–	–		
3.71	1.29	0.83	1.75	–	2.08	3.2	41	24
3.81	1.33	–	1.85	–	1.96	2.9	42	13
3.4	1.0	0.33	1.63	0.79	1.92	3.2	40	32
3.38	0.94	0.38	1.73	0.63	1.9	3.0	37	
3.38	0.96	0.38	1.67	1.0	2.31	3.0	42	

* Males

TABLE 1.2 Feeding on the eggs of T. urticae by the different stages of P. persimilis

Protonymphs				Deutonymphs				Pre-Ovi.	Ovi.	Post-Ovi.
1st. 12 hrs.	2nd. 12 hrs.	3rd. 12 hrs.	4th. 12 hrs.	1st. 12 hrs.	2nd. 12 hrs.	3rd. 12 hrs.	4th. 12 hrs.	Average of 3 days	Average of 3 days	Average of 3 days
4	2	0	0	0	9	0	0	10	26	0
2	3	0	0	6	2	0	0	14	24	6
3	1	0	0	0	9	0	0	13	18	5
3	2	0	0	8	2	1	0	12	30	2
5	3	0	0	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–
6	1	0	0	7	2	0	0	–	–	–
3	2	1	0	–	–	–	–	–	–	–
3	1	0	0	7	2	0	0	9	16	6
4	1	0	0	8	1	0	0	8	21	1
1	4	0	0	6	4	0	0	12	22	2
3	2	0	0	8	3	1	0	9	20	3
4	0	0	0	7	2	2	0	9	16	7
–	–	–	–	–	–	–	–	–	–	–
4	2	0	0	6	2	0	0	10	28	–
4	1	0	0	7	1	0	0	13	23	–
5	0	0	0	6	2	0	0	13	–	–
6	0	0	0	4	3	1	0	–	–	–
–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–
3	2	0	0	7	4	0	0	–	–	–
0	7	0	0	7	3	0	0	–	–	–
3	2	1	0	0	8	0	0	–	–	–
5	0	0	0	8	0	1	0	–	–	–
5	0	0	0	8	1	2	0	–	–	–
5	0	0	0	6	2	0	0	–	–	–

TABLE 1.3 The duration of the immature stages of P. persimilis under low levels of feeding on eggs of T. urticae

No. of prey eggs offered per day	Duration of protonymph stage in days												Mean ± S.E.
	1	2	3	4	5	6	7	8	9	10	11	12	
1	4.3	3.0	2.7	2.7	2.5	3.0	3.0	2.6	4.0	5.7	3.7	3.8	3.41 ± .27
2	3.0	2.0	2.0	2.1	2.1	2.2	2.0	2.0	2.6	2.6	2.2		2.25 ± .10
3	2.0	2.3	2.3	2.1	2.3	2.0	2.2	2.4					2.2 ± .05
4	1.9	2.1	2.0	1.9	1.9	2.1	2.0	2.0					1.99 ± .03

No. of prey eggs offered per day	Total no. of eggs fed during protonymph stage												Mean ± S.E.
	1	2	3	4	5	6	7	8	9	10	11	12	
1	3	3	2	2	2	3	2	2	4	4	3	3	2.75 ± .22
2	4	3	4	4	4	4	4	4	2	2	3		3.45 ± .25
3	3	6	4	4	4	3	5	4					4.12 ± .35
4	4	4	4	4	4	5	5	4					4.25 ± .16

No. of prey eggs offered per day	Duration of deutonymph stage in days												Mean ± S.E.
	1	2	3	4	5	6	7	8	9	10	11	12	
1	4.0	4.5	7.5	5.0	12.0	7.7	6.2	6.0	9.0				6.88 ± .84
2	3.0	2.7	3.0	3.4	3.6	2.6	3.0	3.0	3.2	3.2			3.07 ± .09
3	3.1	3.1	3.5	3.5	3.0	3.1	3.2	3.0					3.18 ± .07
4	3.0	3.1	3.1	3.0	3.0	3.0	3.0	3.1					3.03 ± .02

No. of prey eggs offered per day	Total no. of eggs fed during deutonymph stage												Mean ± S.E.
	1	2	3	4	5	6	7	8	9	10	11	12	
1	4	3	6	3	11	6	5	4	5				5.22 ± .81
2	6	7	4	4	4	4	4	4	4	4			4.5 ± .34
3	6	6	9	6	6	6	7	7					6.62 ± .37
4	8	8	6	8	9	6	8	9					7.75 ± .41

APPENDIX 2

Data of the functional response experiments conducted on 16cm^2 bean leaf discs.

A. 8 hour experiments

TABLE A1 - Functional response experiment (8hr.)

Predator - Protonymph *P. persimilis*

Prey - Eggs of *T. urticae*

Density of Prey	Number of prey killed					
	R_1	R_2	R_3	R_4	R_5	Mean
1	0	0	1	1	1	0.6
2	1	0	2	2	1	1.2
4	2	2	1	2	2	1.8
8	2	2	2	3	3	2.4
16	3	3	2	3	3	2.8
32	3	4	2	3	3	3.0

TABLE A2 - Functional response experiment (8hr.)

Predator - Protonymph *P. persimilis*

Prey - Larvae of *T. urticae*

Density of Prey	Number of prey killed					
	R_1	R_2	R_3	R_4	R_5	Mean
1	1	1	1	1	1	1.0
2	1	2	1	2	1	1.4
4	3	2	2	2	2	2.2
8	4	2	3	3	4	3.2
16	4	3	4	6	2	3.8
32	6	4	4	3	3	4.0

TABLE A3 - Functional response experiment (8hr.)

