POPULATION DYNAMICS OF A HOST-PARASITOID SYSTEM WITH PARTICULAR REFERENCE TO AGE-STRUCTURE EFFECTS

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ABSTRACT

An experimental study of laboratory populations of the stored-products moth, Cadra cautella Walker (Lepidoptera: Phycitidae) and its larval parasitoid, Venturia canescens Gravenhorst (Hymenoptera: Ichneumonidae) identified and quantified density- and age-dependent demographic characteristics of the host-parasitoid system. Host imago longevity and fecundity depended on larval weight at pupation. Observed effects of C. cautella larval competition for food on larval mortality, stage duration, and weight at pupation were successfully captured in a mathematical model. Host larval age significantly influenced inter-stage cannibalism and susceptibility to mortality resulting from parasitoid oviposition wounds. Both larval parasitoid developmental rates and adult parasitoid attack rates depended on host larval age. Long-term population experiments of host and host-parasitoid populations revealed that host populations fluctuated with a period slightly in excess of host generation time and that parasitoid populations were in synchrony with host populations.

ABREGE

Une étude expérimentale conduite en laboratoire sur des populations d'une pyrale des produits entreposés, Cadra cautella Walker (Lepidoptera: Phycitidae) et de son parasitoïde, Venturia canescens Gravenhorst (Hymenoptera: Ichneumonidae), s'attaquant à la larve, permettait d'identifier et de quantifier pour ce complexe hôte-parasitoïde, des caractéristiques démographiques dépendantes de la densité et de l'âge. La longévité et la fécondité de l'hôte adulte dépendaient du poids larvaire à la pupaison. Un modèle mathématique des effets de la compétition larvaire de C. cautella pour la nourriture en fonction de la mortalité et de la durée du stade larvaire, et du poids à la pupaison a pu être développé. L'âge larvaire de l'hôte influençait significativement le cannibalisme entre les stades et le risque de succomber aux blessures de ponte du parasitoïde. Les taux de croissance de la larve et de prédation de l'adulte du parasitoïde sont tous les deux dépendants de l'âge du stade larvaire de l'hôte. Des études de populations de l'hôte et du complexe hôte-parasitoïde démontraient que le temps de développement des populations de l'hôte excédait légèrement le temps de génération de l'hôte et que les populations du parasitoïde suivaient de développement des populations de l'hôte.

Suggested Short Title: Population Dynamics of a Host-Parasitoid System

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CLAIM TO ORIGINALITY

This study represents one of the most comprehensive studies concerning the demography of a host-parasitoid system.

The majority of the demographic characteristics, including density-dependent and age-specific phenomena, have been quantified for the first time for this host-parasitoid system.

The growth model is original and represents a major advance in our understanding and ability to describe the dynamic behaviour of populations of stored-products Lepidoptera.

The experimental manipulation of demographic characteristics (fecundity and longevity) of a species in long-term population experiments, is, to the best of the author's knowledge, completely novel.

The two strategic population models outlined in the final chapter, have not previously been proposed.

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INTRODUCTION AND LITERATURE REVIEW

The consensus among ecologists concerning the degree to which insect populations are regulated by density-dependent processes appears to fluctuate to the same extent as insect populations. A recent paper by Dempster (1983) represents the latest resurrection of this debate (Howard & Friske 1911; Nicholson 1933; Andrewartha & Birch 1954; Varley & Gradwell 1970). If nothing else, the apparent immortality of this controversy underlines the need for further research, a need that has been dramatically illustrated by the recent work of Hassell (1985). Only through a thorough integration of theory and empirical work, both in the laboratory and field, will significant progress be made towards understanding insect population dynamics. One critical area where a more comprehensive integration of theory and experimental work is needed is that of age structure and age-structured effects on insect population dynamics.

The importance of age structure on the behaviour and stability of natural populations is well recognized and in recent years has been the subject of an increasing number of theoretical studies (Oster & Takahashi 1974; Gurtin & Levine 1979; Cushing 1980; Gurney & Nisbet 1980; Hastings 1983, 1984a,b; Gurney & Nisbet 1985; Nunney 1985a,b,c; Murdoch, Nisbet, Blythe, Gurney & Reeve in press).

Several studies concerned with age-structured effects have focussed on the mechanisms responsible for creating large amplitude fluctuations in population numbers with periods approximately equal to the egg to adult maturation time, (Auslander, Oster & Huffaker 1974; Gurney & Nisbet 1985). There have been a number of examples of laboratory insect populations that display large population fluctuations with periods close to the generation time (Mertz 1969; Takahashi 1973; Bellows, 1982; Gurney, Nisbet & Lawton 1983). Indeed entomological folklore would have it that populations exhibiting discrete generations are rather common in both field and laboratory. Populations cycles of this nature, that is cycles that appear as discrete generations, are unpredicted; most age-structured population models predict a rapid broadening of age distributions into a pattern of overlapping continuous generations.

The phenomenon of insect population fluctuation and the mechanisms responsible for producing population cycles of this nature provided the underlying impetus for the work described in this study.

The recent and rapidly expanding literature concerned with the effects of age structure has, however, produced yet another example of the cyclical relationship between theory and empirical evidence so common in population biology. Many of the theoretical studies are, at best, only weakly tied to experimental observations. In particular the theoretical studies concerned with the mechanisms that produce discrete generations in insect populations have been inspired by a number of long-term laboratory studies involving stored-products moths of the family Phycitidae and a predator or parasitoid of the moth in free-running population cages (Flanders & Badgley 1963; Flanders 1968; White & Huffaker 1969a,b; Takahashi 1973; Benson 1974; Podoler 1974a; Gurney, Nisbet & Lawton 1983). In these long-term studies, a range of population behaviours and stability properties have been observed and a number of hypotheses have been formulated to account for these patterns. The hypotheses have invoked mechanisms either occurring entirely within the moth population or resulting from the action of the predator or parasitoid on the age structure of the population.

The development of population models that attempt to describe a particular system or restricted set of systems requires that a balance be achieved between realism and tractability. Increased realism often leads to the inability to identify those factors that are critical in producing a particular pattern of population behaviour, although a priori simplification of a population model runs the risk of neglecting important factors. Furthermore, valid tests of a model can only be achieved when the parameter values of the model are measured independently from the data against which the model is tested.

It is clear from the theoretical literature on age-structured effects on single-species and predator-prey or host-parasitoid population dynamics, and from the literature concerned with the biology and long-term population dynamics of stored-products Lepidoptera that population processes occurring in these laboratory populations are complex. This complexity necessitates a very thorough qualitative and quantitative

understanding of the demographic characteristics specific to an individual species, if reasonably realistic population models are to be formulated.

Furthermore, although a considerable amount of work has been done on the biology of stored-products Lepidoptera, these studies have used many different strains and species of moth, and environmental conditions and type of food have varied markedly. Therefore, there is a lack of solid data for any one species. In addition, although a number of density-dependent or age-dependent phenomena have been shown to occur, their effects have been only crudely quantified.

These insights made it very apparent that the first requirement of an investigation into the phenomenon of discrete versus overlapping generations in stored-products moths was an intensive experimental study of those aspects of the biology related to their population dynamics.

This thesis begins with a brief introduction to the importance of age structure on the dynamic behaviour of single-species and predator-prey systems and is followed by an introduction to the host-parasitoid system selected for this study: the stored-products moth, Cadra cautella (Walker) (Lepidoptera: Phycitidae) and the thelytokous larval parasitoid, Venturia canescens (Gravenhorst) (Hymenoptera: Ichneumonidae). Previous work with laboratory populations of stored-products Lepidoptera is then reviewed. The results of experiments undertaken to identify and quantify the demographic characteristics of host and parasitoid are presented together with a mathematical model formulated to describe the growth, duration and survival of the larval stage of C. cautella. The results of a series of long-term experiments based on free-running populations of the host alone, and host and parasitoid together, are presented. The thesis finishes with a general discussion of some of the implications of the experimental results and presents areas where future work is needed.

POPULATION DYNAMICS AND AGE STRUCTURE

The passing of time is a phenomenon that affects all organisms. Increasing age affects individuals and consequently populations. This is nowhere more apparent than in human populations. Age dictates to a great extent, for example, our legal rights, and our social status. Age plays as important a role in non-human species, where the probability that an

individual reproduces, dies or emigrates from a population is often strongly age-dependent. The enormous diversity in animal and plant 'life histories' is in part a result of the interaction between the passing of time (aging) and the maximization of individual reproductive success. Stearns (1980) and Charlesworth (1980) provided reviews of the evolution of age structure and life history patterns. As the demographic characteristics of a particular species are a function of evolutionary events, so are the demographic characteristics a function of the dynamic behaviour.

The impact of age structure on the dynamic behaviour of single-species population models has been investigated using a variety of approaches based on both discrete and continuous-time formalisms. The earliest efforts using a continuous-time approach were by Sharpe & Lotka (1911) and von Foerster (1959), although Leslie (1945, 1948) approached the problem using a discrete-time formalism. Subsequent work has expanded these models to include density dependence, variable environments, and stochasticity. Goodman (1967), Charlesworth (1980) and Nisbet & Gurney (1982) have presented discussions of the various formalisms and have provided extensive references to the work that has been done in this area. The studies have been based on complex and intimidating mathematics. With the exception of the discrete-time approaches of Leslie (1945, 1948) they have been primarily of theoretical interest and have not been a commonly-used approach to practical population modelling.

Most of these models predict a broadening of population age distribution until a stable age distribution is achieved, where the proportion of individuals in each age class remains constant through time and where a number of generations are present at any point in time. The incorporation of age structure has been found to influence the quantitative rather than the qualitative aspects of dynamic behaviour of single-species populations. Exceptions to these conclusions do occur and age-structured populations may oscillate in response to external stimuli such as annual climatic changes (Oster & Takahashi 1974; Gurney & Nisbet 1980).

Recently, the mathematical rigor of the continuous-time formalism of von Foerster (1959) for age-structured populations has been modified to produce an approach based on the use of analytically and numerically

simple time-delay mathematical models (Gurney, Nisbet & Lawton 1983). The assumptions are based on the description of the life history of a species as a sequence of arbitrary stages, defined such that individuals in a given stage are functionally identical; that is, all individuals of a given stage have the same per capita death and reproductive rates. This approach, although applicable to a wide range of animal species, is particularly appropriate for the description of insect life histories, where these stages are not only functionally but biologically real entities. This approach is being continually modified (Nisbet & Gurney 1983; Blythe, Nisbet & Gurney 1984) and is now a very powerful tool for use in the mathematical representation of insect populations.

Using these techniques, Gurney Nisbet & Lawton (1983) and Gurney & Nisbet (1985) have explored phenomena directly relevant to the theme of this study. In insects where the critical factor limiting population growth is larval food supply, they found that the manner in which the effect of larval competition for food is incorporated into the models can have profound effects on the dynamic behaviour of the population. If the effects of larval food limitation are manifest in the vital rates of a subsequent stage, for example reduced adult fecundity, the resulting population cycles typically have periods slightly in excess of twice the egg-to-adult maturation period. If the effects of larval competition are expressed directly on the larvae (usually in the form of increased mortality) cycle periods will be close to the insect's maturation period and larval competition will produce discrete generations. These authors have also found that the precise nature of the population cycles is critically dependent on the form of adult survivorship.

Mathematical models predicting self-sustaining discrete generations have also been formulated by Bellows (1982). In an excellent study combining theory and experimental work, he produced a discrete-time simulation model describing laboratory populations of the weevils Callosobruchus chinensis and C. maculatus. Bellows argued that the discrete generations resulted from highly asymmetric inter-instar competition.

Single-species population models incorporating age structure have been shown to generally differ only quantitatively from single-species models without age structure. The same situation does not occur when age

structure is incorporated into models of predator-prey or host-parasitoid systems. In particular age-specific predation introduces a range of possible stability properties and behaviours for these two-species systems (Oster & Takahashi 1974; Gurtin & Levine 1979; Hastings 1983, 1984a,b; Nunney 1985a,b,c; Murdoch, Nisbet, Blythe, Gurney & Reeve 1987). The behaviour and stability properties depend on, for example, the relative durations of adult and juvenile predator and prey stages, or the existence of invulnerable prey stages. Auslander, Oster & Huffaker (1974) have shown, using a complicated continuous-time model that a parasitoid can sufficiently affect the age structure of the host population to shift it from a continuous generation mode to a discrete generation mode.

The next section of this review will serve to introduce the reader to some of the basic biological attributes of the species chosen as the animal model for this study.

INTRODUCTION TO THE ANIMAL MODEL

A great many of the biological attributes of C. cautella and V. canescens relevant to the aim of the present work have been investigated experimentally as part of this study. Comparisons of the observed experimental results with those previously reported, and the presentation of published data pertinent to this study but not investigated experimentally, will be found in the discussion sections of the appropriate chapters. The purpose of this section is to provide a general overview and introduction to the biology of the host and parasitoid. It will be followed by a review of the previous studies that have examined the population dynamics of stored-products Lepidoptera.

The Host

Cadra cautella Walker (Lepidoptera: Phycitidae) is an economically important pest of stored grains, cocoa, dried fruit and nuts (Munro 1966). Its extensive geographic distribution is generally restricted to tropical and sub-tropical regions where it is found in association with stored-products (Benson 1973). Natural populations also occur (Richards & Thomson 1932).

Adults tend to emerge from pupae in the late afternoon (Steele 1970) and peak flight activity occurs in the late evening (Graham 1970). Pheromone levels in females increase to a peak about 3 h after the moth emerges and rapidly decline following mating (Kuwahara, Kitamura, Takahashi & Fukami 1968). Steele (1970) reported that the peak in mating activity occurs just after dusk. Females 'calling' males adopt a characteristic posture, where the abdomen is extruded and flexed upwards. Males respond to calling females by rapidly vibrating their wings, although erratically walking or flying about the female and releasing pheromones to stimulate copulation in the female (Benson 1973). The morphology of the sex pheromone glands of both sexes has been described by Dickins (1936). The male and female reproductive systems have been described by Joubert (1967, 1969).

Burges & Haskins (1964) investigated the development and survival of C. cautella under different temperature and humidity conditions. At 70% relative humidity they found that the limiting temperatures for development were 15 and 36°C, with the optimum temperature being 31°C. They found that temperature influenced the duration of all developmental stages but that humidity had a significant influence only on the larval stage. Larvae live within the food and construct galleries composed of silk frass and food. The dietary requirements of the larvae have been investigated by Fraenkel & Blewett (1946). Feeding larvae and larvae coming into contact with other larvae produce a secretion, originating in the mandibular gland, which causes the larvae to disperse (Corbet 1971; Mudd & Corbet 1973). Hagstrum & Sharp (1975) reported the occurrence of C. cautella larvae in diapause as part of a study on this species carried out in a citrus pulp warehouse. Hagstrum & Silhacek (1980) reported that larval diapause induction is a function of the interaction between genotype and the degree of larval crowding.

In addition to C. cautella there are a number of other Lepidoptera commonly associated with stored products: Sitotroga cerealellae (Ol.) (Gelechiidae), as well as Ephestia elutella (Hubner), Anagasta kuehniella (Zeller), C. calidella Guen., C. figulilella Gregs., and Plodia interpunctella (Hubner), all members of the Phycitidae. Richards & Thomson (1932) and Benson (1973) have reviewed the literature concerning

the biology of many of these stored-products moths. References to and comparisons with these species will be made in the present work.

The Parasitoid

Venturia canescens (Gravenhorst) (Hymenoptera: Ichneumonidae) has a virtually cosmopolitan distribution (Richards & Thomson 1932). Twenty-two species of Lepidoptera have been reported to serve as hosts for this parasitoid. Natural hosts include members of the Pyralidae, Tinaeidae and Yponomeutidae, although species of Oecophoridae and Gelechiidae have served as laboratory hosts (Salt 1976).

The parasitoid has a thelytokous reproductive mechanism, whereby diploid females produce only diploid female offspring. Males are extremely rare and functionless (Slobodchikoff & Daly 1971). Slobodchikoff (1982), in a study of morphological wing characteristics, was able to distinguish between individuals from wild and laboratory strains. He was unable to distinguish between clones initiated from a single laboratory strain, and he attributed this to a high degree of genetic heterozygosity among the wasps.

V. canescens is an endoparasite of the host's larval stage. Parasitoid larvae are found in host pupae, but oviposition in the pupal stage is uncommon (Diamond 1929; Ahmad 1936). Imagos feed on nectar, sugar or honey solutions but are not thought to feed on host fluids (Rogers 1970).

A number of studies have used V. canescens as an animal model to investigate foraging behaviour and patch time allocation, in the context of optimal foraging theory (Taylor 1974; Cook & Hubbard 1977; Hubbard & Cook 1978; Waage 1979; Cook & Hubbard 1980; Marris, Hubbard & Hughes 1986).

Volatile components released from the host, host silk and faeces serve as stimuli (Thorpe & Jones 1937; Thorpe 1938; Williams 1951; Matsumoto & Huffaker 1973a) that function to attract the wasp to areas where hosts are present. Once in these areas, contact with non-volatile components of the host's mandibular gland secretions 1) stimulates the parasitoid to tap the food medium with its antennae and to probe the food with the ovipositor (Corbet 1971; Corbet 1973; Mudd & Corbet 1973) and 2)

elicits specific orthokinetic and klinotactic behaviours that serve to keep the wasp in areas where hosts are present (Waage 1978).

Once a host is located, oviposition takes seconds. Following oviposition a characteristic cocking motion moves an egg from the ovaries to the tip of the ovipositor; this must occur before another host can be parasitized. Ovipositor morphology and the cocking motion were described by Rogers (1972a). Only one egg is laid per host encounter and there is incomplete avoidance of superparasitism (Simmonds 1943; Fisher 1961a; Rogers 1975). The morphological characteristics of eggs, the five larval instars, and pupae have been described by Corbet & Rotheram (1965). Only one parasitoid is able to complete development in a host and when superparasitism occurs it is the oldest larvae that survives. If both parasitoid larvae are in their first instar, the older larva destroys the younger by direct physical attack (Fisher 1961b). Greater age differentials between the parasites result in the physiological suppression of egg and 1st instar development due to the low oxygen tension in the host haemocoele (Fisher 1963). Eggs or larvae damaged or killed by direct attack or physiological suppression are subjected to a haemocytic response by the host (Fisher 1961b). Rogers (1970) reported that the final larval stage of C. cautella was able to mount a successful defense reaction to a primary infection of the parasite. He felt that this response was the result of damage to the egg during oviposition. Eggs and young first instar larvae of V. canescens are thought to have a coating on their surface that prevents recognition by host defense mechanisms (Salt 1968).