Predator - Protonymph P. persimilis

Prey - Protonymph of T. urticae

Density of Prey	Number of prey killed					
	R_1	R_2	R_3	R_4	R_5	Mean
1	1	1	1	1	1	1.0
2	1	2	1	1	1	1.2
4	2	2	3	2	2	2.2
8	4	3	2	3	3	3.0
16	4	2	3	3	3	3.0
32	2	3	3	4	4	3.2

TABLE A4 - Functional response experiment (8hr.)

Predator - Protonymph P. persimilis

Prey - Female deutonymph of T. urticae

Density of Prey	Number of prey killed					
	R_1	R_2	R_3	R_4	R_5	Mean
1	1	0	1	0	1	0.6
2	1	1	1	1	1	1.0
4	1	1	1	1	2	1.2
8	1	2	1	2	2	1.6
16	1	2	2	2	2	1.8
32	3	2	2	2	2	2.2

TABLE A5 - Functional response experiment (8hrs.)

Predator - Deutonymph P. persimilis

Prey - Eggs of T. urticae

Density of Prey	Number of prey killed					
	R_1	R_2	R_3	R_4	R_5	Mean
1	0	1	0	1	1	0.6
2	2	1	2	0	1	1.2
4	4	4	3	4	4	3.8
8	5	6	6	5	5	5.4
16	5	7	5	7	7	6.2
32	7	6	7	5	6	6.2
48	5	7	6	6	6	6.0

TABLE A6 - Functional response experiment (8hr.)

Predator - Deutonymph P. persimilis

Prey - Larvae of T. urticae

Density of Prey	Number of prey killed					
	R_1	R_2	R_3	R_4	R_5	Mean
1	1	1	1	1	1	1.0
2	2	2	2	1	2	1.8
4	4	4	3	4	4	3.8
8	6	6	5	5	6	5.6
16	8	8	9	9	7	8.2
32	8	10	10	8	8	8.8
48	7	11	10	8	9	9.0
64	10	8	9	9	10	9.2

TABLE A7 - Functional response experiment (8hr.)

Predator - Duetonymph P. persimilis

Prey - Protonymph of T. urticae

Density of Prey	Number of prey killed					
	R_1	R_2	R_3	R_4	R_5	Mean
1	1	1	1	1	1	1.0
2	2	2	1	2	1	1.6
4	3	4	3	3	4	3.4
8	5	4	5	4	5	4.6
16	4	7	6	5	6	5.6
32	7	6	6	7	5	6.2

TABLE A8 - Functional response experiment (8hr.)

Predator - Deutonymph P. persimilis

Prey - Female deutonymph of T. urticae

Density of Prey	Number of prey killed					
	R_1	R_2	R_3	R_4	R_5	Mean
1	1	1	1	1	1	1.0
2	2	2	2	2	2	2.0
4	2	2	3	2	3	2.4
8	3	2	3	2	2	2.4
16	2	2	2	3	2	2.2
32	2	3	3	3	3	2.8

B. 24 Hour experiments

TABLE B1 - Function response experiments (24hr.)

Predator - Protonymph P. persimilis

Prey - Eggs of T. urticae

Density of Prey	Number of prey killed										
	R_1	R_2	R_3	R_4	R_5	R_6	R_7	R_8	R_9	R_{10}	Mean
1	1	1	1	1	1	0	0	0	1	1	0.7
2	2	1	1	2	1	0	1	1	2	1	1.2
4	2	1	2	2	2	4	4	2	2	2	2.3
8	3	3	5	4	5	4	5	5	4	4	4.2
16	5	6	5	5	4	4	3	4	4	4	4.4
32	4	4	5	4	4	4	4	4	4	4	4.1
48	6	6	5	3	5	5	4	3	5	5	4.7

TABLE B2 - Functional response experiment (24hr)

Predator - Protonymph P. persimilis

Prey - Larvae of T. urticae

Density of Prey	Number of prey killed										
	R_1	R_2	R_3	R_4	R_5	R_6	R_7	R_8	R_9	R_{10}	Mean
1	1	1	1	1	1	0	1	1	1	1	0.9
2	2	2	2	2	2	1	2	2	2	2	1.9
4	2	4	3	2	3	4	3	3	3	3	3.0
8	5	5	4	3	3	5	3	4	5	3	4.0
16	5	4	6	4	7	7	6	7	4	5	5.5
32	6	5	7	5	6	7	6	7	5	5	5.9
48	5	8	7	8	7	6	6	7	8	7	6.9

TABLE B3 - Functional response experiments (24hr.)

Predator - Protonymph P. persimilis

Prey - Protonymph of T. urticae

Density of Prey	Number of prey killed										
	R_1	R_2	R_3	R_4	R_5	R_6	R_7	R_8	R_9	R_{10}	Mean
1	1	1	1	1	1	1	1	0	1	1	0.9
2	2	2	1	2	2	1	1	2	2	2	1.8
4	3	2	2	3	3	3	4	2	3	4	2.9
8	4	5	6	4	4	6	5	4	4	4	4.6
16	4	4	6	4	4	4	4	4	4	3	4.1
32	5	4	5	5	5	3	5	7	3	5	4.7

TABLE B4 - Functional response experiment (24hr.)

Predator - Protonymph P. persimilis

Prey - Female deutonymph of T. urticae

Density of Prey	Number of prey killed										
	R_1	R_2	R_3	R_4	R_5	R_6	R_7	R_8	R_9	R_{10}	Mean
1	1	1	1	1	1	1	1	1	1	1	1.0
2	2	1	2	2	2	1	1	2	2	2	1.7
4	2	2	1	1	2	3	2	2	2	2	1.9
8	2	3	2	3	3	4	2	2	2	3	2.6
16	2	4	3	2	3	4	2	2	3	3	2.8
32	2	3	4	3	3	4	3	3	2	2	2.9

TABLE B5 - Functional response experiment (24hrs.)

Predator - Deutonymph *P. persimilis*

Prey - Eggs of *T. urticae*

Density of Prey	Number of prey killed										
	R_1	R_2	R_3	R_4	R_5	R_6	R_7	R_8	R_9	R_{10}	Mean
1	1	1	0	1	1	1	0	1	1	0	0.7
2	1	2	0	2	1	2	1	2	2	1	1.4
4	3	4	4	4	4	4	3	4	2	4	3.6
8	6	4	7	8	8	6	7	7	7	7	6.7
16	6	8	9	8	7	8	8	9	8	8	7.9
32	9	9	8	8	8	9	9	8	7	8	8.3
48	8	6	8	9	10	8	9	9	10	7	8.4

TABLE B6 - Functional response experiment (24hrs.)

Predator - Deutonymph *P. persimilis*

Prey - Larvae of *T. urticae*

Density of Prey	Number of prey killed										
	R_1	R_2	R_3	R_4	R_5	R_6	R_7	R_8	R_9	R_{10}	Mean
1	1	1	1	1	1	1	1	1	1	1	1.0
2	2	2	2	2	2	1	2	2	2	2	1.9
4	4	4	4	4	4	3	3	4	4	3	3.7
8	6	6	6	5	6	7	5	6	6	7	6.0
16	8	8	10	9	9	9	6	9	9	9	8.6
32	8	10	11	10	11	10	11	9	9	10	9.9
48	10	9	9	10	13	11	8	10	14	8	10.2

TABLE B7 - Functional response experiment (24hr.)

Predator - Deutonymph P. persimilis

Prey - Protonymph of T. urticae

Density of Prey	Number of prey killed										
	R_1	R_2	R_3	R_4	R_5	R_6	R_7	R_8	R_9	R_{10}	Mean
1	1	1	1	1	0	1	1	1	1	1	0.9
2	2	1	2	2	2	2	2	0	1	2	1.6
4	4	3	4	4	3	3	3	4	4	3	3.5
8	6	7	4	3	6	4	5	6	5	5	5.1
16	6	8	6	8	6	6	8	7	8	8	7.1
32	10	4	6	6	11	7	5	6	8	6	6.9

TABLE B8 - Functional response experiment (24hr.)

Predator - Deutonymph P. persimilis

Prey - Female deutonymph of T. urticae

Density of Prey	Number of prey killed										
	R_1	R_2	R_3	R_4	R_5	R_6	R_7	R_8	R_9	R_{10}	Mean
1	1	1	1	1	1	1	1	0	1	1	0.9
2	2	1	1	2	1	1	2	1	2	2	1.5
4	3	2	3	2	3	3	4	3	2	3	2.8
8	3	3	4	5	3	3	3	2	4	4	3.4
16	4	5	4	4	5	3	4	4	4	3	4.0
32	5	6	4	3	4	3	3	4	4	3	3.9

TABLE B9 - Functional response experiments (24hr.)

Predator - Adult female *P. persimilis*

Prey - Eggs of *T. urticae*

Density of Prey	Number of prey killed										
	R_1	R_2	R_3	R_4	R_5	R_6	R_7	R_8	R_9	R_{10}	Mean
1	1	0	1	1	1	1	0	0	0	1	0.6
2	1	2	2	2	2	2	1	2	2	2	1.8
4	4	4	3	4	3	4	3	3	4	2	3.4
8	7	8	6	7	5	7	6	7	5	8	6.6
16	11	11	13	13	12	14	9	11	13	7	11.4
32	19	20	21	19	21	23	20	18	16	20	19.7
64	23	21	20	19	22	23	23	23	20	22	21.6
96	27	23	26	27	23	26	28	24	24	22	25.0

TABLE B10 - Functional response experiments (24hr.)

Predator - Adult female *P. persimilis*

Prey - Larvae of *T. urticae*

Density of Prey	Number of prey killed										
	R_1	R_2	R_3	R_4	R_5	R_6	R_7	R_8	R_9	R_{10}	Mean
1	1	0	1	1	1	1	1	1	1	0	0.8
2	0	2	1	1	0	2	1	1	0	2	1.0
4	0	2	1	2	1	3	3	4	1	3	2.0
8	6	4	4	3	5	1	4	1	1	3	3.2
16	8	2	7	5	7	7	9	8	4	5	6.2
32	16	10	8	6	5	8	11	7	16	3	9.0
48	17	20	11	22	20	15	16	15	18	16	17.0
64	21	21	10	25	13	20	14	19	15	25	18.3
96	30	33	22	18	19	27	26	19	18	23	23.5

TABLE B11 - Functional response experiment (24hr.)

Predator - Adult female P. persimilis

Prey - Protonymph T. urticae

Density of Prey	Number of prey killed										
	R_1	R_2	R_3	R_4	R_5	R_6	R_7	R_8	R_9	R_{10}	Mean
1	1	0	0	1	1	1	1	1	1	1	0.8
2	1	2	1	1	2	1	1	0	1	1	1.1
4	3	3	3	3	3	3	3	1	3	4	2.9
8	3	4	4	2	5	5	2	5	4	6	4.0
16	4	9	5	3	9	6	5	5	6	5	5.7
32	8	9	13	10	10	9	8	6	14	10	9.7
48	10	7	11	18	8	11	15	11	11	12	11.4
64	11	12	11	17	9	14	13	14	11	11	12.3

TABLE B12 - Functional response experiment (24hr.)