DYNAMIC BEHAVIOUR OF LABORATORY POPULATIONS OF STORED-PRODUCTS LEPIDOPTERA

Since the experiments of Utida (1941), Crombie (1945, 1946) and Park (1948), stored-products insects have been popular laboratory animal models for the study of insect population dynamics. In addition to the work involving stored-products beetles, weevils (Bellows 1982) and Lepidoptera have been used by investigators wishing to study the long-term behaviour of laboratory populations. The very fact that these are stored-products insects has been the reason that they are so often

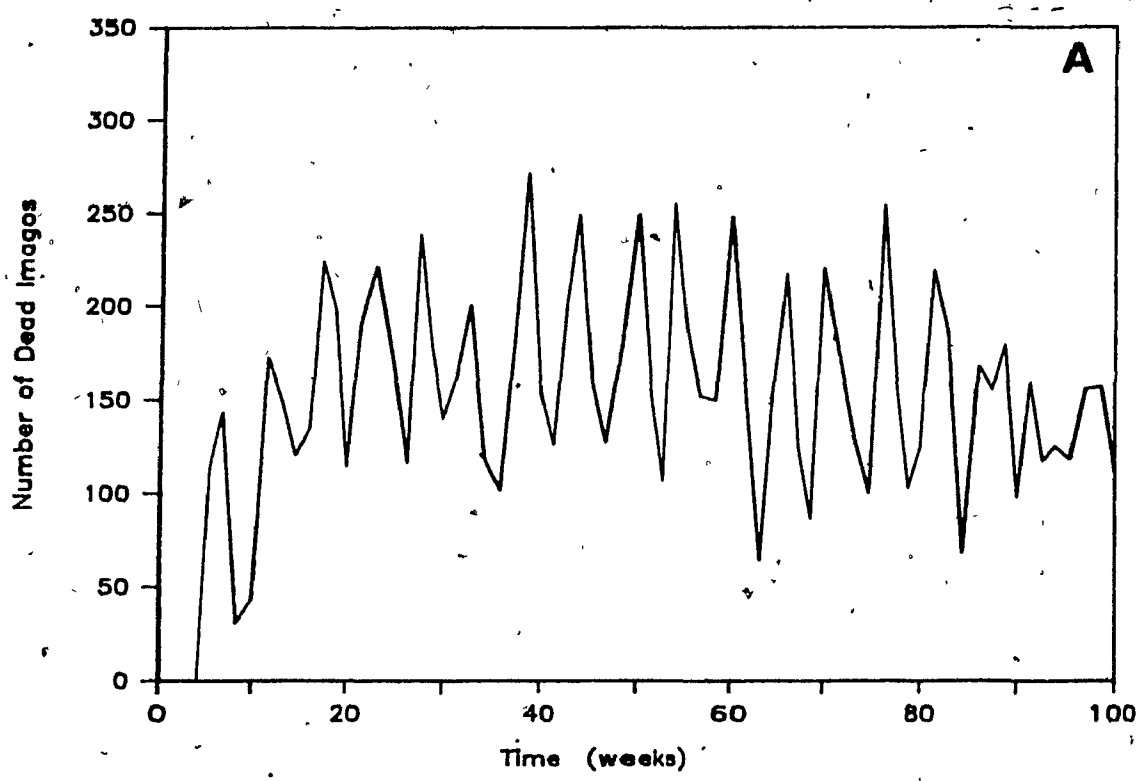
selected for these studies. First their habit of living in stored agricultural products results in their being considered pests in many parts of the world and, as such, knowledge of their biology is of applied importance. Furthermore, stored products are an inviable food source easily obtained, manipulated and quantified, freeing the culturing of the insects from the availability of a living food source.

There have been a number of studies that have investigated the dynamic behaviour of laboratory populations of stored-products Lepidoptera, both in the context of single-species populations and two-species populations involving parasitic bacteria, predators and parasitoids. The results of studies involving single-species and host-parasitoid populations will be briefly summarized. The studies employ a basic experimental protocol whereby food is added to a cage at a fixed rate per unit time and remains in the cage for some fixed period of time. Populations are censused by removing and counting dead imagos in the cage at some fixed time interval.

Cadra cautella and Venturia canescens were the host and parasitoid of choice in an extensive series of experiments by Takahashi (1959, 1973). The results of one of Takahashi's single species population cages and one of the host-parasitoid population cages are presented in Fig. 1.1. These experiments were run in small cages (0.0156 m^3) at 30°C, using rice bran, added at the rate of 20 g/week. Single-species populations were food-limited and showed a distinct cyclical behaviour, with a cycle period of about 40 days, a value slightly in excess of the minimum developmental period. Both species in the host-parasitoid cages tended to show synchronous cyclical behaviour with periods of about 36 days. Takahashi (1959) found that as the depth of the food in the experimental cages increased, thereby decreasing the searching efficiency of the parasitoid, populations were less likely to become extinct and the amplitude of the fluctuations in the host population decreased.

In a long series of experiments (Flanders & Badgley 1963; Flanders & Hall 1965; Flanders 1968), Anagasta kuehniella was used in conjunction with the deliberate or accidental introduction of Bacillus thuringiensis, Tribolium confusum, the predatory mite Blattisocius tarsalis, and/or V. canescens. The experiments were conducted at 27°C in cages with a volume of 0.13 m^3; the rate of food replacement varied from 3.85 g/week to 7.7

Figure 1.1. Ten day counts of dead imagos of Cadra cautella and Venturia canescens in long-term population cages. Data from Takahashi (1973, Fig. 3). A. Single-species population cage. B. Host-parasitoid population cage. The black line denotes the host (C. cautella) although the red line depicts the parasitoid (V. canescens).


A
Number of Dead Imagos
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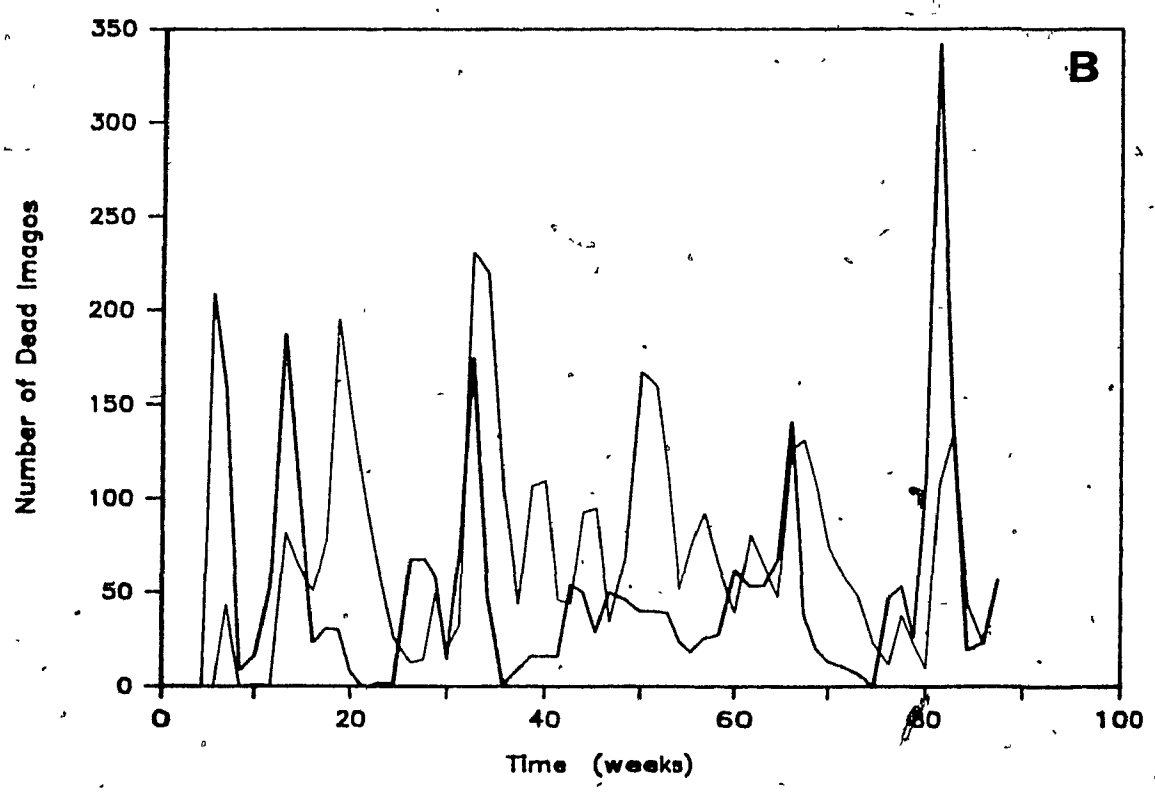
60
80
100
Time (weeks)


B
Number of Dead Imagos
350
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50
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40
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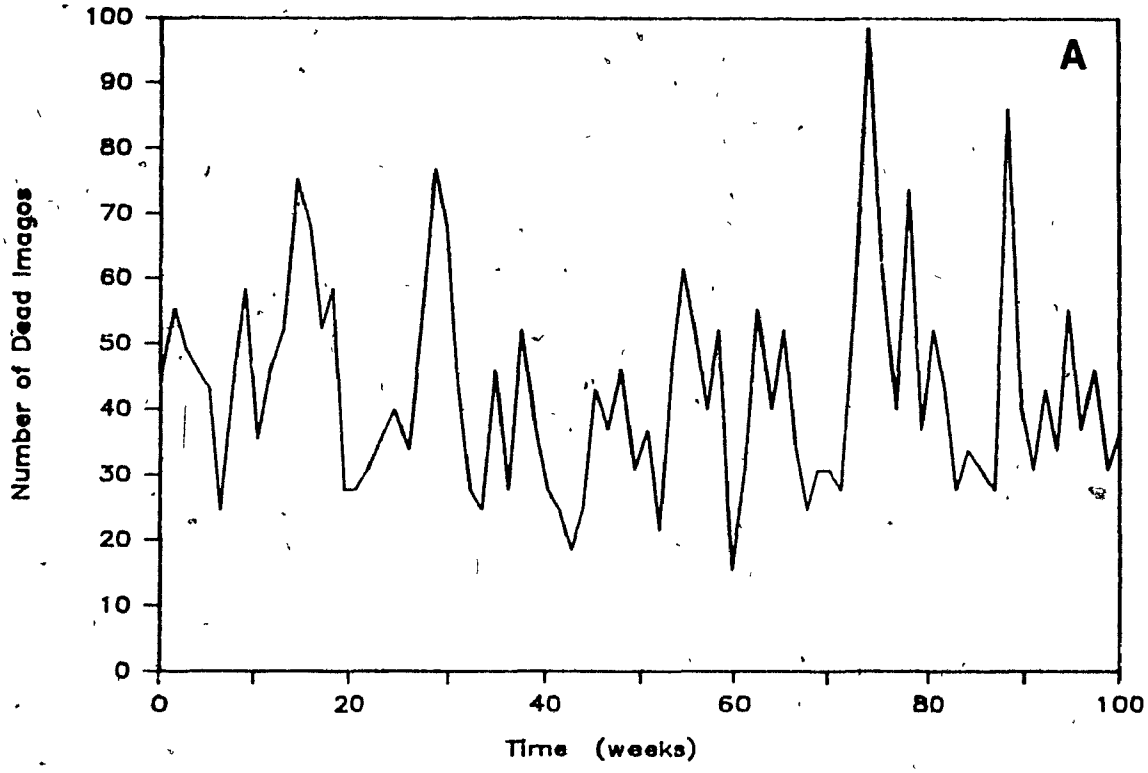
80
100
Time (weeks)

g/week. A large number of cages were established and the shape and size of the containers in which the food was placed varied among cages. In addition the food in some cages was covered with different depths of expanded mica ('vermiculite'). The vast majority of the population cages were 3 or more species systems and as a result of different treatments there was virtually no replication. Observations made in this set of studies include a distinct periodicity in the population fluctuations of the host, with cycle periods being slightly in excess of the host developmental period. It was suggested that this periodicity was due to intense competition (cannibalism and territoriality) amongst 1st instar larvae. The amplitude of host population cycles depended on the size of the container in which food was placed and on the depth of expanded mica over the food, with amplitudes decreasing with increased amounts of vermiculite. Parasitoid numbers were found to fluctuate in synchrony with the host population, regardless of whether or not the parasitoid was regulating the host population, although the stability of the system, as measured by the frequency of extinctions, decreased as the area for host refuge increased.

White & Huffaker (1969a,b) performed a series of long-term experiments using A. kuehniella, B. tarsalis and V. canescens. The experiments were conducted at 26°C in cages with a volume of 0.12 m^3; the rate of food addition was 8 g/week. Examples of the results from their single-species cages and host-parasitoid cages are presented in Fig. 1.2. They concluded that in the absence of the parasitoid, host populations fluctuate randomly about an equilibrium, show no indication of periodicity or discrete generations, and are regulated by food availability coupled with competition among early larval stages. Host-parasitoid populations were found to exhibit distinct host generations with parasitoid populations fluctuating in synchrony with the host. These generations were separated by a period of 54 days, 12 days more than the minimum developmental period of the host (42 days). Overlaid on population fluctuations due to the discreteness of host generations were population cycles with a period of four generations. White and Huffaker (1969b) concluded that the action of the parasitoid on the age structure of the host population was responsible for producing discrete generations in the host population. "The discreteness arises from the effective

Figure 1.2. Three and a half day counts of dead imagos of Anagasta kuehniella and Venturia canescens in long-term population cages. A. Single-species population cage. Data from White & Huffaker (1969a, Fig. 3) B. Host-parasitoid population cage. Data from White & Huffaker (1969b, Fig. 2). The black line denotes the host (A. kuehniella) although the red line depicts the parasitoid (V. canescens).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Number of Dead Imagos
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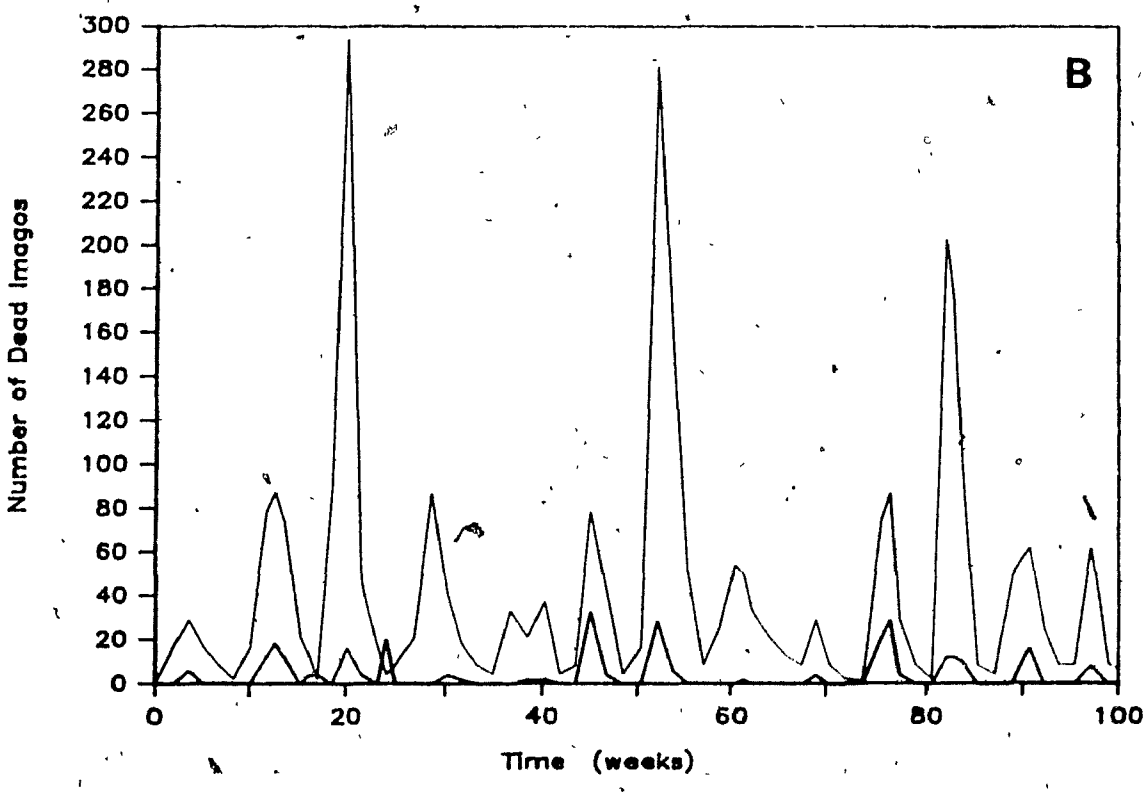
B
Number of Dead Imagos
Time (weeks)
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60
80
100

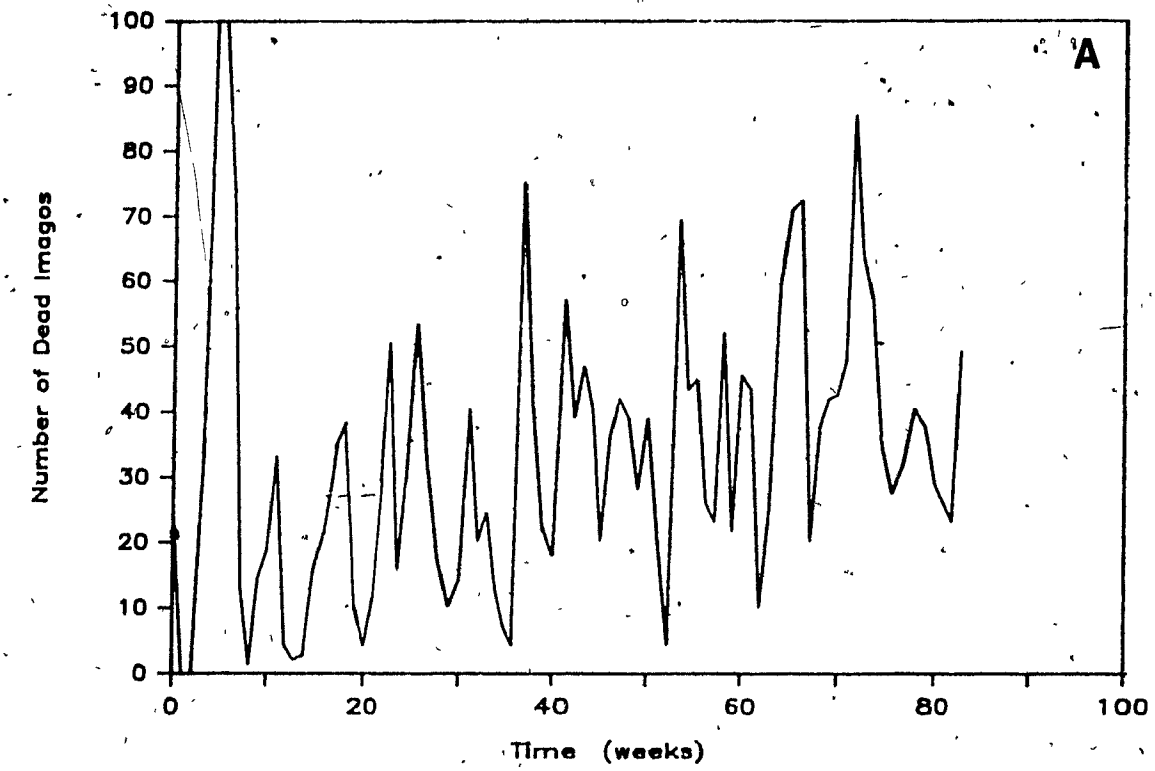
parasitization of all the earliest and latest-developing immature host larvae in a given generation, thereby synchronizing the emergence of adults" (White & Huffaker 1969b).