Predator - Adult female P. persimilis

Prey - Female deutonymph of T. urticae

Density of Prey	Number of prey killed										
	R_1	R_2	R_3	R_4	R_5	R_6	R_7	R_8	R_9	R_{10}	Mean
1	0	1	0	1	1	1	1	0	1	1	0.7
2	0	2	2	1	0	1	1	1	2	2	1.2
4	2	1	3	3	3	2	4	3	2	2	2.5
8	5	3	5	3	5	2	5	6	4	2	4.0
16	3	4	5	7	7	4	4	7	3	4	4.8
32	10	9	6	6	7	6	8	8	6	9	7.5
64	7	7	11	8	8	9	6	9	6	6	7.7

C. Functional response to two-prey situation

TABLE C1 - The feeding by protonymph P. persimilis when eggs and female deutonymphs of T. urticae were offered in combination.

Prey combinations			Replicates											
Prey	No.	%	1	2	3	4	5	6	7	8	9	10	Mean	% in diet
E	16	80	3	3	4	2	4	4	3	4	4	2	3.3	
D	4	20	1	0	0	1	1	0	1	0	0	1	0.5	13.2
E	12	60	2	2	1	2	3	1	6	3	4	2	2.6	
D	8	40	2	1	1	1	0	2	0	1	1	3	1.2	31.6
E	10	50	4	2	1	1	2	4	1	2	3	2	2.2	
D	10	50	0	1	2	2	1	0	2	2	1	2	1.3	37.1
E	8	40	3	0	3	3	2	1	1	1	3	0	1.7	
D	12	60	1	2	1	1	2	2	3	1	3	3	1.9	52.8
E	4	20	2	1	0	0	1	2	2	1	0	0	0.9	
D	16	80	1	2	2	4	2	2	1	1	3	2	2.0	68.9

E - Eggs of T. urticae
D - Deutonymph of T. urticae

TABLE C2 - The feeding by protonymph P. persimilis when larvae and female deutonymphs of T. urticae were offered in combination.

Prey combinations			Replicates											
Prey	No.	%	1	2	3	4	5	6	7	8	9	10	Mean	% in diet
L	16	80	4	4	4	2	5	5	6	5	5	6	4.6	
D	4	20	0	1	1	2	0	0	0	0	0	0	0.4	8.0
L	12	60	3	1	1	3	2	4	2	4	4	4	2.8	
D	8	40	1	2	1	1	1	1	1	1	1	2	1.2	30.0
L	10	50	3	3	4	0	4	2	2	1	1	3	2.3	
D	10	50	1	2	1	3	1	1	2	2	3	1	1.8	43.9
L	8	40	1	1	2	3	3	2	2	3	0	2	1.9	
D	12	60	1	1	1	1	1	3	1	1	2	1	1.3	40.6
L	4	20	1	1	2	0	0	0	0	0	1	1	0.6	
D	16	80	1	1	2	2	3	2	2	2	2	1	1.8	75.0

L - Larvae of T. urticae
D - Deutonymph of T. urticae

TABLE C3 - The feeding by deutonymph P. persimilis when eggs and female deutonymphs of T. urticae were offered in combination.

Prey combinations			Replicates							
Prey	No.	%	1	2	3	4	5	6	Mean	% in diet
E	16	80	3	4	7	5	6	7	5.3	84.2
D	4	20	2	1	0	2	1	0	1.0	
E	12	60	2	4	2	5	4	6	3.8	69.7
D	8	40	3	2	3	0	1	1	1.7	
E	10	50	3	6	2	2	3	3	3.1	63.3
D	10	50	1	0	2	3	3	2	1.8	
E	8	40	2	1	2	1	4	1	1.8	45.8
D	12	60	2	2	3	3	1	3	2.1	
E	4	20	1	2	2	1	0	0	1.0	26.1
D	16	80	2	3	2	3	3	4	2.8	

E - Eggs of T. urticae
D - Deutonymph of T. urticae

TABLE C4 - The feeding by deutonymph P. persimilis when larvae and female deutonymphs of T. urticae were offered in combination

Prey combinations			Replicates							
Prey	No	%	1	2	3	4	5	6	Mean	% in diet
L	16	80	7	5	7	6	4	8	6.1	80.4
D	4	20	1	2	2	0	3	1	1.5	
L	12	60	3	1	3	4	4	1	2.7	51.6
D	8	40	2	3	3	2	2	3	2.5	
L	10	50	2	3	3	2	3	3	2.7	48.5
D	10	50	3	3	3	3	2	3	2.8	
L	8	40	1	1	3	2	1	3	1.8	42.3
D	12	60	2	3	2	2	3	3	2.5	
L	4	20	1	1	0	1	1	2	1.0	24.0
D	16	80	3	3	3	3	4	3	3.1	

L - Larvae of T. urticae
D - Deutonymph of T. urticae

TABLE C5 - The feeding by adult female P. persimilis when eggs and female deutonymphs of T. urticae were offered in combination

Prey combinations			Replicates																					
Prey	No.	%	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Mean	% in diet
E	16	80	10	9	9	9	12	12	12	8	12	7	14	14	14	13	15	12	13	15	12	12	11.7	89.1
D	14	20	1	0	1	1	2	3	0	0	2	2	2	2	2	3	0	2	1	2	2	2	1.5	
E	8	60	4	9	7	6	7	7	5	6	10	8	6	8	7	8	1	7	8	1	8	11	6.7	71.5
D	12	40	1	0	2	1	2	2	2	2	2	3	5	3	5	4	3	2	2	4	1	2	2.4	
E	10	50	4	3	7	8	6	6	7	7	8	8	6	8	7	9	6	3	5	9	10	3	6.5	66.5
D	10	50	4	2	1	2	4	3	4	4	2	2	2	6	4	2	4	4	3	3	4	3	3.15	
E	8	40	6	4	6	3	5	8	5	4	6	7	1	5	4	6	6	4	6	5	6	7	5.2	58.0
D	12	60	2	4	3	4	2	3	2	3	3	3	4	5	7	5	4	4	6	3	2	5	3.7	
E	14	20	1	3	3	2	3	2	2	2	2	1	2	0	1	1	3	2	2	0	2	3	1.85	27.4
D	16	80	4	2	5	4	4	4	4	6	6	5	9	3	3	8	5	4	5	4	4	6	4.75	

E - Eggs of T. urticae

D - Deutonymphs of T. urticae

TABLE C6 - The feeding by adult female P. persimilis when larvae and female deutonymphs of T. urticae were offered in combination

Prey combinations			Replicates																					
Prey	No.	%	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Mean	% in diet
L	16	80	10	4	7	3	4	2	3	2	2	3	0	5	3	5	5	9	3				4.12	
D	4	20	3	4	3	2	4	2	2	2	3	1	3	3	3	3	2	1	2				2.53	42.4
L	12	60	2	2	0	1	4	1	4	0	2	0	3	4	3	0	5	2	1	3	1	6	2.2	
D	8	40	8	6	4	3	4	4	3	4	4	3	4	3	5	4	4	4	5	3	5	4	4.2	70.0
L	10	50	4	2	1	2	1	0	3	2	1	1	2	1	2	2	1	1	2	0	3	1	1.6	
D	10	50	7	7	5	3	5	4	5	2	5	5	6	3	2	6	4	2	3	5	4	6	4.45	73.6
L	8	40	2	0	0	0	3	1	1	2	2	1	2	0	2	0	0	1	1	2	0	3	1.15	
D	12	60	7	4	4	3	4	4	5	6	6	5	5	6	4	3	7	6	5	5	5	5	4.95	83.6
L	4	20	2	1	0	2	1	0	0	0	1	1	1	1	0	0	2	0	0	1	0	0	0.65	
D	16	80	8	4	9	7	4	3	4	5	3	3	5	8	4	5	4	5	5	3	5	6	5.0	89.1

L - Larvae of T. urticae

D - Deutonymph of T. urticae

APPENDIX 3

PROGRAMME PREDICT LISTING

```
      PROGRAM PREDICT (INPUT,OUTPUT,TAPE5=INPUT,TAPE6=OUTPUT)
C
C     PROGRAM PREDICT
C
C     THIS PROGRAM SOLVES THE TWO-PREY-TYPE ROGERS RANDOM PREDATOR
C     EQUATION USING NEWTONS APPROXIMATION IN A DOUBLE CONVERGING LOOP
C
C     INPUT : 1.  SEARCH EFFICIENCY + HANDLING TIME FOR EACH PREY TYPE -
C                 (A1,B1,A2,B2)
C             2.  TOTAL TIME AVAILABLE - (T)
C             3.  NUMBER OF PREY DENSITIES FOR PREY TYPE 1 AND
C                 PREY TYPE 2 - (NPI,NPV)
C             4.  NPI VALUES OF PREY DENSITY FOR TYPE 1.
C             5.  NPV VALUES OF PREY DENSITY FOR TYPE 2.
C
      DIMENSIONS XNOI(50),XNOV(50)
      READ(5,1000)A1,B1,A2,B2
      READ(5,1001)T
      READ(5,1002)NPI,NPV
      READ(5,1003)(XNOI(J),J=1,NPI)
      READ(5,1003)(XNOV(J),J=1,NPV)
      WRITE(6,2000)A1,B1,A2,B2,T
      WRITE(6,2001)
      DO 3000 J=1,NPI
      XNI=XNOI(J)
      DO 3000 K=1,NPV
      XNV=XNOV(K)
      EI1-0. $ EV1=0
      EI2=100. $ EV2=100.
3011  IF(XNI.EQ.0.)GOTO3006
      EI1=XNEWT(B2,A1,B1,XNI,EI1,EV1,T)
      DI=ABS((EI1-EI2)/EI1)
      EI2=EI1
      GOTO3008
3006  DI=0. $ EI1=0.
3008  IF (XNV.EQ.0.)GOTO3009
      EV1=XNEWT(B1,A2,B2,XNV,EV1,EI1,T)
      DV=ABS((EV1-EV2)/EV1)
      EV2=EV1
      GOTO3010
3009  DV=0. $ EV1=0.
3010  IF(DI.GT.0.0001.OR.DV.GT.0.0001)GOTO3011
      WRITE(6,2002)XNI,XNV,EI1,EV1
3000  CONTINUE
1000  FORMAT(4F10.5)
1001  FORMAT(F10.5)
1002  FORMAT(215)
1003  FORMAT(1X,16F5.0)
2000  FORMAT(1H1,* PROGRAM ROGTWO : RESULTS :*,
     1/,* A FOR PREY TYPE 1 : *,E14.6,
     2/,* TH FOR PREY TYPE 1 : *E14.6,
     3/,* A FOR PREY TYPE 2 : *,E14.6,
     4/,* TH FOR PREY TYPE 2 : *E14.6,
     5/,* TOTAL TIME AVAILABLE *,E14.6)
2001  FORMAT(///,* 1ST PREY PRESENT . 2ND PREY PRESENT . 1ST PREY
     EATEN 1 2ND PREY EATEN *)
2002  FORMAT(2X,E14.6,5X,E14.6,4X,E14.6,3X,E14.6)
      STOP
      END
```