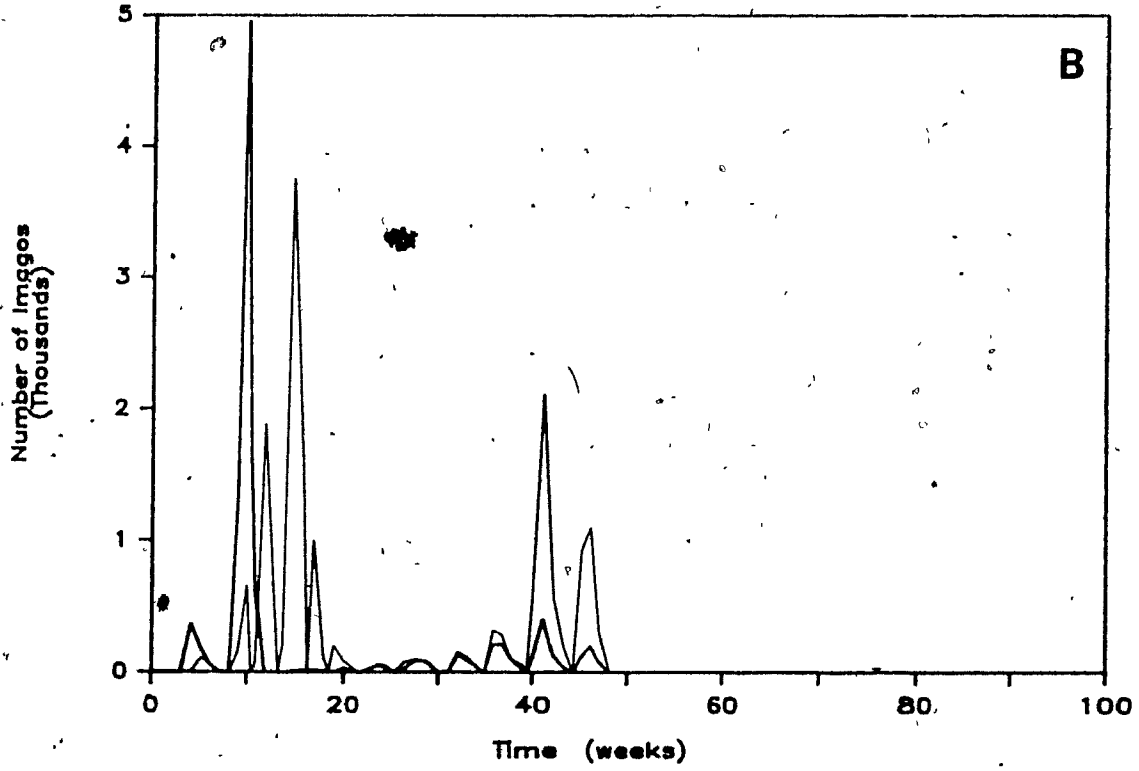
Conclusions reached by the above authors were based on the interpretation of the degree of food utilization and the number of host or parasitoid imagos produced. Without knowledge of the events occurring in the other life-history stages, these conclusions can only be considered as hypotheses. Following the development of techniques for the analysis of insect life-table data (Varley & Gradwell 1960) a number of workers applied these techniques to the analysis of long-term host-parasitoid populations involving stored-products Lepidoptera.

Hassell & Huffaker (1969) analysed a series of data collected from long-term populations of A. kuehniella and V. canescens carried out in very large population cages (13.8 m^3) at 25°C at a food replacement rate of 24 g/week or 144 g/week. Host and parasitoid populations exhibited largely discrete generations allowing the use of life-table analysis. The authors concluded that parasitism and early larval mortality were the important mortalities determining host and parasitoid population densities. Early larval mortality was thought to be due to competition of early instars for space and food and/or due to the delayed effects of larval food limitation on adult host fecundity. Early larval mortality was also thought to be due to wounds inflicted by the parasite during oviposition.

Podoler (1974a) investigated the dynamics of a population of Plodia interpunctella and V. canescens. Figure 1.3b presents the change in the numbers of host and parasitoid through time. The experiments were carried out at 30°C in a 0.73 m^3 cage. Podoler concluded that parasitism contributes most to the changes in total mortality, but that egg mortality was important in determining the level of total mortality. Reductions in adult egg fecundity as a result of larval food competition were a component of egg mortality as were changes in sex ratio and a lack of sychronization in male and female imago emergence. Podoler also identified significant density dependence in pupal mortality that he attributed to cannibalism by 5th instar larvae. Figure 1.3a presents data from Gurney, Nisbet & Lawton (1983) and has been included to show

Figure 1.3. Host (Plodia interpunctella) and parasitoid (Venturia canescens) imago population densities in long-term population cages. A. Seven day totals in a single-species population cage. Data from Gurney, Nisbet & Lawton (1983, Fig. 5). B. Population densities in a host-parasitoid population cage. Data from Podoler (1974a, Fig. 1). The black line denotes the host (P. interpunctella) and the red line depicts the parasitoid (V. canescens).


A
Number of Dead Imagos
0
10
20
30
40
50
60
70
80
90
100
0
20
40
60
80
100
Time (weeks)


B
Number of Imagos (Thousands)
0
1
2
3
4
5
0
20
40
60
80
100
Time (weeks)

comparable data on the single- species dynamics of P. interpunctella (cage volume 0.005 m^3, rate of food replacement 7 g/week).

Benson (1974) conducted long-term experiments on the dynamics of C. cautella and Bracon hebetor, a gregarious ectoparasite of the larvae. Benson suggested that the key factors causing change in the host population were egg and early larval mortality, caused either by larval competition for food and space, or by variation in imago fecundity. He also presented data suggesting delayed density-dependent mortality of 3rd and 4th instar larvae caused mainly by the action of the parasite.

Although these studies employing life-table analyses are an improvement over the earlier studies concerning the dynamic behaviour of these host- parasitoid populations, life-table analyses can contribute little to the understanding of processes occurring within a generation. This point has been demonstrated in recent work by Hassell (1985), who illustrated the problems in detecting density dependence from typical life-table data. Furthermore, life-table analysis, and the discrete-time population models resulting from such analyses are inherently unable to describe the dynamics of populations with overlapping generations and as a result do not form a generally suitable approach to the study of single-species populations of these stored-products insects.

This review has described the importance of age structure in population dynamics and has emphasized the need for a thorough qualitative and quantitative understanding of the demographic characteristics of a species, if one wishes to understand what factors are important in determining stability and behaviour even in relatively simple laboratory populations. For example, previous experimental work has shown that, in stored-products Lepidoptera, larval competition for a limited food resource may express itself either directly on the larval population through increased mortality or indirectly through its effect on the survival or fecundity of subsequent stages. Theoretical work has shown that the pattern of population cycling may be critically dependent on which of these two results of larval competition is dominant in a population.

GENERAL MATERIALS AND METHODS

The original cultures of C. cautella and V. canescens were obtained in 1982 from the Stored-Product Insects Research and Development Laboratory, United States Department of Agriculture, Savannah, Georgia, and were maintained at Macdonald College through the course of this research.

Environmental conditions for basic culture maintenance and all experimental work were 27±1°C, 85±5% R.H. (mean ± range), and 12:12 L:D. Food for the moth larvae consisted of commercially obtained wheat flakes, prepared by briefly heating (about half a minute) whole wheat kernels to a temperature of about 60°C and then passing the kernels through a roller mill. This process ruptures the seed coating and produces round flakes 1-2 mm thick and 5-10 mm in diameter. Handling results in breakage of these flakes into smaller pieces, but relatively little flour dust is produced. Prior to use, wheat flakes were steam-sterilized in 1 l containers for 30 minutes. Normally moth and wasp imagos were not provided with food or water. However some experiments did examine the effects of providing imagos with 2 g honey dissolved in 10 cc distilled water; this solution was changed daily.

Host eggs were obtained by lightly anaesthetizing imagos with CO_2 gas and transferring the adults to a 2 l round container. This container was inverted over a sieve (0.6 mm mesh) resting above a 150 mm petri dish. Eggs laid by the adults passed through the sieve into the petri dish. If eggs were collected from more than one container of adults at a time, eggs from all containers were pooled. This technique allowed the collection of large numbers of known-age host eggs which were counted individually as required for experiments. Partially collapsed or discoloured eggs were rejected.

Host cultures were started with 1000-2000 eggs and 400-500 g wheat flakes in 2.5 l glass containers with a wire mesh lid (1 mm mesh size) lined with #1 filter paper. The parasitoid was cultured by adding wasp imagos to host cultures containing larvae at least 10 days old. Cultures were maintained until the majority of imagos had emerged.

Experiments concerned with the longevity of host and parasitoid imagos and C. cautella fecundity used closed glass oil-lamp chimneys.

Ventilation occurred through a foam stopper. Transparent, polystyrene containers used in the other experiments were covered with fine mesh screening (60 μm) held in place by opaque snap-on polyethylene lids with at least 50% of the surface area cut away. Container dimensions will be given as length x width x height, or diameter x height.

DATA PRESENTATION AND STATISTICAL ANALYSES

In general individual insects are considered to represent an experimental unit. Thus sample size is the number of insects counted and not the number of vials. Exceptions to this will be noted in the text.

Unless otherwise stated values presented in the text will represent the mean±1 standard error of the mean (S.E.). Figures generally illustrate the mean±95% confidence interval; if a confidence interval does not appear it is because the interval is smaller than the size of the symbol used to represent the data point. Figures presenting proportion as the dependent variable do not include the appropriate binomial confidence limits if the purpose is to simply show patterns. Further information concerning experimental results illustrated in figures are presented in a series of Data Appendices numbered in correspondence with the figure number. In an attempt to keep the number of figures within reasonable bounds, only data sets depicting the range of results obtained from an experiment are presented; the data not illustrated in figures have been presented in the Data Appendices.

Cohort age is defined as the number of days elapsed from the birth of the egg, while stage age is defined as the number of days from the start of a stage.

The level of significance was set at alpha=0.01. Exact probability levels are presented for all statistical analyses. Parameter estimation involving non-linear functions was by non-linear regression (Secant Method) (SAS 1982). The cubic spline technique used from STATGRAPHICS (1985), is a procedure that connects a series of data points with a smooth curve using a cubic function. The resulting curve is a strictly empirical representation.

DEMOGRAPHIC CHARACTERISTICS OF CADRA CAUTELLA

The purpose of this chapter is to present results of a series of experiments designed to determine the effects of egg and larval density on larval and pupal development, and on imago survival and fecundity. In addition, inter-stage competition was investigated.

MATERIALS AND METHODS

Egg to Imago Development

The duration of the egg stage was determined by isolating groups of eggs (6 h old) in 60 mm petri dishes, containing a very thin layer of wheat flour. A total of 1676 eggs hatched from 6 petri dishes. The containers were examined at intervals and all hatched larvae were counted and removed.

The number of larval instars and sex differences in instar and pupal duration were determined by placing single eggs in 30 mm petri dishes containing 0.1, 0.3, 0.5 or 0.8 g wheat flakes. The dishes were examined daily and the stage and instar of the moth recorded. Larval molts were recognised by the presence of a pale head capsule and the presence of the molted head capsule from the previous instar. Molted head capsules were removed. Only those individuals which completed development were used in the analyses. This experiment was not designed to obtain accurate estimates of instar duration, or to examine the effect of food density on larval development. It was assumed that while the daily disturbance of the larvae would very likely affect absolute instar duration, the effects of handling would be equivalent for both sexes. Observed pupal durations are probably valid estimates, as the daily checks resulted in almost no disturbance of pupae.

Information on the effect of density on total developmental time and mortality was obtained by establishing groups of vials with varying initial numbers of eggs and recording the age and number of imagos emerging. Eggs (12 h old) were added to vials (3.0 x 6.0 cm) containing 1.7 g food at egg densities of 0.58 eggs/g (288 vials), 5.9 (60), 14.7 (60), 29.4 (90), 44.1 (90), 58.8 (90), 88.2 (149), and 117.6 (135). Eggs from a single pool were used for each density up to and including 29.4

eggs/g. The large number of eggs required and the time involved in preparing the vials for the higher densities required that three pools of eggs be used for each density. The vials were examined daily once adults started to emerge and the age and sex of each emerged imago was recorded.

More detailed information concerning the effect of larval density on duration and mortality of the individual stages was obtained by adding varying number of eggs (12 h old) to groups of vials (3.0 x 6.0 cm) containing 1.7 g wheat flakes. Initial egg numbers were 1 (0.58 eggs/g), 10 (5.88), 25 (14.71), 50 (29.4), 75 (44.1), and 100 (58.8). The vials for a particular density were established from a single pool of known-age eggs. Each density was established on a different day. At regular intervals, daily for earlier ages and every other day as the cohort aged, a number of vials were examined for each density: . 0.58 eggs/g (60 vials/sample), 5.9 and 14.7 (10), 29.4 and 44.1 (6), and 58.8 (5). The number of moths in each stage was recorded and the vials were discarded. The duration and survival of the larval instars and pupal stage were determined using the method of Ives & Gordon (in prep.).[1]

Additional data concerning pupal mortality were obtained by adding eggs (12 h old) to vials (3.0 x 6.0 cm) containing 1.0 g food. Thirty vials were prepared per density and the initial egg densities were: 1, 2, 4, 6, 8, 10, 12, 14, 18, 22, 26, 30, 40, 60, 80, 100. All densities were initiated using the same pool of eggs. The total number of moths emerging per vial was recorded and once all insects had emerged, the food in the vials was examined and the number of dead pupae recorded.[1]

Imago Survivorship and Fecundity

A number of experiments were undertaken to determine the factors which may influence the life span and fecundity of C. cautella. The basic experimental procedure consisted of placing newly emerged imagos (12 h old) in chimneys (8.3 x 17.5 cm) resting in 10 cm petri dishes. The petri dishes were changed daily and the numbers of eggs laid were recorded. In general moth eggs did not stick to the sides of the chimney, but any eggs

---

[1] The paper presenting this technique for estimating stage durations and through stage survivals is in preparation. The method is broadly similar to the one developed by Bellows & Birley (1981), but incorporates a number of improvements.

which did stick were counted and removed. Imago age at death was recorded. In order to summarize the data collected on age-specific fecundity into a single statistic, the age at which a female imago laid 50% of her eggs was calculated by multiplying female age by the number of eggs laid at that age and summing these values over the lifetime of the female. This sum was then divided by the total lifetime egg production.

The effect of larval density on fecundity and life span of resulting imagos was determined by placing 1 female and 2 males raised at the same density in a chimney. Imagos for this experiment were selected from those emerging from the last experiment described in the previous section. In order to determine what proportion of the eggs laid by females were viable, samples of 20 eggs were removed at random from the eggs produced by a female in a day. Samples were selected from females raised at different densities and at different ages. The eggs were placed in vials (1.0 x 4.0 cm) with a 'pinch' of wheat flour. The vials were examined after 3 days and the numbers of hatched eggs and eggs containing developed larvae were determined.

The effect of imago density on imago fecundity and survival was determined by isolating varying numbers of adults in chimneys. The imagos used in this experiment were reared at an initial density of 10 eggs in 1.7 g food. The numbers of imagos per chimney and number of chimneys were: 2 (28), 4 (16), 6 (10), 8 (11), 10 (11), 12 (10), 20 (10). Attempts were made to keep a 1:1 sex ratio, but some mistakes in sexing did occur. The number of eggs per female was calculated as the total number of eggs produced per chimney divided by the number of females per chimney. As a result chimneys were considered to represent the experimental unit for fecundity. Individuals were considered the experimental unit for testing treatment effects on imago life span.

Adults raised at an initial egg density of 10 eggs/1.7 g food were used to assess the effect of providing imagos with a food source (honey solution). Six chimneys containing 5 males and 5 females served as controls with no food, while 5 chimneys containing 5 males and 5 females were provided with a honey solution. The food source was placed in a small cotton-stopped vial inserted in a hole in the foam stopper. The same criteria as described above were used for testing treatment effects in this experiment.

Imagos emerging from the experiment concerning pupal mortality were used to determine the inter-relationship between imago weight and imago fecundity and life span, as well as the effect of initial egg density on imago weight at emergence. Newly emerged females were lightly anaesthetized with CO_2, weighed and placed in a chimney together with 2 males. The total number of eggs produced and the age of the female at death were recorded.

Inter-stage Interactions

A series of experiments were undertaken to determine if cannibalism occurred between the various stages of C. cautella. It was assumed that older instars would feed on younger stages; that is, while 5th instars might prey on 1st instars the reverse would not occur. Cannibalism by larval stages on pupae was also examined. The basic experimental protocol consisted of adding varying numbers of the older stage ('predator') to a fixed number of the younger stage ('prey'), in a fixed amount of food. After a period of 2 days 70% ethanol was added to the vials The vials were then examined and the number of older and younger stages determined. Based on the results from other experiments the following values were chosen to be the most appropriate ages (cohort age) to use for the various stages at the start of the experiment; egg stage, 0.5 days, 1st instar, 5; 2nd instar, 9; 3rd instar, 11; 4th instar, 15; 5th instar 20; pupal stage, 27 d. Preliminary analyses of these data consisted of regressing the number of 'prey' (y) recovered at the end of the experiment against the natural log of the number of 'predators' recovered (x) + 1. Slopes not significantly different from 0 were assumed to indicate the absence of cannibalism.

In order to determine if C. cautella larvae prey on the egg stage, 60 moth eggs (12 h old) were added to vials (1.5 x 5.0 cm) containing either 0.1 g (1st, 2nd, 3rd instars) or 0.2 g food (4th and 5th instars). A varying number of known-age larvae, raised at a density of 10 eggs/g food, were removed from the food and placed into the vials prior to the addition of the eggs. After 2 days the vials were examined and the number of intact eggs and larvae determined.

Inter-larval cannibalism was investigated in the following manner. The basic experimental protocol consisted of preparing a series of vials (3.0 x 6.0 cm) containing various numbers of eggs (12 h old). When the larvae were of the appropriate age, the contents (food and larvae) of the vials containing the older larvae were added to the vials containing the younger larvae. For each instar combination, there were 6 densities of the older larvae and 5 vials per density. Table 3.1 outlines the various initial egg densities used for the different instar combinations.

Cannibalism of pupae by larvae was investigated by preparing 60 vials (3.0 x 6.0 cm) containing 10 eggs in 1.7 g food and maintaining them until pupation had occurred (27 days). Larvae were reared by adding 100 eggs (1st and 2nd instars), 75 eggs (3rd), 50 eggs (4th) and 20 eggs (5th) to each of ten vials (3.0 x 6.0 cm) containing 1.7 g food. At the appropriate ages the contents of the vials containing the larvae were added to the vials containing the pupae. Ten vials served as controls and had 1.7 g of food added to them but no larvae.

RESULTS

Egg to Imago Development

The duration of the egg stage was found to be 3.5±0.2 days. The proportion of unhatched viable eggs is presented in Fig. 3.1a. Egg viability was found to be a function of female age but not a function of the density at which imagos were raised (age effect, $F_{(11,347)}=7.36$, $p<0.0001$; density effect, $F_{(7,347)}=1.99$, $p>0.056$). Figure 3.1b illustrates the observed decline in egg viability with increasing imago age (densities pooled). The data of Fig. 3.1b, together with results presented on age-specific fecundity (Fig. 3.8) were used to calculate the average proportion of viable eggs over the lifetime of an imago. The number of eggs produced per day was weighted by the proportion viable for a female of that age. On average 68.4% of the eggs produced by a female hatched.

The experiment which followed the course of development of single hosts showed that there were 5 larval instars. Table 3.2 presents a summary of the results of this experiment. No differences were detected between sexes in the durations of 1st, 2nd and 3rd instars. Females spent

Table 3.1. Initial egg densities used to investigate inter-instar cannibalism in the larval stage of Cadra cautella.