PROGRAMME PREDICT LISTING

```
1           FUNCTION XNEWT (B2,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.0.0001)GOTO1
9           XNEWT=E
10          RETURN
11          END
```

APPENDIX 4

THE RAW DATA OBTAINED FROM EXPERIMENTS ON MUTUAL INTERFERENCE

TABLE 4.1 Predator - Protonymphs of P. persimilis
Prey - 150 larvae of T. urticae on 32 cm^2 leaf disc
Duration of experiment - 8 hours

Predator density	Number killed in each replicate				Total	Average
	1	2	3	4		
1	6	5	4	5	20	5.00
4	16	16	18	18	68	17.00
8	33	35	31	34	133	33.25
16	53	57	60	62	232	58.00

TABLE 4.2 Predator - Protonymphs of P. persimilis
Prey - 150 larvae of T. urticae on 32 cm^2 leaf disc
Duration of experiment - 24 hours

Predator density	Number killed in each replicate					Total	Average
	1	2	3	4	5		
1	7	8	7	7	6	35	7.0
2	13	14	16	12	13	68	13.6
4	28	27	28	29	27	139	27.8
8	52	52	46	51	45	246	49.2
16	89	85	97	92	103	466	93.2

TABLE 4.3 Predator - Protonymphs of P. persimilis
Prey - 150 deutonymphs of T. urticae on 32 cm^2 leaf disc
Duration of experiment - 24 hours

Predator density	Number killed in each replicate				Total	Average
	1	2	3	4		
1	3	2	3	3	11	2.75
2	5	5	7	6	23	5.75
4	9	10	10	11	40	10.00
8	19	21	17	18	75	18.75
16	35	41	41	34	151	37.75

TABLE 4.4 Predator - Deutonymphs of P. persimilis
Prey - 150 larvae of T. urticae on 32 cm^2 leaf disc
Duration of experiment - 24 hours

Predator density	Number killed in each replicate				Total	Average
	1	2	3	4		
1	15	13	12	12	52	13.00
2	23	25	20	25	93	23.25
4	46	40	44	50	180	45.00
8	89	72	84	80	325	81.25
16	139	140	134	137	550	137.50

TABLE 4.5 Predator - Adult females of P. persimilis
Prey - 150 larvae of T. urticae on 32 cm^2 leaf disc
Duration of experiment - 24 hours

Predator density	Number killed in each replicate					Total	Average
	1	2	3	4	5		
1	23	21	20	23	20	107	21.4
2	34	33	36	35	30	168	33.6
4	34	34	41	45	45	199	39.8
8	44	58	59	60	62	283	56.6
16	77	75	81	69	103	405	81.0

TABLE 4.6 Predator - Adult females of P. persimilis
Prey - 150 deutonymphs of T. urticae on 32 cm^2 leaf disc
Duration of experiment - 24 hours

Predator density	Number killed in each replicate						Total	Average
	1	2	3	4	5	6		
1	10	11	11	12	7	9	60	10.0
2	19	19	20	18	20	15	111	18.5
4	28	30	32	27	23	25	165	27.5
8	38	44	52	61	51	36	282	47.0
16	57	82	96	93	82	62	472	78.7
32	112	107	97	100	100	108	624	104.0

TABLE 4.7 Predator - Adult females of *P. persimilis*
Prey - 150 deutonymphs of *T. urticae* on a trifoliate bean leaf
Duration of experiment - 24 hours

Predator density	Number killed in each replicate					Total	Average
	1	2	3	4	5		
1	10	11	9	9	7	46	9.2
2	16	19	17	15	20	87	17.4
4	25	32	29	28	34	148	29.6
8	53	52	51	63	57	276	55.2
16	90	86	80	71	92	419	83.8
32	121	121	125	127	108	602	120.4

APPENDIX 5

THE RAW DATA OBTAINED FROM EXPERIMENTS ON BEHAVIOURAL RESPONSES

Leaf No.		1					2					3					4					5					"Stem"				
Pred. density		1	2	4	8	16	1	2	4	8	16	1	2	4	8	16	1	2	4	8	16	1	2	4	8	16	1	2	4	8	16
Hours	1	.6	1.0	2.25	4.0	8.0	.4		.5	1.2	.2		.4	.25	.8	1.2		.4		.6	.6		.25	.2	2.4			.2	.75	1.2	2.0
Hours	2	.6	1.4	2.5	4.6	6.8	.2	.2	.5	.6	1.3		.2	.25	.8	1.2				.2	1.2			1.2	1.6			.2	.75	.6	1.8
Hours	3	.8	1.2	2.5	4.4	5.0		.2	.5	.8	1.2			.5	.4	.6		.2		.8	2.0		.25	1.0	1.4		.2	.4	.25	.4	2.8
Hours	4	1.0	1.4	2.25	5.0	4.2			.75	.8	1.2			.25	.6	1.2		.2		.4	1.4			.8	1.2			.4	.75	.2	2.4
Hours	5	1.0	2.0	2.5	5.0	4.2			.5	.6	1.2			.25	.2	.6			.25	.2	2.1			1.2	1.0				.25	.4	1.2
Hours	6	1.0	2.0	2.5	4.6	5.0			.5	.6	1.4			.5	.2	.4			.25	.4	1.8			1.2	.8					.4	1.6
Hours	7	1.0	2.0	2.75	5.0	5.4			.25	.6	.8			.5	.6	.2				.8	1.4			.2	1.0				.25	.2	1.6
Hours	8	1.0	2.0	3.0	5.4	5.4			.25	.2	.6			.25	.6					.4	1.2			.8	1.2				.25		1.8
Hours	22	1.0	2.0	3.25	5.6	6.0			.25	.2	.4				.2	.4				.4	1.0			.6	.8						1.2
Hours	23	1.0	2.0	3.25	5.6	5.8			.25	.4	1.2				.2	.6					.8			.4	.6					.4	.6
Hours	24	1.0	2.0	3.25	5.8	5.6			.25		1.0				.4	.8					.2			.2	.6					.4	1.4