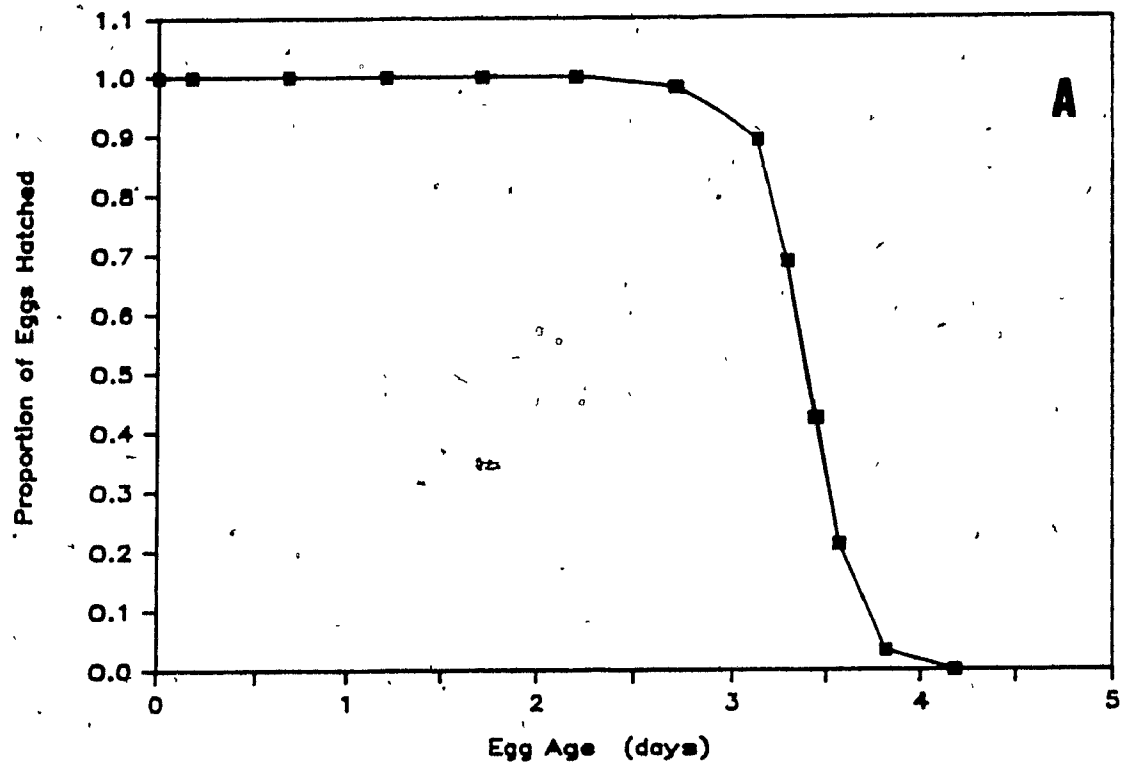
Interaction	Initial Egg Numbers						
	Younger Larvae	Older Larvae					
2nd on 1st	75	0	25	50	75	100	150
3rd on 1st	75	0	10	20	30	40	50
4th on 1st	75	0	10	15	20	25	30
5th on 1st	75	0	5	10	15	20	25
3rd on 2nd	50	0	10	20	30	40	50
4th on 2nd	50	0	10	15	20	25	30
5th on 2nd	50	0	5	10	15	20	25
4th on 3rd	50	0	10	15	20	25	30
5th on 3rd	50	0	5	10	15	20	25
5th on 4th	30	0	5	10	15	20	25

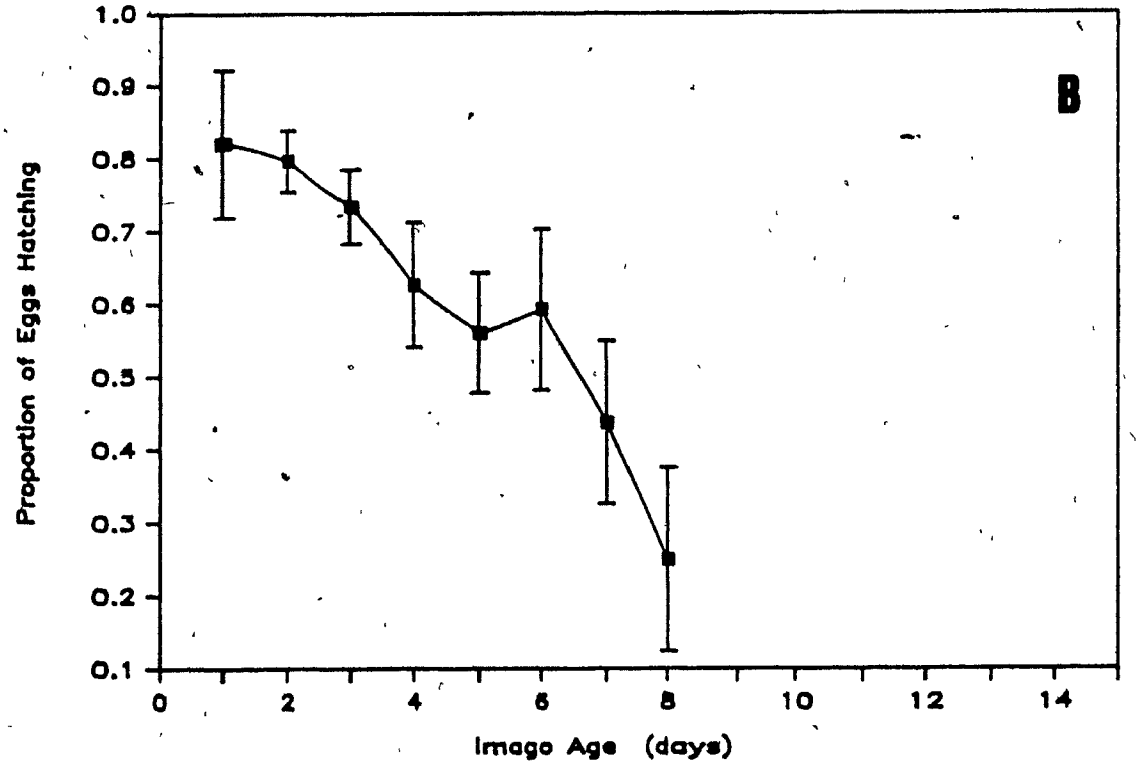
Table 3.2. Stage durations and imago weights for Cadra cautella raised individually.

STAGE	STAGE DURATION (days) MALES MEAN	S.D.	FEMALES MEAN	S.D.	PROB[1] $P > X^2$
1st Instar	4.0	0.5	3.9	0.6	> 0.222
2nd Instar	3.1	0.4	3.1	0.5	> 0.624
3rd Instar	3.1	0.7	3.3	0.5	> 0.094
4th Instar	4.3	0.7	4.7	0.6	< 0.004
5th Instar	7.6	3.4	8.0	2.1	< 0.001
Pupal Stage	8.2	0.5	7.7	0.5	< 0.001
Total Development	30.4	3.9	30.7	2.7	< 0.105

[1] Kruskal-Wallis Test for differences between sexes in stage duration.

Figure 3.1. Egg hatching in Cadra cautella. A. The duration of the egg stage. B. Changes in egg viability as a function of the age of the imago when the eggs were laid.


A
Proportion of Eggs Hatched
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
1
2
3
4
5
Egg Age (days)


B
Proportion of Eggs Hatching
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
2
4
6
8
10
12
14
Imago Age (days)

significantly more time as 4th and 5th instars, but less time as pupae, resulting in there being no difference between male and female pre-imaginal periods.

Initial egg density was found to have a significant effect on the pre-imaginal period of C. cautella (males, $F_{(7,1592)}$=174.1, p<0.0001, females, $F_{(7,1812)}$=192.3, p<0.0001). Both sexes responded in a similar manner to the effects of larval density (Fig. 3.2). At low larval densities males tended to emerge slightly earlier than females, but once larval densities exceeded 29 eggs/g there were no differences in pre-imaginal periods between the sexes. The proportion of imagos emerging was also found to depend on larval density ($F_{(7,667)}$=489.34, p<0 0001) The average number of imagos emerging per vial is presented in Fig. 3.3a, while Fig. 3.3b presents the relationship between mortality and larval density expressed as k-values (log # Eggs -log # Imagos). Density was found to have no effect on the sex ratio of the emerged imagos ($F_{(7,483)}$=2.21, p>0 04); the proportion of males emerging per vial was 0.48±0.09.

Two examples of the effects of larval density on the development of C. cautella are illustrated in Fig. 3.4, while Table 3.3 presents the stage durations and average daily probability of stage survival for all of the densities examined. Total developmental periods and probabilities of surviving through a stage are shown in Fig. 3.5. These data show that the pre-imaginal period is strongly determined by initial egg density The effect of increasing density is first apparent in the 5th instar, but as densities increase further, 4th and then 3rd instar durations are lengthened. These data suggest that pupal duration is not influenced by initial egg density. Survival of 2nd, 3rd and 4th instars is high and does not appear to depend on initial density. First instars suffer higher levels of mortality than 2nd, 3rd or 4th instars but the mortality does not appear to be a function of density. Increases in initial egg density had a detrimental effect on the survival of 5th instars, with survival rapidly decreasing with increasing density. Pupal survival in this series of experiments was high and did not appear to be affected by initial egg density.

Further data on the magnitude of pupal mortality and the effect of initial density are presented in Fig. 3.6. Mortality, expressed as

Figure 3.2. Effect of initial egg density on Cadra cautella age at imaginal emergence. Changes in age at emergence with initial egg density for males (A) and females (B).

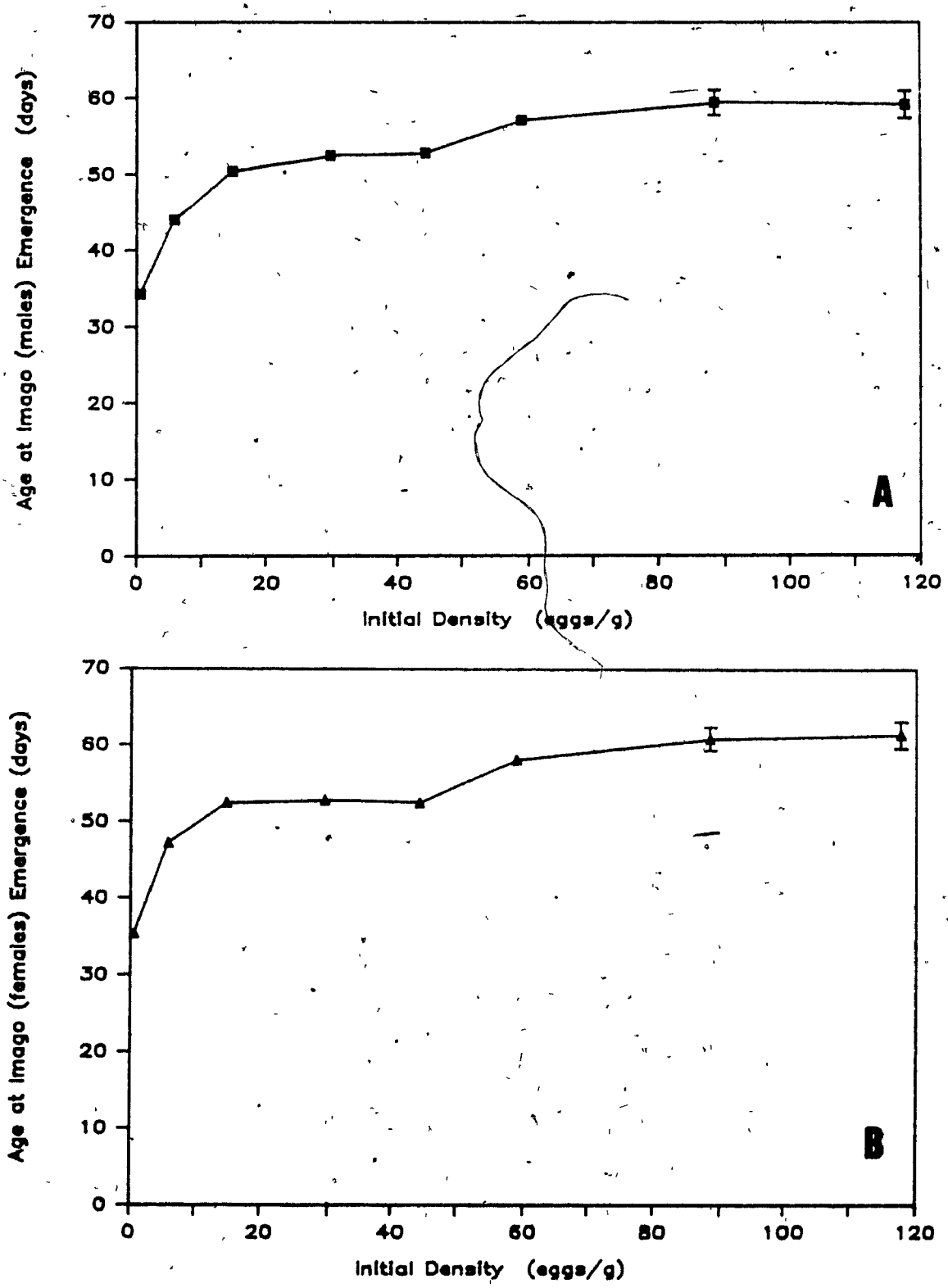
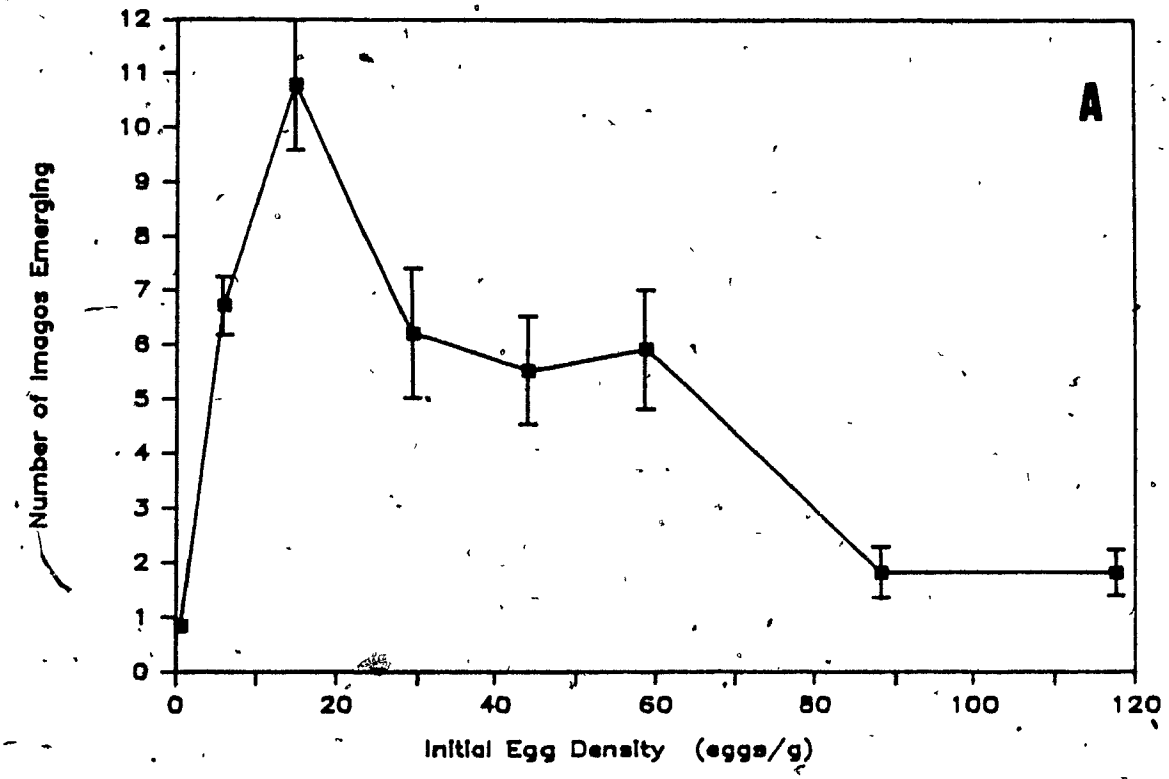

Age at Imago (males) Emergence (days)
70
60
50
40
30
20
10
0
0
20
40
60
80
100
120
Initial Density (eggs/g)
A
Age at Imago (females) Emergence (days)
70
60
50
40
30
20
10
0
0
20
40
60
80
100
120
Initial Density (eggs/g)
B

Figure 3.3. Effect of initial egg density on level of pre-imaginal mortality in Cadra cautella. A. Number of imagos emerging per vial as a function of initial egg density. B. Change in mortality levels as a function of initial egg density.


A
Number of Imagos Emerging
0
1
2
3
4
5
6
7
8
9
10
11
12
0
20
40
60
80
100
120
Initial Egg Density (eggs/g)

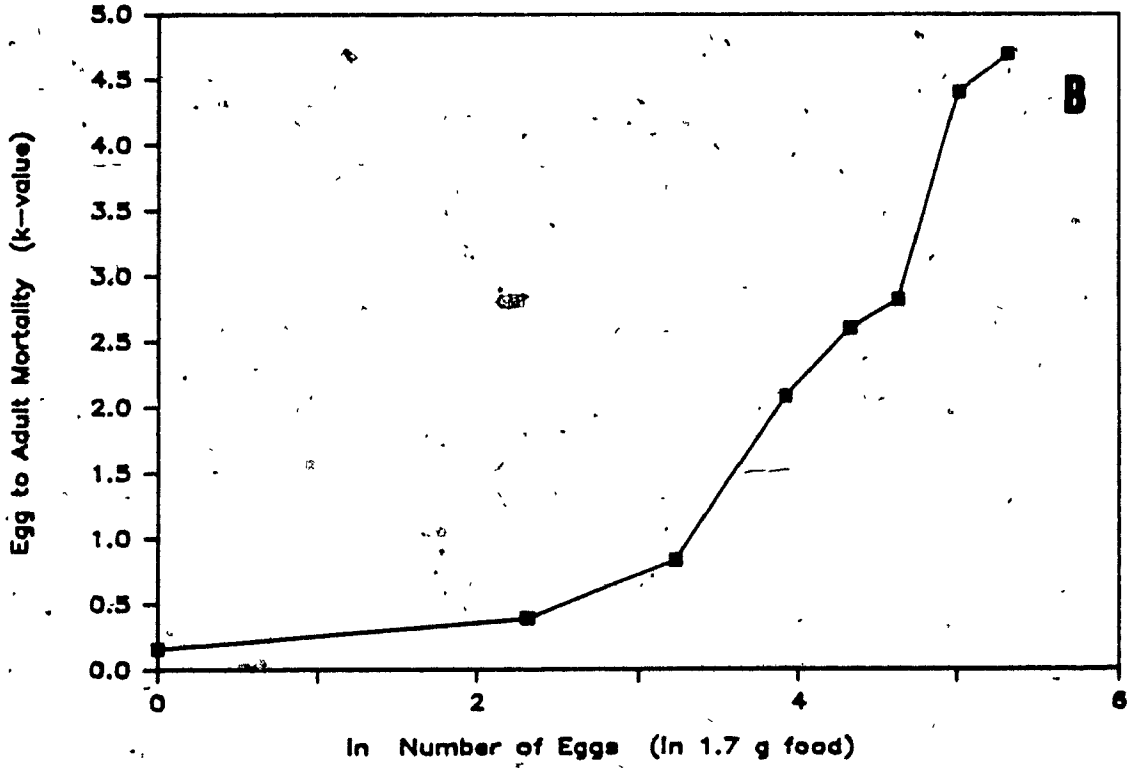
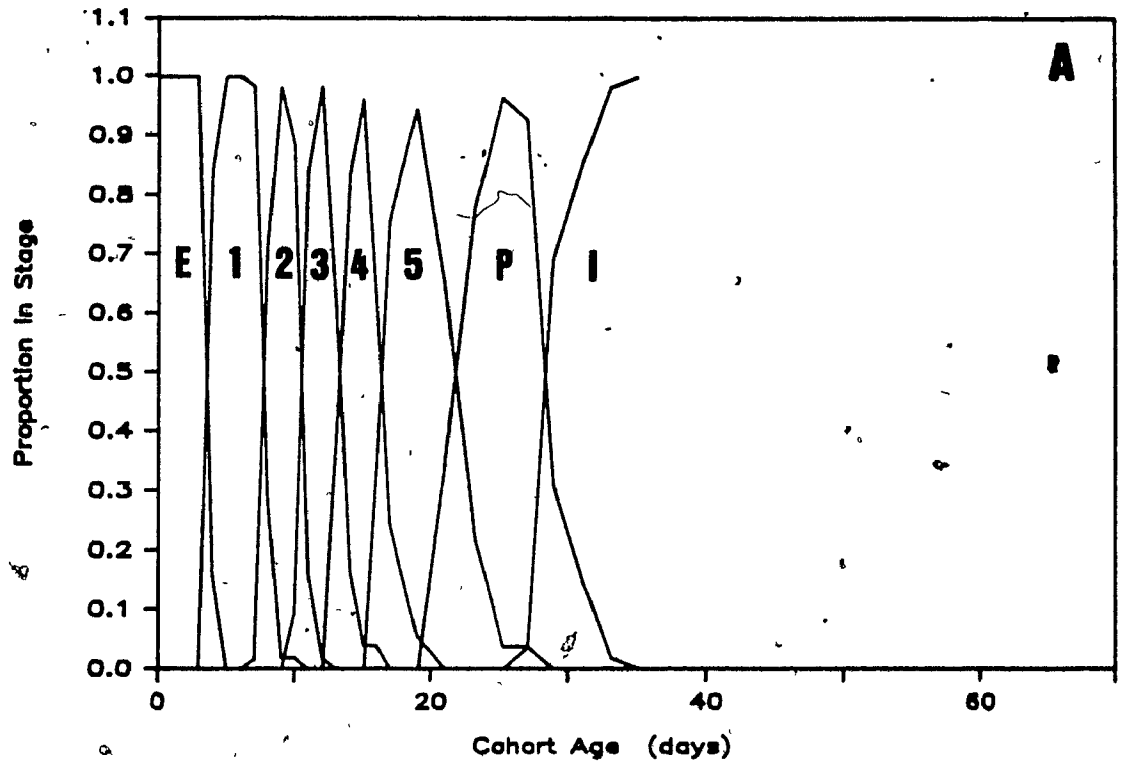

B
Egg to Adult Mortality (k-value)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
0
2
4
6
ln Number of Eggs (ln 1.7 g food)

Figure 3.4. Two examples illustrating effect of initial egg density on stage durations in Cadra cautella. Changes with time in proportion of individuals in a stage. A. Initial number of eggs: 1/vial (0.58 eggs/g). B. Initial number of eggs: 100/vial (58.8 eggs/g). Stages are identified on the graphs; E, egg stage; 1-5, 1st through 5th larval instars; P, pupal stage; I, imago stage.


A
E
1
2
3
4
5
P
I
Proportion in Stage
Cohort Age (days)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
0
20
40
60

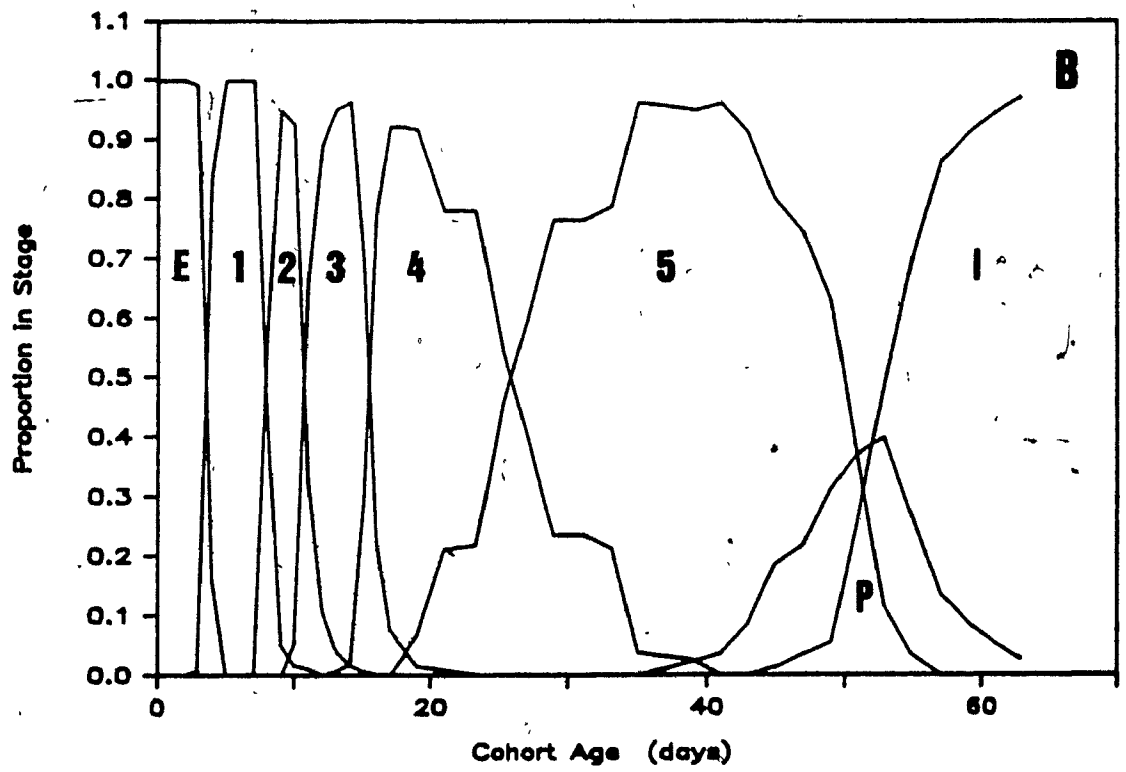

B
E
1
2
3
4
5
P
I
Proportion in Stage
Cohort Age (days)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
0
20
40
60

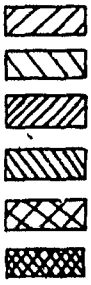
Table 3.3. Effect of initial egg density on stage duration and probability of survival in Cadra cautella.

DENSITY[1]	STAGE	DURATION (days) MEAN	VARIANCE	SURVIVAL[2,3]
0.58	1st	4.1	0.2	0.98
	2nd	2.8	0.2	1.03
	3rd	2.7	0.3	0.99
	4th	3.0	0.4	0.99
	5th	5.3	1.4	1.01
	Pupa	6.9	0.9	1.00
5.88	1st	4.5	0.2	0.98
	2nd	3.3	0.3	1.00
	3rd	2.8	0.7	1.00
	4th	3.8	1.8	1.00
	5th	5.4	0.2	1.00
	Pupa	7.7	4.2	1.00
14.7	1st	4.3	0.2	1.00
	2nd	2.8	0.1	1.00
	3rd	3.1	0.3	0.99
	4th	3.8	0.8	1.02
	5th	9.4	10.2	0.95
	Pupa	6.8	2.0	0.99
29.4	1st	4.6	0.6	0.97
	2nd	3.3	0.1	1.01
	3rd	3.4	1.3	0.98
	4th	6.0	1.6	1.03
	5th	10.9	21.7	0.86
	Pupa	8.6	0.2	1.06
44.1	1st	4.2	0.2	0.97
	2nd	3.4	0.6	1.02
	3rd	4.0	2.7	0.99
	4th	9.3	14.0	1.01
	5th	14.4	11.7	0.85
	Pupa	7.1	16.6	1.03
58.8	1st	4.3	0.2	0.99
	2nd	2.8	0.1	0.98
	3rd	4.6	0.2	0.99
	4th	10.7	45.4	1.00
	5th	18.7	0.7	0.83
	Pupa	9.7	6.1	1.00

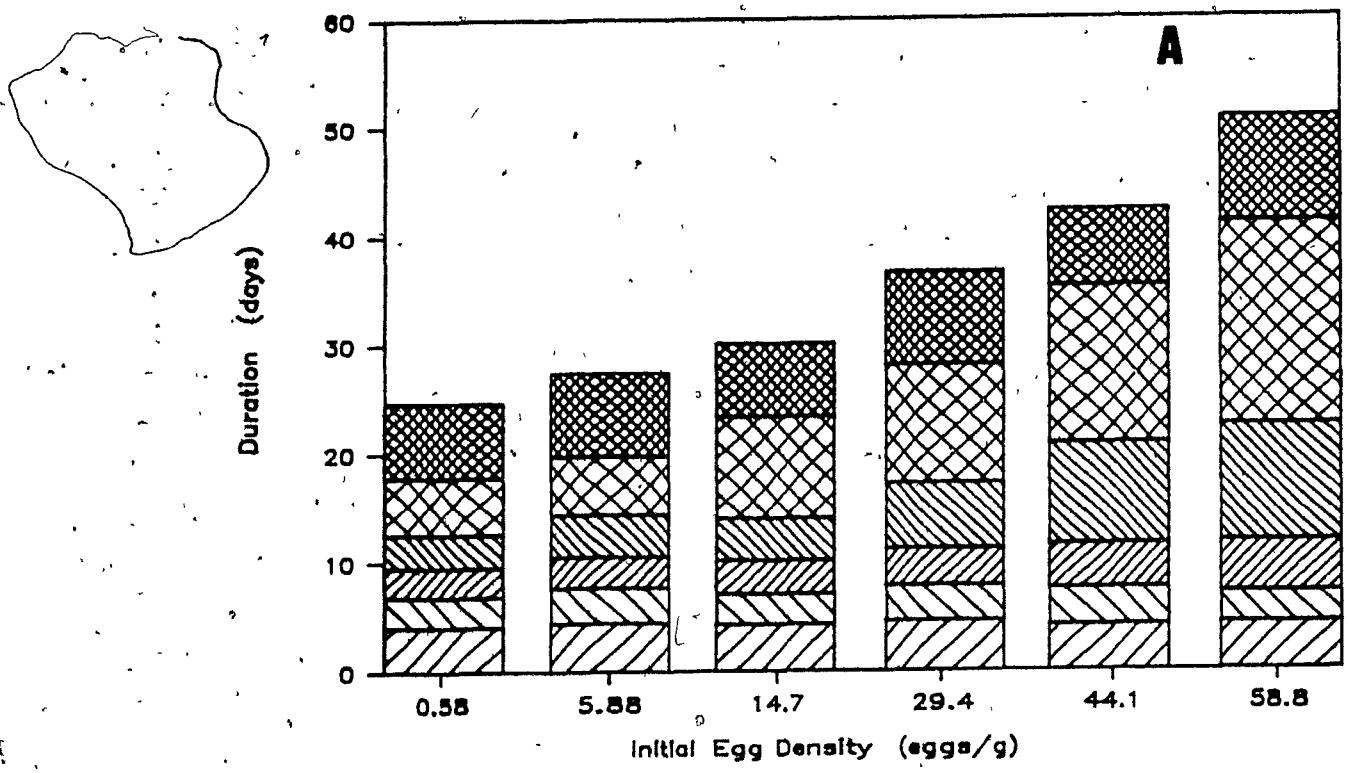
[1] Initial egg density (eggs/g food).
[2] Average stage-specific probability of survival.
[3] Probabilities may be estimated as >1 as the data was gathered using a destructive sampling method.

Figure 3.5. Effect of initial egg density on stage duration and survival of Cadra cautella. A. Effect of density on the duration of larval and pupal stages. B. Effect of density on probability of surviving through a stage. (Survival probabilities have been truncated to be <= 1.)

A. Effect of density on stage durations.



B. Effect of density on stage survival.


A
Duration (days)
0
10
20
30
40
50
60
0.58
5.88
14.7
29.4
44.1
58.8
Initial Egg Density (eggs/g)

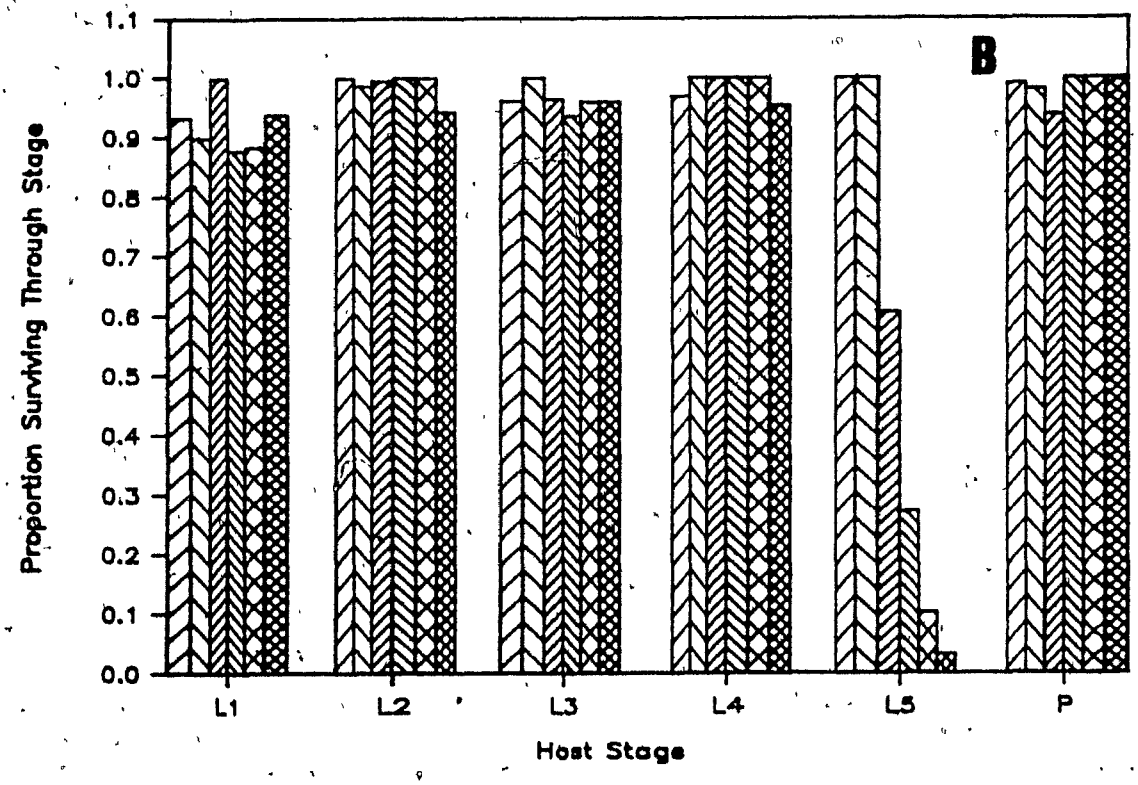
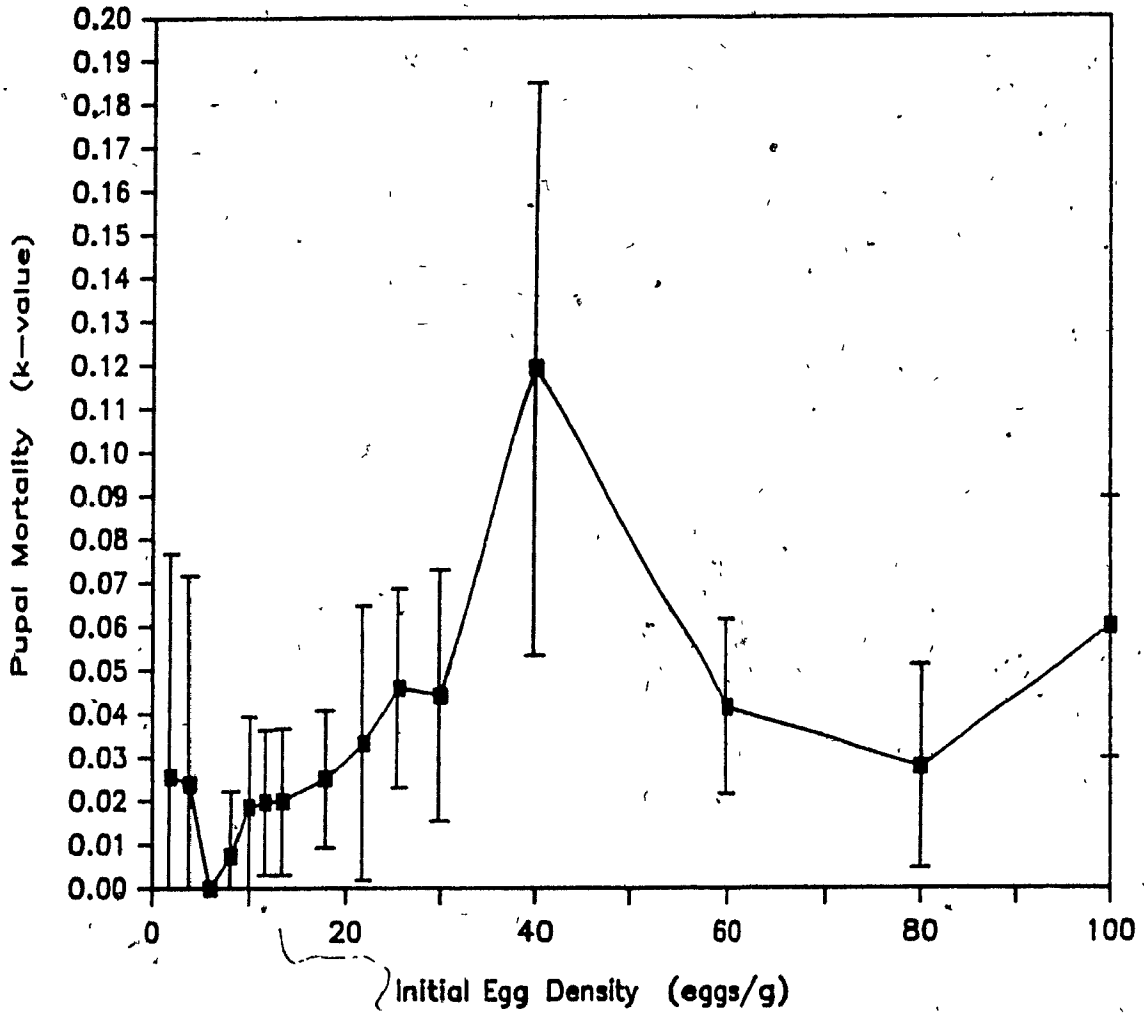

B
Proportion Surviving Through Stage
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
L1
L2
L3
L4
L5
P
Host Stage

Figure 3.6. Effect of initial egg density on mortality of Cadra cautella pupae.


Pupal Mortality (k—value)
0.20
0.19
0.18
0.17
0.16
0.15
0.14
0.13
0.12
0.11
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
0
20
40
60
80
100
Initial Egg Density (eggs/g)

k-values, was found to be significantly influenced by density ($F_{(14,411)}$=3.25, p<0.0001), but the significance of the analysis was entirely due to the higher k-values for pupal mortality observed in the 40 egg/g density. The average k-value for all densities was 0.034±0.004.

The impact of initial egg density on the survival and fecundity of C. cautella can be summarized by the classic demographic statistics, reproductive value and generation time. The statistics are presented in Table 3.4 and were calculated by standard methods (Krebs 1985) using the observed results presented in Figs 3.1b, 3.2, 3.3, 3.7, and 3.8, and assuming initial cohorts of viable female eggs and a 1:1 sex ratio.

Imago Survivorship and Fecundity

The density at which imagos were reared had a significant influence on imago life span (males, $F_{(7,784)}$=37.18, p<0.0001; females, $F_{(7,499)}$=78.64, p<0.0001). This is illustrated in Fig. 3.7, where Figs 3.7a,b illustrate two examples of the proportion of imagos surviving in relation to imago age. The relationship between observed life span and initial density is presented in Fig. 3.7c.

Initial egg density also had a significant effect on the pattern of age-specific fecundity, with average female age at 50% egg production ranging from 3.0 to 4.1 days ($F_{(7,468)}$=3.72, p<0.001). Figures 3 8a,b present two examples of the proportion of total eggs laid with respect to imago age. A decline in lifetime fecundity with increasing density (Fig. 3.8c) was also observed ($F_{(7,495)}$=57.86, p<0.0001).

The number of imagos per oviposition container was found to influence imago life span (males, $F_{(6,340)}$=12.68, p<0.0001; females, $F_{(6,358)}$=8.13, p<0.0001). Figures 3.9a,b present two examples of the proportion of imagos surviving with increasing imago age, while Fig. 3.9c illustrates the relationship between imago life span and imago density.

There was no effect of adult C. cautella density on imago fecundity, with respect to either the average age at 50% egg production (Figs 3.10a,b) ($F_{(6,89)}$=2.70, p>0.018), or lifetime egg production (Fig. 3.10c) ($F_{(6,89)}$=2.33, p>0.038).