TABLE 5.1 The number of predators in different densities found in the prey infested leaf (leaf No. 1) during the first 8 hours and 22nd, 23rd and 24th hours after introduction. (Average of 5 replicates). Density of prey - 150 female deutonymph *T. urticae*

TABLE 5.2 The aggregative response of predators to an uneven distribution of the prey, female deutonymphs of T. urticae, on 5 bean leaflets.

TABLE Density of predator - 1, Density of prey ( )

Prey	(0)					(20)					(40)					(80)					(160)					"Stem"				
Hours	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5
1						1					1					1							1	1						
2											1					1	1				1			1						
3							1				1										1			1					1	
4							1												1		1		1	1						
5							1				1										1		1	1						
6							1		1												1		1	1						
7							1		1												1		1	1						
21																					1	1	1	1	1					
22													1								1	1	1		1					
23									1				1								1	1	1							
24													1						1		1	1	1							

TABLE 5.3 Density of predator - 2, Density of prey ( )

Prey	(0)					(20)					(40)					(80)					(160)					"Stem"				
Hours	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5
1		1										1		1	1			2		1	2			1						
2													1				2	1		1	2			2	1					
3															1		1	1		1	2	1	1	2						
4				1							1	1	1								1	1	1	2	1					
5						1			1			1	1			1		1				1		2	1					
6						1			1							1		1				2	1	2	1					
7						2			1									1				2	1	2	1					
21						2												1	2			2	1	2						
22						2												1	2			2	1	2						
23						1										1		1	2			2	1	2						
24						2											1	1	2			1	1	2						

TABLE 5.4 Density of predator 4, Density of prey ( )

Prey	(0)					(20)					(40)					(80)					(160)					"Stem"				
Hours	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5
1			1			1	1	1				1	1	2		1		1	1	1	1	2		1	2	1				1
2	1	1				1	1		1	1			2			1			1		1	1	1	2	3		1	1		
3								1		1	1	1		1		1	2			1	1	2	3	3	2	1				
4		1	1							1	1			1	1	1		1			2	3	1	3	2			1		
5		1									1		1			1	1			1	2	2	3	4	3					
6							1				1		1			2			1	1	1	2	3	3	3		1			
7											1	1	1			2	1		1	1	1	2	3	3	3					
21								1			1	1			1			1		1	3	3	1	3	2			1	1	
22								1	1		1	1			1	1				1	2	3	2	3	2			1		
23							1	2			1	2	1			1				1	2	1		4	3			1		
24								2			1		1			1		1		1	1	4		4	3	1				

TABLE 5.5 Density of predator 8, Density of prey ( )

Prey	(0)					(20)					(40)					(80)					(160)					"Stem"				
Hours	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5
1	1	1		1	1			1	1		3	2	1	1	2	1	3			1		2	6	4	3	3			1	1
2				1				1			4	3	1		2	1	2			1	2	3	6	6	4	1			1	1
3			1					1	1		1	3		1	1	2	2	1	1	2	4	3	3	4	4	1		2	1	1
4						1	1		1	1	1		2		1	2	1	2		1	3	6	4	6	5	1			1	
5						1	1	2	1	1	2		1		1	2		2		1	3	7	3	5	5				2	
6						1	1	1	1	1	2		1	3	1	1		3	2	2	3	7	3	2	4	1				
7	1					2	1	1	2	1	1		1		1			3	2	1	4	7	3	4	5					
21							1					1		1		1	2	2	1	2	6	4	4	5	5	1		2	1	1
22	1										2	1			1	1	3	4		2	2	4	3	8	4	2		1		1
23				1			1		2	1	3		1		1	1	2	3		1	3	3	3	5	4		2	1		1
24								1	1	1	1		1	1	1	1	2	2	1	1	4	4	4	5	4	2	2			1

TABLE 5.6 Density of predator - 16, Density of prey ( )

Prey	(0)					(20)					(40)					(80)					(160)					"Stem"				
Hours	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5	R_1	R_2	R_3	R_4	R_5
1	1	1			2	2		2	1	1	5	4	1	1	1	3	3	2	5	5	5	4	4	9	4		3	3		3
2	1		2		2	2			2	2	4		2	2	1	3	4	4	4	3	5	9	6	8	5	1	1	1		3
3	4		1			1		1	3		2	2	2	1	1	1	2	5	5	5	7	11	5	6	8	1	1	1		2
4	2					1	2	1	3		2	1	1	1	3	3	1	4	5	3	5	9	7	7	8	3	2	2		2
5	1		1				1	1	1	3	3	4	1	2	3	5	2	6	7	1	4	8	7	6	6	3		1		3
6			1		1	1			1	2	2		4	1	3	8	2	5	7	3	2	11	5	7	6	3	2	1		1
7	1					1			1	3	3		1	1	1	4	2	8	6	5	6	10	5	7	5	1	3	1	1	1
21		3					2	1		3	6	2	2	1	2	2	4	5			4	4	7	14	10	4			1	1
22		5			1	2		1		4	3	4		1	3	3	5	6			4	1	4	13	7	4		5	2	1
23		5	4	2	1	1	1		2	2	4	5	1	1	2	4	2	2	1		4	2	3	9	9	3		4	1	2
24		5	2		1	2	1		1	3	2	3		1	1	4	3	1	5		5	2	7	9	9	3		3		