Providing imagos with food increased the life span of female imagos from 7.0±0.2 to 8.6±0.4 days ($F_{(1,53)}$=12.60, p<0.0009), but had no effect on male life span (unfed, 9.4±0.5 days; fed, 9.8±0.4 days) ($F_{(1,48)}$=0.35,

Table 3.4. Effect of initial egg density on basic life-table statistics for Cadra cautella.

INITIAL DENSITY	REPRODUCTIVE VALUE	GENERATION TIME
0.6	105.4	37.1
5.9	76.8	49.5
14.7	50.0	54.4
29.4	8.3	54.9
44.1	4.0	55.4
58.8	4.8	59.9
88.2	0.5	62.3
117.6	0.2	63.6

Figure 3.7. Effect of initial egg density on survival characteristics of Cadra cautella imagos. Proportion of imagos surviving as a function of imago age, when imagos were reared at an initial egg density of 5.88 eggs/g food (A) or 117.6 eggs/g (B). C. Effect of initial density on average lifespan. ■ male and ▲ female imagos.

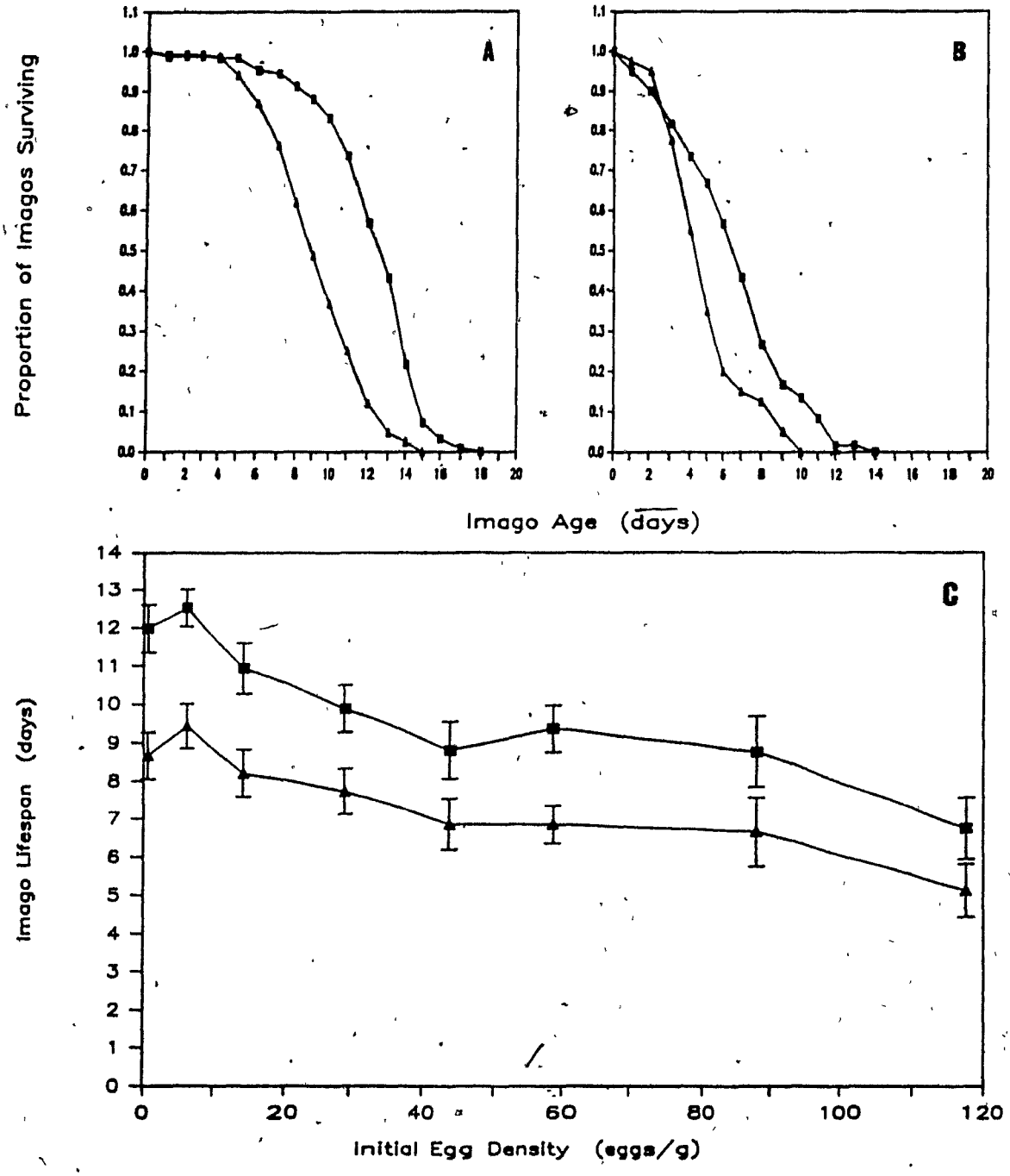

Proportion of Imagos Surviving
A
B
Imago Age (days)
C
Imago Lifespan (days)
Initial Egg Density (eggs/g)

Figure 3.8. Effect of initial egg density on reproductive characteristics of Cadra cautella imagos. Fraction of total eggs laid per day when imagos were reared at an initial density of 5.88 eggs/g (A) or 29.4 eggs/g (B). C. Effect of initial egg density on lifetime egg production of females.

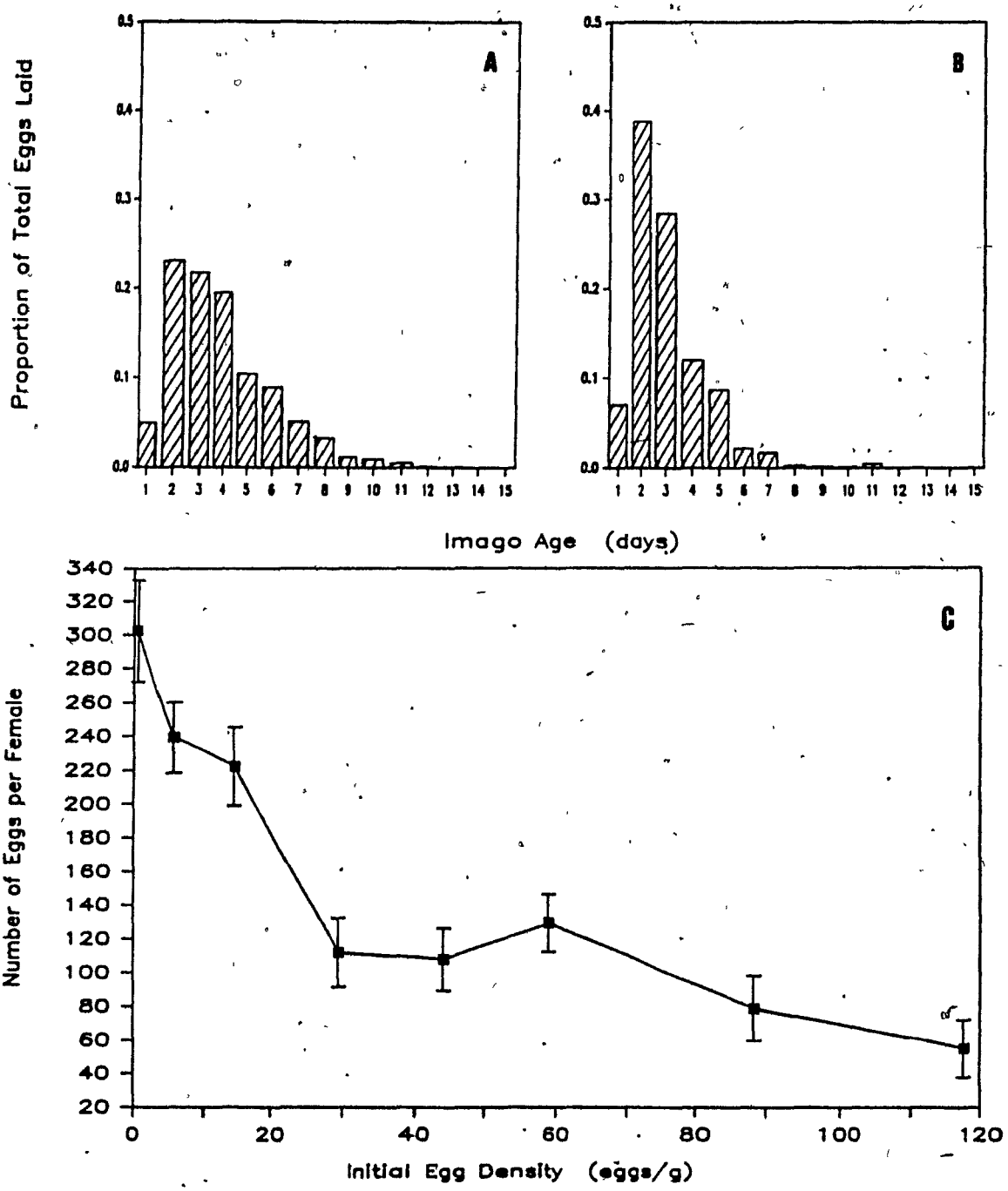

A
B
C
Proportion of Total Eggs Laid
Imago Age (days)
Number of Eggs per Female
Initial Egg Density (eggs/g)

Figure 3.9. Effect of imago density on survival characteristics of Cadra cautella imagos. Proportion of imagos surviving as a function of imago age, when imago density was 2/container (A) or 20/container (B). C. The effect of imago density on average lifespan. ■ male and ▲ female imagos.

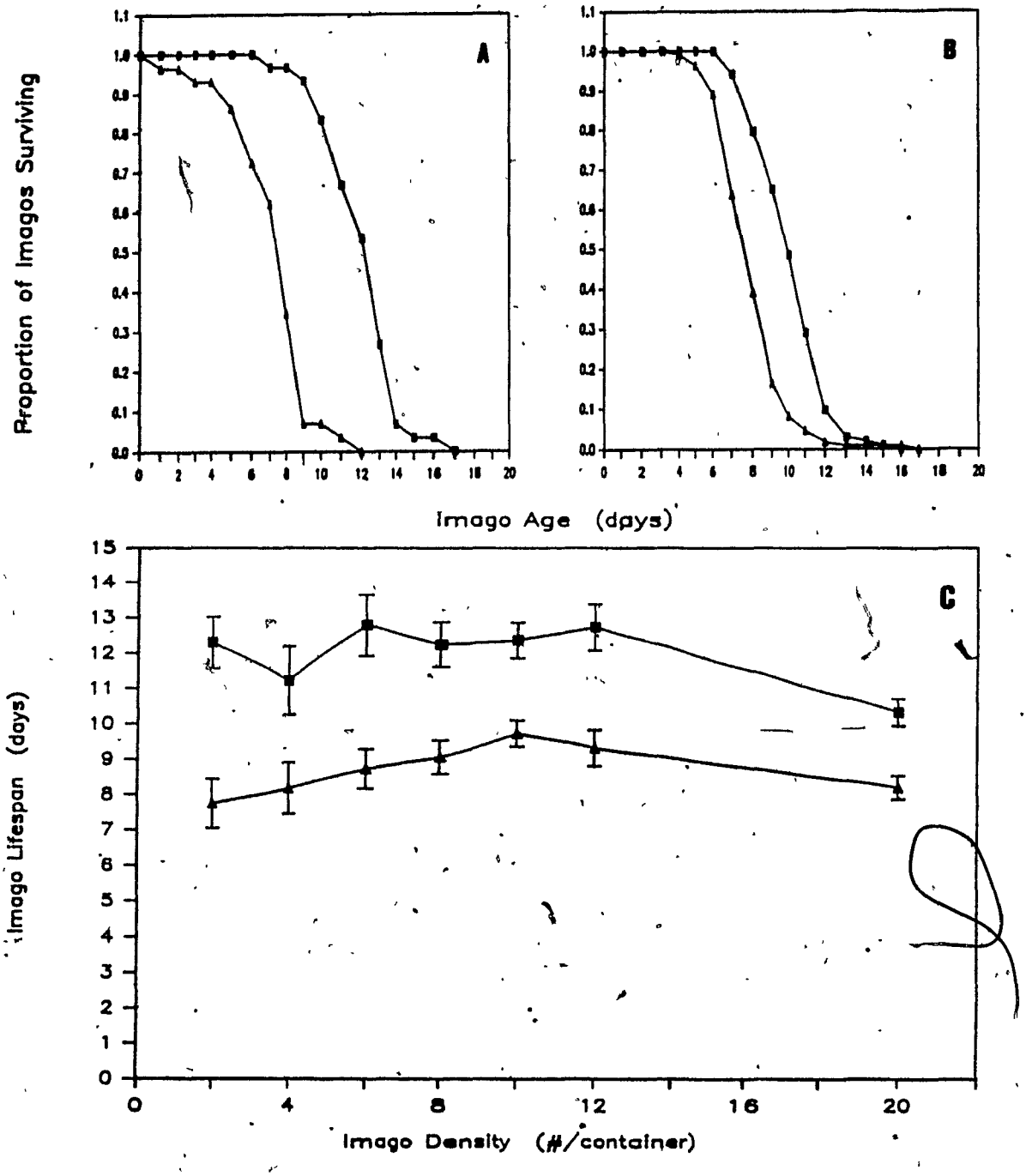
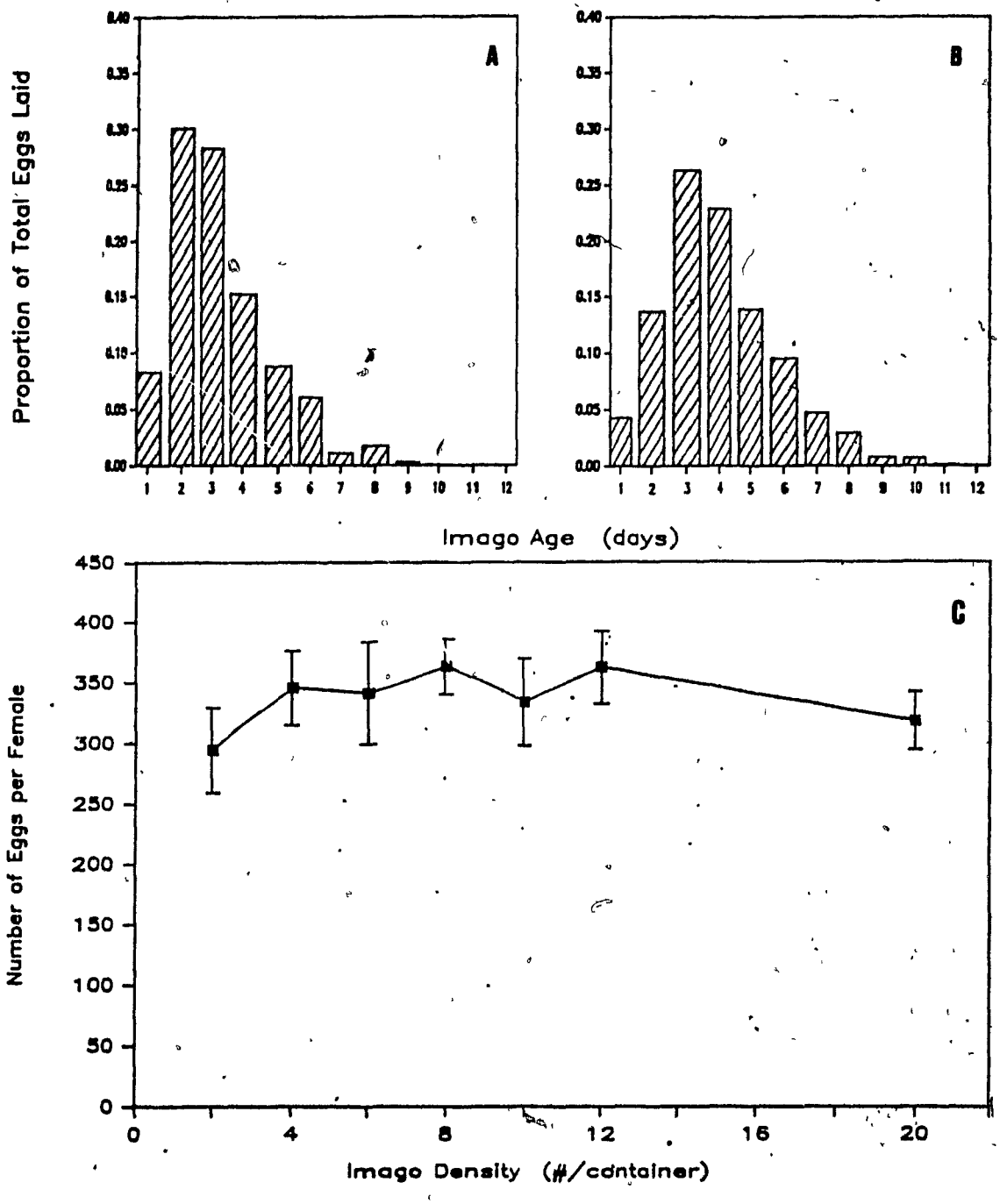

A
B
C
Proportion of Imagos Surviving
Imago Age (days)
Imago Lifespan (days)
Imago Density (#/container)

Figure 3.10. Effect of imago density on reproductive characteristics of Cadra cautella imagos. Fraction of total eggs laid per day at an imago density of 4/container (A) or 10/container (B). C. Effect of imago density on lifetime egg production of females.


Proportion of Total Eggs Laid
A
B
Imago Age (days)
C
Number of Eggs per Female
Imago Density (#/container)

$p \geq 0.55$). The proportions of unfed and fed imagos surviving with imago age are presented in Figs 3.11a,b.

The presence of food increased lifetime fecundity from 341.5±23.0 to 483.5±18.6 eggs/female ($F_{(1,9)}=21.72$, $p<0.002$), but had no effect on the age at 50% egg production (unfed, 2.8±0.2 d, fed 2.7±0.1 d) ($F_{(1,9)}=0.06$, $p>0.81$). The age-specific fecundity for fed and unfed imagos is presented in Figs 3.11c,d.

Figure 3.12 illustrates the relationship between imago weight at emergence and imago fecundity and life span. It also presents the relationship between initial egg density and imago weight at emergence. A linear relationship was the best description of the effect of imago weight on total fecundity ($R^2=0.76$), while a power curve provided a reasonable description on the relationship between female life span and weight ($R^2=0.63$). The parameter estimates for the regressions are presented in the figure description.