TABLE 5.7 Averages of 5 replicates

Predator	1					2					4					8					16				
Prey	0	20	40	80	160	0	20	40	80	160	0	20	40	80	160	0	20	40	80	160	0	20	40	80	160
1		0.2	0.2	0.2	0.4	0.2		0.6	0.6	0.6	0.2	0.6	0.8	0.8	1.2	0.8	0.4	1.8	1.0	3.0	0.8	1.2	2.4	3.6	5.2
2			0.2	0.4	0.4			0.2	0.8	1.0	0.4	0.8	0.4	0.4	1.6	0.2	0.2	2.0	0.8	4.2	1.0	1.2	1.8	3.6	6.6
3		0.2	0.2		0.4			0.2	0.6	1.2		0.4	0.6	0.6	2.2	0.2	0.4	1.2	1.6	3.6	1.0	1.0	1.6	3.6	7.4
4		0.2		0.2	0.6			0.6		1.2	0.4	0.2	0.6	0.4	2.2		0.8	0.8	1.2	4.8	0.4	1.4	1.6	3.2	7.2
5		0.2	0.2		0.6		0.4	0.4	0.4	0.8	0.2		0.4	0.6	2.8		1.2	0.8	1.0	4.6	0.4	1.2	2.6	4.2	6.2
6		0.4			0.6		0.4		0.4	1.2		0.2	0.4	0.8	2.4		1.0	1.4	1.6	3.8	0.4	0.8	2.0	5.0	6.2
7		0.4			0.6		0.6		0.2	1.2			0.6	1.0	2.4	0.2	1.4	0.6	1.2	4.6	0.2	1.0	1.2	5.0	6.6
21					1.0		0.4		0.6	1.0		0.2	0.6	0.4	2.4		0.2	0.4	1.6	4.8	0.6	1.2	2.6	2.2	7.8
22			0.2		0.8		0.4		0.6	1.0		0.4	0.6	0.4	2.4	0.2		0.8	2.0	4.2	1.2	1.4	2.2	2.8	5.8
23		0.2	0.2		0.6		0.2		0.8	1.0		0.6	0.8	0.4	2.0	0.2	0.8	1.0	1.4	3.6	2.4	1.2	2.6	1.8	5.4
24			0.2	0.2	0.6		0.4		0.8	0.8		0.4	0.4	0.6	2.4		0.6	0.8	1.4	4.2	1.6	1.4	1.4	2.6	6.4

APPENDIX 6

THE DATA OBTAINED FROM EXPERIMENTS ON POPULATION INTERACTION OF P. PERSIMILIS AND T. URTICAE

TABLE 6.1 The interaction when one predator was introduced per plant two weeks after the infestation with prey

Days from infestation	Mite Stages	R_1		R_2		R_3		R_4	
		Prey	Pred.	Prey	Pred.	Prey	Pred.	Prey	Pred.
	eggs	156		139		214		381	
	larvae	54		73		89		90	
	protonymph	147		122		159		78	
	deutonymph	73		118		67		48	
	females	11		08		03		7	
	males	12		11		00		3	
	total	453	00	471	00	532	00	607	00
	eggs	1074	14	2551	12	743	01	1169	03
	larvae	66	00	22	02	11	00	36	07
	protonymph	135	03	10	00	42	00	64	01
	deutonymph	100	00	51	00	97	01	67	00
	females	143	01	118	01	77	02	114	01
	males	84	00	39	00	47	00	25	00
	total	1602	18	2791	15	1017	04	1475	12
	eggs	3289	20	2929	38	2288	05	4022	65
	larvae	145	00	1398	00	437	00	659	00
	protonymph	65	02	154	01	129	02	257	00
	deutonymph	32	00	58	01	66	03	31	00
	females	116	07	122	15	58	08	46	11
	males	52	00	53	04	65	03	25	01
	total	3699	29	4714	59	3043	21	5040	77
	eggs	2816	63	3047	13	6626	142	4286	84
	larvae	872	22	668	13	2452	29	903	02
	protonymph	595	18	2160	17	2261	56	1933	05
	deutonymph	277	10	389	09	636	19	306	00
	females	74	06	53	05	186	56	115	11
	males	94	03	74	00	144	13	26	02
	total	4728	122	6391	57	12305	315	7569	104
	eggs	83	182	267	130	743	205	1108	203
	larvae	135	34	136	44	320	35	388	15
	protonymph	355	26	243	11	1544	06	2040	14
	deutonymph	185	16	230	03	614	05	1211	03
	females	55	57	183	60	162	33	261	16
	males	77	14	65	07	184	07	295	08
	total	890	329	1124	255	3567	284	5303	259
	eggs	00	00	02	42	24	117	Discontinued	
	larvae	00	00	01	25	11	72		
	protonymph	00	13	00	23	40	66		
	deutonymph	00	07	00	39	27	62		
	females	00	313	00	263	05	358		
	males	00	18	00	10	07	99		
	total	00	351	03	402	114	774		