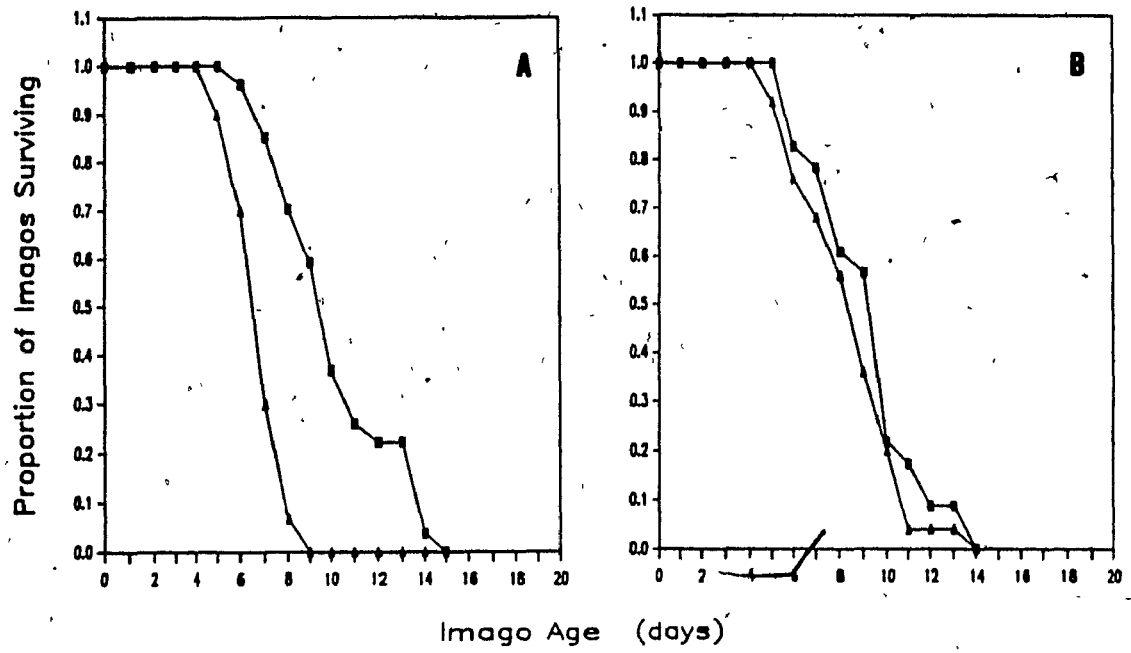
Inter-stage Interactions

The results of the preliminary statistical analyses for interactions between eggs and instars and among instars are presented in Table 3.5 All larval instars were found to cause significant reductions in the number of eggs present. Reductions in the numbers of 1st instars were also found when they were maintained in the presence of 2nd and 3rd instar larvae. No reduction was found in the number of pupae/vial when they were exposed to the various larval instars (Kruskal-Wallis: $X^2_{(5)}=0.34$, $p>0.996$); the numbers of pupae/vial were: control, 7.5±0.3; 1st instar, 7.7±0.3; 2nd instar, 7.6±0.3; 3rd instar, 7.5±0.3; 4th instar, 7.7±0.4; 5th instar, 7.5±0.3.

Further analyses were carried out on the observed egg cannibalism and on 1st instar cannibalism by the older larval instars. All instars were considered in this analysis even though not all of the interactions were found to be significant in the preliminary analyses. The following equation was used to describe egg cannibalism,

$$N_a = N_t [1-\exp(-a_e L_s T)] \qquad \text{Eq. 3.1}$$

Figure 3.11. Effect of feeding on survival and reproductive characteristics of Cadra cautella imagos. Proportion of imagos surviving with respect to imago age when imagos are unfed (A) or when imagos were provided with honey dissolved in water (B). ■ male and ▲ female imagos. Fraction of total eggs laid as females age when imagos are unfed (C) or fed (D).


A
B
Proportion of Imagos Surviving
Imago Age (days)

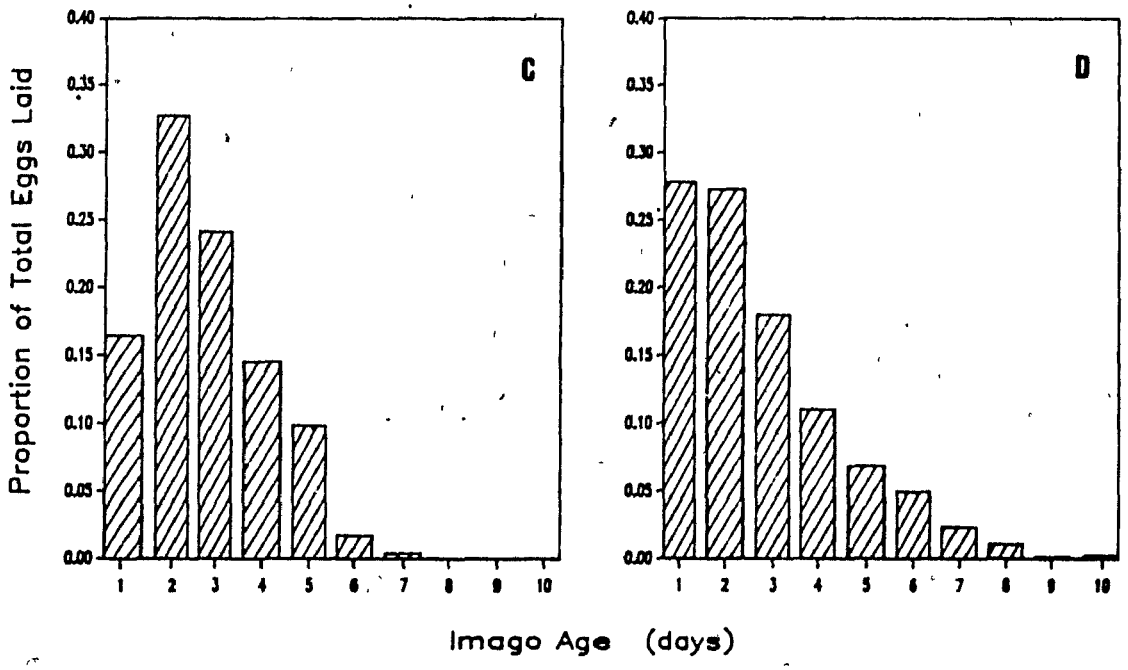
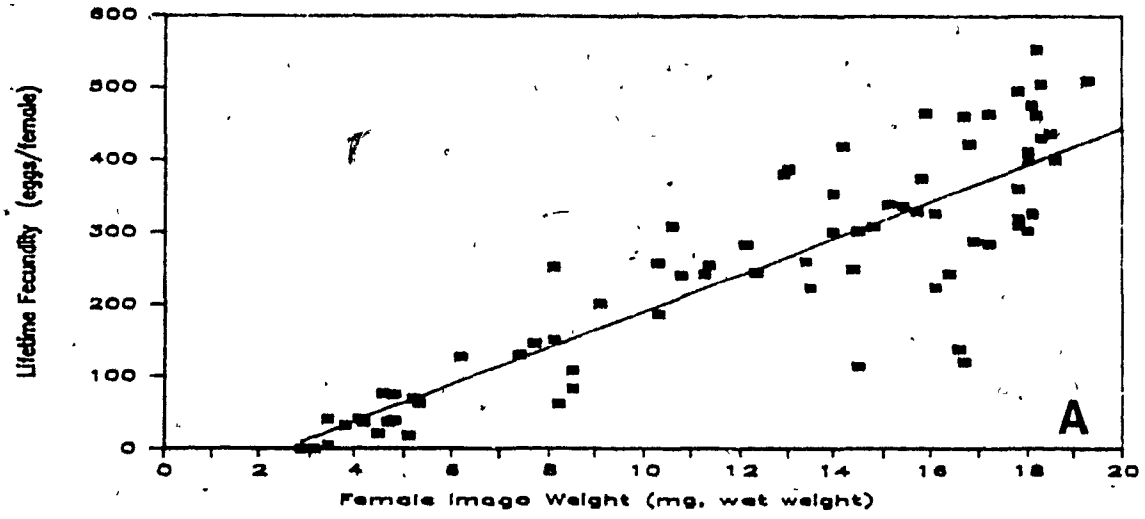
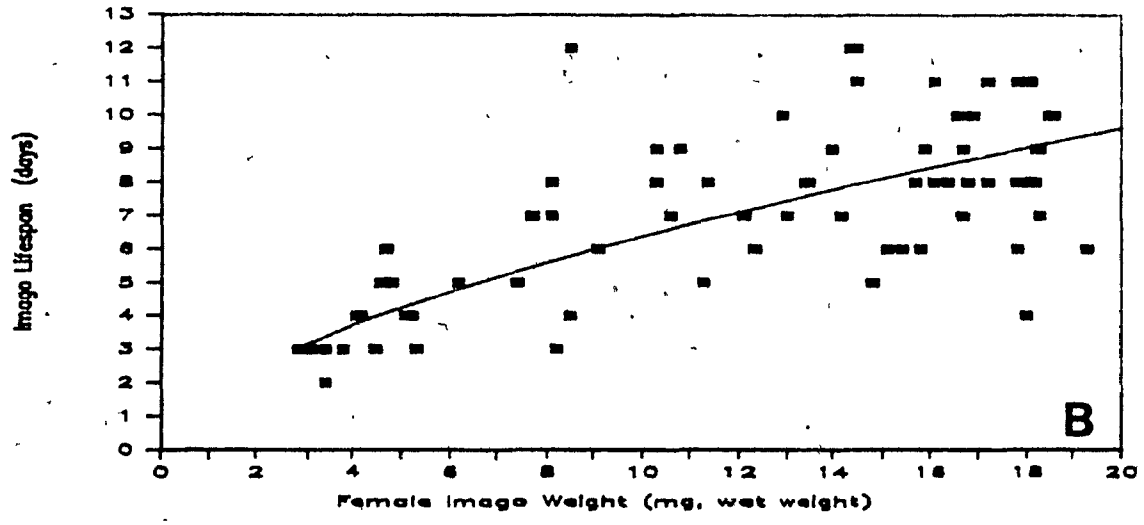

C
D
Proportion of Total Eggs Laid
Imago Age (days)

Figure 3.12. Relationship between Cadra cautella imago weight at emergence and female fecundity and life span. A. Relationship between female fecundity and imago weight at emergence. Parameters of the regression line are intercept = -61.8±75.7 and slope = 25.3±1.65. B. Relationship between female life span and imago weight at emergence. Parameters of the curve are intercept = 0.502±0.271, exponent = 0.586±0.056. C. Effect of initial egg density on female imago weight at emergence.


Lifetime Fecundity (eggs/female)
Female Imago Weight (mg, wet weight)
A


Imago Lifespan (days)
Female Imago Weight (mg, wet weight)
B

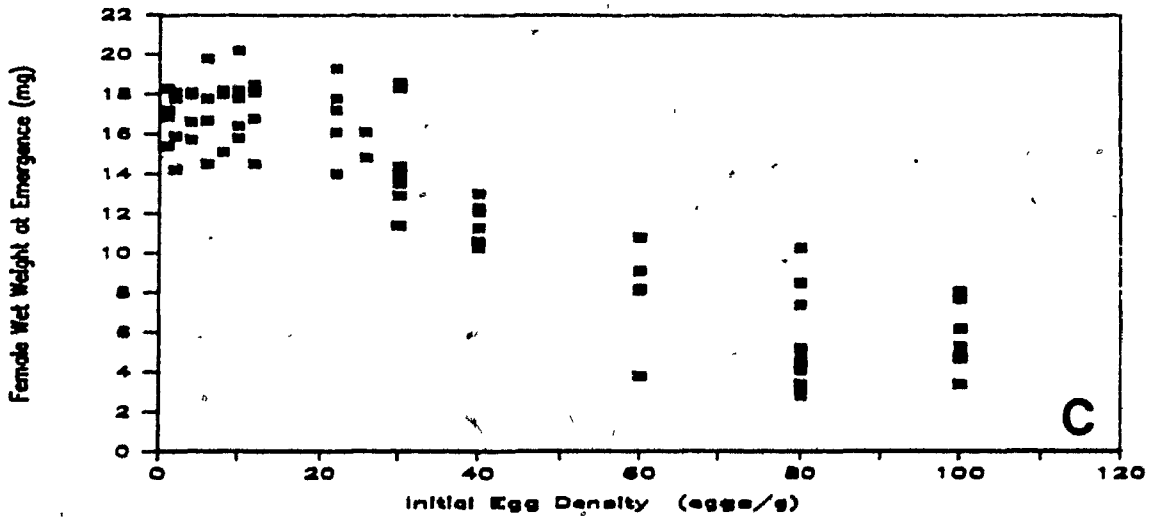

Female Wet Weight at Emergence (mg)
Initial Egg Density (eggs/g)
C

Table 3.5. Test statistics for preliminary analysis for interactions between the stages of Cadra cautella.

	'PREDATOR'				
'PREY'	1st	2nd	3rd	4th	5th
Egg	25.95[1]	186.43	194.73	81.61	15.94
	<0.0001[2]	<0.0001	<0.0001	<0.0001	<0.0002
1st		17.61	11.38	6.23	1.14
		<0.0002	<0.0024	<0.019	<0.2955
2nd			1.38	0.01	2.50
			>0.2494	>0.9871	>0.1250
3rd				0.01	0.16
				>0.9433	>0.6942
4th					0.87
					>0.3595

[1] Calculated F-statistic.

[2] Probability of > F-statistic.

where N_a = number of 'prey' attacked (eggs)

N_t = number of 'prey' available

L_s = number of 'predators' (larvae) per g food

T = time available for search, days

and a_e = instantaneous search rate for eggs, $g/(L_s \cdot T)$.

In estimating the relationship between eggs attacked and instar density, the search rate (a_e) was the only unknown parameter as the initial number of eggs available was known (60).

In the case of cannibalism of 1st instars N_t was also an unknown parameter and it was more appropriate to estimate the parameters using

$$N_{na} = N_t' \exp (-a_1 L_s T) \qquad \text{Eq. 3.2}$$

where N_{na} = number of 'prey' not attacked (1st instar)

and a_1 = instantaneous search rate for 1st instars, $g/(L_s \cdot T)$.

The time available for search was 2 days for both the egg and 1st instar data. Figure 3.13 illustrates the relationship between the number of eggs consumed and instar density for the five larval instars together with the predictions of Eq. 3.1. Figure 3.14 presents the predictions of Eq.3.2 together with the observed data on number of 1st instars surviving in the presence of 2nd, 3rd, 4th and 5th instars. The parameter estimates are presented in Table 3.6. Figure 3.15 illustrates the relationship between search rates and larval instar.

DISCUSSION

The observed duration of the egg stage (3.5±0.2 days) is in close agreement with the durations reported by Burges & Haskins (1964). The proportion of viable eggs in a sample was found not to depend on the density at which imagos were reared, but to depend on the age of the imago. The reasons for the decline in egg viability with increasing imago age (Fig. 3.1b) are unknown, but may relate to declining energy reserves

Table 3.6. Estimates of search rates (a_e and a_l) for cannibalism of eggs and 1st instar larvae by larvae of Cadra cautella.

PREDATOR INSTAR	STAGE ATTACKED			
	EGG		1st INSTAR	
	a_e	S.E.	a_l	S.E.
1st	0.00045	0.000055	-	-
2nd	0.00155	0.000097	0.00492	0.00140
3rd	0.00397	0.000284	0.01060	0.00222
4th	0.00480	0.000383	0.01406	0.00458
5th	0.00441	0.000576	0.0[1]	-

[1] Parameter estimate not significantly different from 0

Figure 3.13. Egg cannibalism by larvae of Cadra cautella. Observed data together with the predictions of Eq. 3.1. Parameter values for the functional response are presented in Table 3.6. Number of eggs consumed by 1st instar larvae (A) 2nd instars (B) 3rd instars (C) 4th instars (D) and 5th instars (E)

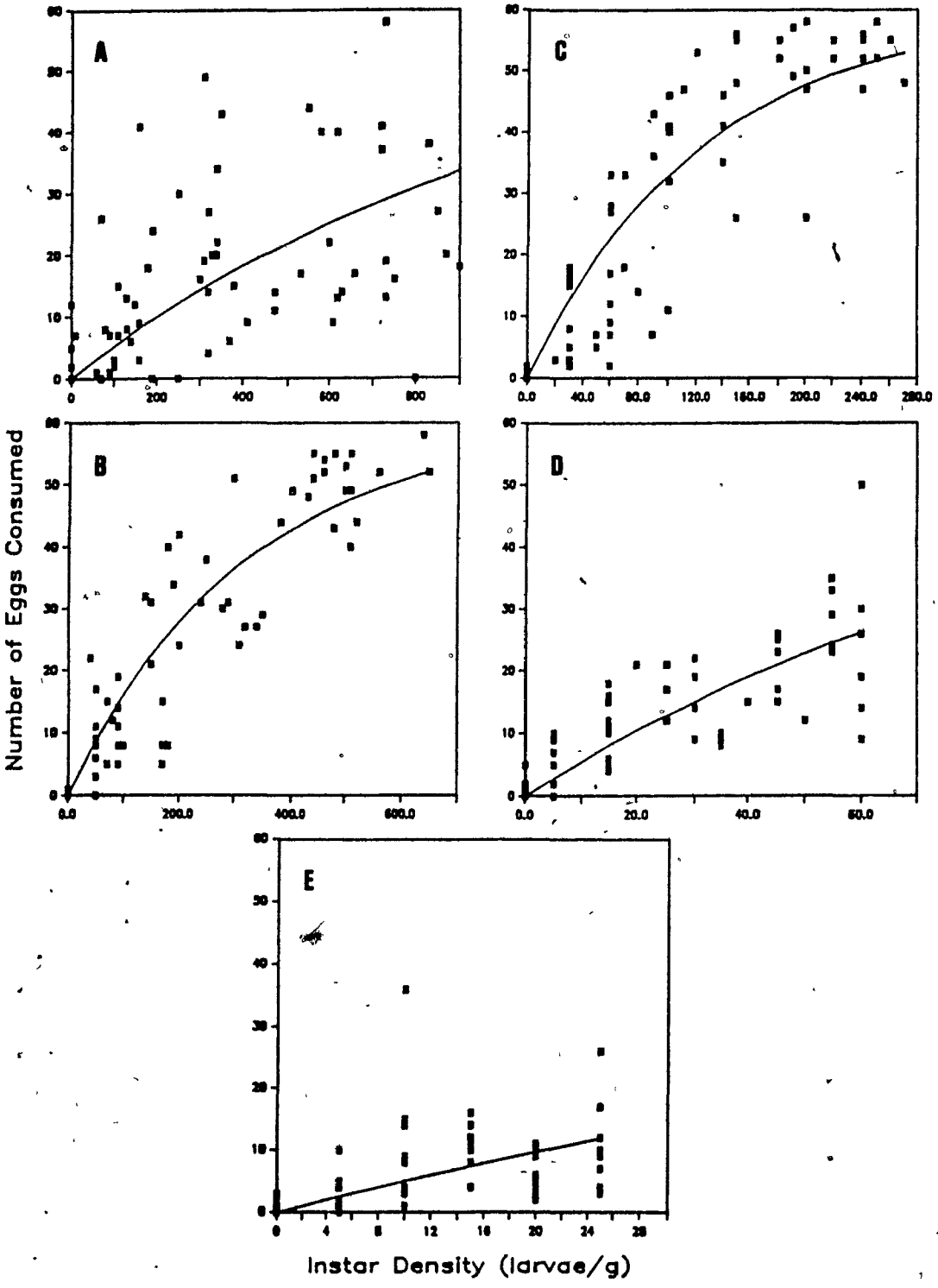
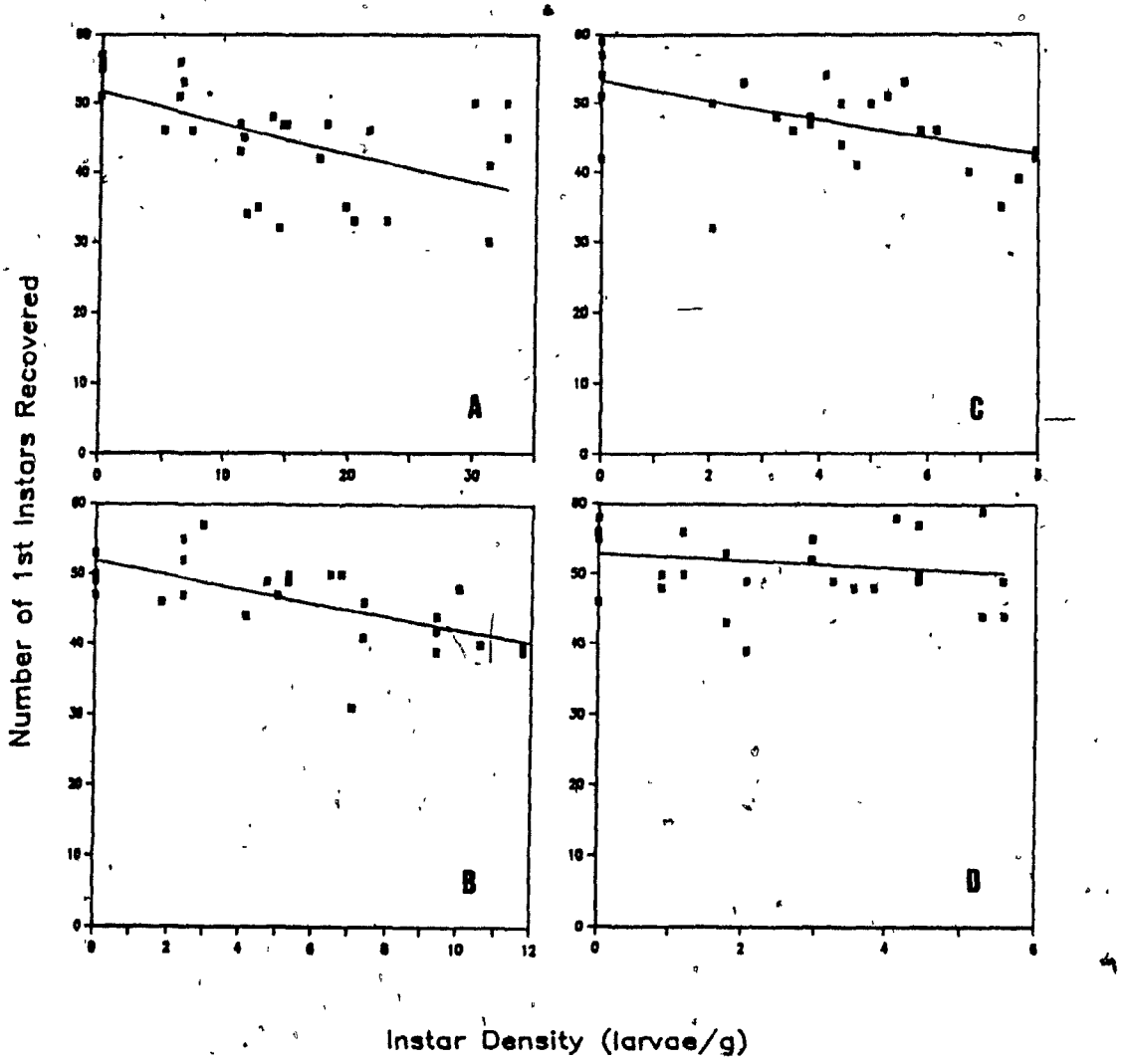

A
B
C
D
E
Number of Eggs Consumed
Instar Density (larvae/g)

Figure 3.14. Cannibalism of 1st instars by larvae of Cadra cautella. Observed data on number of larvae not attacked in relation to 'predator' density, together with the predictions of Eq. 3.2. Parameter values for the functional response are presented in Table 3.6. Number of 1st instar larvae not attacked by 2nd instars (A) 3rd instars (B) 4th instars (C) and 5th instars (D).


Number of 1st Instars Recovered
A
B
C
D
Instar Density (larvae/g)

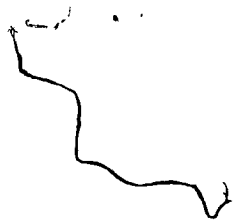
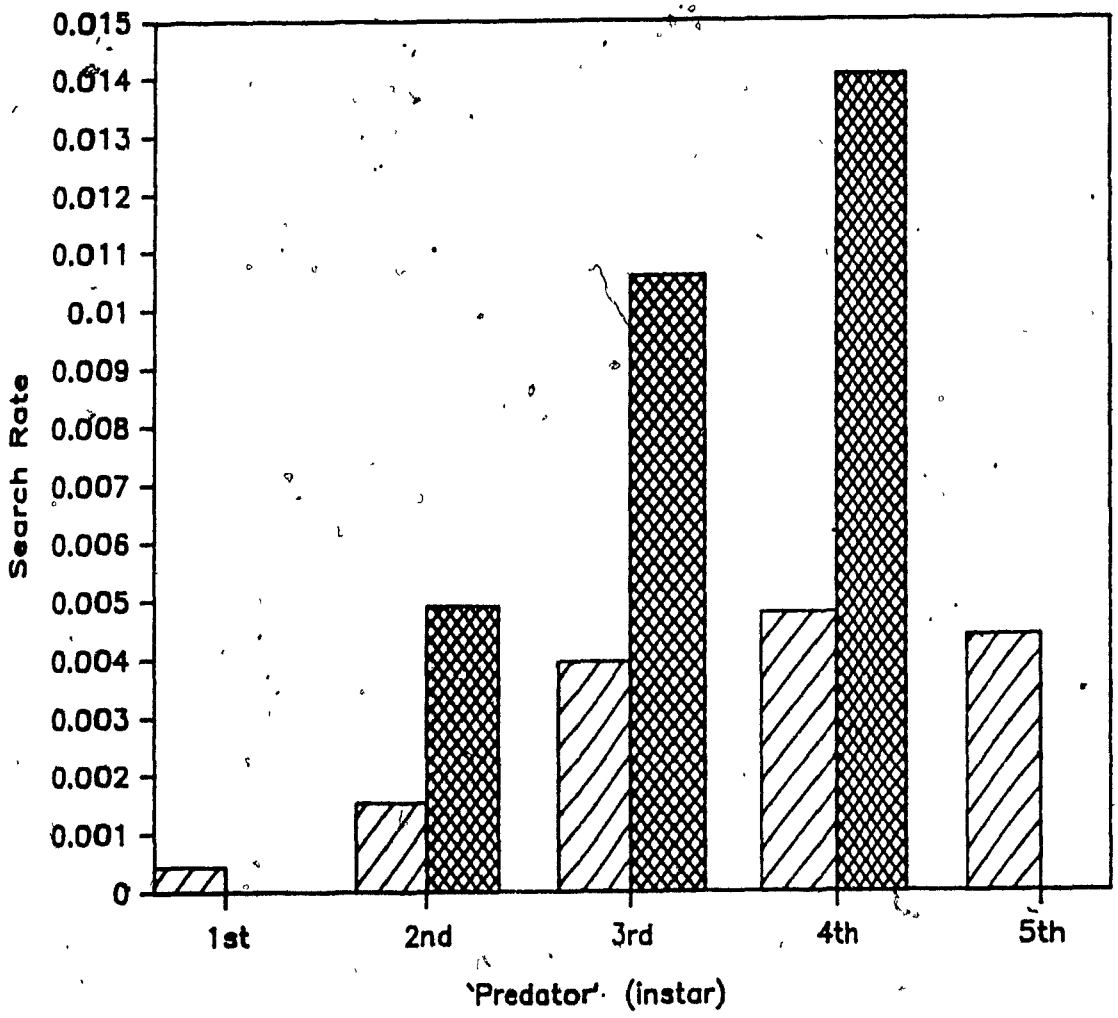


Figure 3.15. Stage-specific instantaneous attack rates for egg and 1st instar cannibalism by larvae of Cadra cautella. Single-hatched bars denote the attack rates (a_0) for egg cannibalism and double-hatched bars the attack rates (a_1) for 1st instar cannibalism.


0.015
0.014
0.013
0.012
0.011
0.01
0.009
0.008
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0
Search Rate
1st
2nd
3rd
4th
5th
'Predator' (instar)

in the female or sperm limitation. Eggs laid late in an imago's life often have an abnormal external morphology, and are usually laid in strings as opposed to singly as is usual for eggs laid earlier in life (personal observation). There is a great deal of variability in published values for egg viability, both within and between species of stored-products Lepidoptera. For example, Gurney, Nisbet & Lawton (1983) reported that the proportion of viable eggs in P interpunctella varied from 0.28-0.75. Ahmad (1936) found that A kuehniella egg viability depended on conditions of humidity and temperature during the oviposition period, where spermatogenesis was retarded and sperm motility reduced with increasing temperatures (Raichoudhury 1936). The results of this study and the work cited above suggest that the observed differences in egg viability are not significantly determined by imago developmental history but were determined by environmental effects during the imaginal stage However, imago larval history may play a role as demonstrated by Lum & Flaherty (1969, 1970) who found that sperm quality and quantity P. interpunctella was reduced when males were reared under conditions of continuous light as compared to males raised under alternating light-dark conditions.

Takahashi (1961) found that the number of larval instars increased as larval density (eggs/g food) increased. The results from the experiment where larvae were raised individually showed that there were only five larval instars, even though larval stage durations ranged from 17-37 days. The results of the cohort experiments (Fig. 3.4) indicated that as larval densities increased, the size of the larval head capsule at a molt for a particular instar declined, but there was no suggestion of additional larval molts. The reasons for the differences observed between this study and Takahashi (1961) are not known. Benson (1973) reported that variation in the number of larval instars within and among species is common.

Increases in the initial number of eggs per g food prolonged the pre-imaginal period by up to 25 days (Fig. 3.2). Takahashi (1956b; 1961) reported a similar phenomenon for C. cautella raised on rice bran, but over a comparable range of initial egg densities he only observed about a 10 day increase in developmental time. Increased developmental period with increasing larval density has also been reported for P. interpunctella by Podoler (1974b), and for A. kuehniella by Ullyett &

Merwe (1947). Mortality levels also rose rapidly above densities of about 25 eggs/g food (Fig. 3.3a). Similar patterns in the relationship between mortality (k-values) and larval density (Fig. 3b) have been reported for C. cautella by Takahashi (1956b) and Rogers (1970). These authors found that there was a rapid increase in mortality at initial egg densities between 25 - 30 eggs/g.

The cohort experiments (Fig. 3.5a and Table 3.3) provided more detailed information on the effects of density on the development of C. cautella. As the initial density increased 5th instars were the first stage to be affected, with 5th instar duration increasing with each subsequent increase in density. As larval densities increased, progressively younger instars showed decreases in their rate of development. The duration of the pupal stage appears to be independent of initial egg density and the average pupal duration over all densities (7.8 days) is in close agreement with the results presented in Table 3.2 (8.0 days, sexes pooled).

The results illustrated in Fig. 3.5b suggest that the pattern in numbers surviving (Fig. 3a) can be attributed to the effects of larval density on the survival of 5th instars, the only stage to show any systematic response to initial egg density. Survival of 2nd, 3rd, and 4th larval instars and pupae was uniformly high and independent of initial egg density. The survival of 1st instars tended to be lower than 2nd-4th instars, but showed no consistent trend with density. Increasing larval density seemed to have a primary influence on developmental period and a less dramatic effect on larval mortality. There was a substantial increase in 4th instar duration (Fig. 3.5a) but no corresponding decrease in 4th instar survival (Fig. 3.5b). The probability of surviving through the 5th instar declined with increasing larval density, primarily as a result of the effects of density on stage duration as opposed to an increase in the instantaneous larval death rate. The daily probability of survival decreased from 1.0 to 0.95 between densities of 5.88 and 14.7 eggs/g and then declined to 0.86 and remained virtually constant over the remaining densities (Table 3.3). The additional data on pupal mortality presented in Fig. 3.6 confirmed the results of the cohort experiment; pupal mortality is low and although there appears to be a slight increase in mortality with initial egg density it is not significant.

The initial egg densities from which imagos were reared had significant negative effects on the survival of male and female imagos (Fig. 3.7) and on the lifetime fecundity of females (Fig. 3.8c). Initial egg density also had an effect on the shape of the age-specific fecundity curve (Fig 3.8a,b); the average age at which 50% of the eggs had been laid ranged from 4.1 days (5.88 eggs/g) to 3.0 d (29 4 eggs/g) Takahashi (1956a,c) described reduced imago survival and fecundity as initial density increased in C. cautella, but reported female fecundities ranging from 25 -135 eggs. Takahashi used rice bran as food, compared to wheat flakes used in this study and this may account for the differences in total fecundity and the impact of larval density of fecundity between the two studies. Similar patterns in the effects of larval density on imago survival and fecundity have been shown for A kuehniella by Ullyett & Merwe (1947), for E. elutella by Richards & Waloff (1946) and for P. interpunctella by Snyman (1949) and Podoler (1974b).

Although imago life span was influenced by the number of imagos present per oviposition container, the results were not very consistent (Fig. 3.9). The life span of male imagos remained constant over most densities and only declined at the highest imago density (Fig. 3 9c). The life span of female imagos showed a convex relationship with imago density, increasing initially with increased larval density and then declining, with the average life span of females being longer at the highest density than at the lowest imago density. No effect of imago density on lifetime fecundity or imago age at 50% egg production was detected. Similarly Ullyett (1945) working with A. kuehniella found that the number of eggs/female increased to a maximum and then declined with increasing imago density whereas Snyman (1949) showed that the number of eggs laid in the first 2 days of life in P. interpunctella declined as the number of imagos/container increased. Although similar numbers of imagos were used, the species differences and disparate size of the oviposition containers used by Ullyett (52 cc) and Shyman (37 cc) compared with those used in this study (950 cc), make comparisons difficult. Under very crowded conditions the imagos suffer a considerable degree of physical damage in the form of lost scales and appendages as well as very reduced life spans (personal observation).

Providing imagos with honey dissolved in water increased the life span of female imagos and increased lifetime fecundity by an average of 142 eggs/female (Fig. 3.11). Male life span was unaffected. Norris (1934) found that the life span and fecundity of adult C. cautella were halved if deprived of water. Norris found that providing sugar increased the imago longevity but not fecundity of C. cautella. The results of this study agree with those of Norris for females, but not for males.

Figure 3.12 illustrates the effect of initial larval density on imago weight at emergence. Similar effects have been shown by Takahashi (1953a,c) for this species as well as other stored-products Lepidoptera (Ullyett & Merwe 1947; Snyman 1949).

A significant degree of egg and 1st instar cannibalism by larvae was found to occur (Figs. 3.13 and 3.14). The level of egg cannibalism increased to a plateau as the larvae aged, while the level of 1st instar cannibalism consistently increased with larval stage until the 5th instar, which apparently do not attack 1st instars. With the exception of 5th instars, there was a greater degree of 1st instar cannibalism than egg cannibalism by the larvae. This may be a reflection of the spatial distribution of eggs and larvae. Larvae occur within the wheat flakes while eggs are generally found on top of the food. Why 5th instars prey on eggs but apparently stop attacking 1st instars, may be due to relative immobility of 5th instars which seem to spend less time moving through the food medium than the younger instars. In addition the silk feeding tubes constructed by 5th instars are generally more elaborate than those spun by younger larvae (personal observation) and may exclude 1st instars. These factors may reduce the amount of contact between 1st and 5th instars. The egg has no power of escape or avoidance, and if an egg lies in the path of a feeding 5th instar it will likely be eaten. The lack of any other instar-instar interactions may be due to the increased mobility and robustness of older larvae, better enabling them to avoid attack by larvae older than themselves.

A number of important demographic characteristics have been identified and quantified for C. cautella populations living under the experimental conditions used in this study. The more important of these characteristics are related to density dependent events occurring in the larval stage. These effects are sufficiently strong that on average,

individuals raised at high larval densities have reproductive values less than unity (Table 3.4). The effects of increased larval density are expressed in several ways. There is increased larval mortality (Fig. 3.5b) and a decreased rate of larval development (Fig 3.5a), while the survival and fecundity of the resulting imagos declines (Figs.3.7, 3.8) Increased larval density results in lower larval growth rates and lower imago weights not only in C. cautella but also in other stored-products Lepidoptera (personal observation; Richards & Waloff 1946, Ullyett & Merwe 1947; Snyman 1949; Takahashi 1961; Podoler 1974b). A number of mechanisms have been postulated to account for the effects of increased larval density. Cannibalism and starvation due to food exhaustion have been suggested by Takahashi (1955, 1956b), Rogers (1970) and Podoler (1974b). Corbet (1971) demonstrated increased dispersal and delayed pupation in late final instars of A. kuehniella with increasing larval density, as a result of larval responses to larval mandibular gland secretions. Hagstrum & Silhacek (1980) found that, when larvae of C. cautella originating from inbred diapause lines were reared individually in small quantities of food (0.18 g), adult emergence was delayed from 4 to 10 weeks. They also found that larval diapause was induced when larvae were reared on a mixture of fresh food and residual food (larval faeces) and observed that the diapause-inducing effect of the residual fraction could be removed by chloroform-methanol solvent. Takahashi (1957) working with 'unselected' populations C. cautella reported a similar effect, where pre-imaginal duration increased as the fraction of residual food (faeces) increased. Time to 50% imago emergence ranged from 30-55 days, when the ratio of food:faeces ranged from 20:0 to 20:40.

It appears that many of the effects described are functions of larval growth and intra-larval interactions related to larval density. Any population model that claimed to describe the dynamics of C. cautella would need to incorporate such factors as food utilization, the dynamic effects of larval density on larval mortality and stage duration, as well as larval size and its subsequent impact on imago survival and reproduction. If a model of individual growth could be developed that predicted larval growth, stage duration and survival, substantial progress could be made towards the development of a population model of this single-species system. The following chapter presents a series of

experiments designed to provide further data on the impact of larval density on larval growth, and a growth model incorporating some of the mechanisms that have been discussed in this chapter.

In summary, the demographic characteristics of C. cautella populations have been quantified. The majority of the dynamic processes have been shown to occur in, or be a consequence of, factors influencing larval development. The demographic characteristics of the pupal and imaginal stages are subjected to little or no dynamic control. Egg survival is dynamically related to larval density due to egg cannibalism by larvae, while 1st instar cannibalism by older larvae is an additional dynamic factor operating on the larval stage. The consequences of these demographic characteristics and dynamic processes will be discussed in a subsequent section.

A MODEL OF CADRA CAUTELLA LARVAL GROWTH AND COHORT SURVIVAL

In the previous chapter it was shown that a number of the demographic characteristics of Cadra cautella depend on the initial egg density (eggs/g food) from which cohorts of the moth were reared Increased egg density resulted in increased larval stage duration and mortality, but decreased imago life span and fecundity These results were thought to be entirely due to larval competition for food, where effects on larval stage duration and survival were a direct consequence of larval competition, and effects on imago lifespan and fecundity were the indirect expression of the effects of larval competition on larval weight. In the context of cohort experiments, the duration and through stage survival of the egg and pupal stages are assumed to be simple constants, independent of larval density. Data presented in the previous chapter support these assumptions.

While many of the observed consequences of larval density could be incorporated into a mathematical population model of C cautella in an empirical ad hoc fashion, a more realistic and potentially more useful model would be obtained by describing larval competition as the outcome of the interactions of a number of biological processes. The purpose of this chapter is to present a mathematical model which captures the essential effects of larval density on larval growth, stage duration and cohort survival In order to achieve this objective a series of experiments were carried out to provide information on the larval growth process, to allow preliminary estimates of the required parameters, and to provide a set of observed data with which the model predictions could be compared

MATERIALS AND METHODS

All insect weights reported are dry weights. Insects were briefly immersed in 70% ethanol and dried for 48 h at 60° C prior to weighing. Wheat flakes were stored at 27°C and 85% R.H. for 7 days prior to use. Moisture content of the food stored in this way was 10.3% and was determined by drying the wheat flakes for 72 h at 60° C. Experiments were initiated based on wet weights of food, but dry weights calculated by adjusting for moisture content will be reported. Amount of remaining food

following an experiment was determined by carefully separating uneaten food from faeces and frass and drying the food for 72 h at 60°C prior to weighing. Each experiment was established from a single pool of eggs (3±3 h old, ±range).

Preliminary data on larval growth were obtained by establishing a series of vials (3.0 x 6.0 cm) containing 3.1 g wheat flakes and 25 eggs. At intervals the vials were examined and larvae and pupae were removed and weighed. Smaller larvae were weighed in groups, while 5th instars, pupae and imagos were weighed individually. Imagos were weighed on the day that they emerged.

The effect of larval density on larval growth was investigated by adding 0.9 g food to a series of vials (3.0 x 6.0 cm). There were 11 initial egg densities (eggs/vial): 5, 8, 12, 18, 26, 40, 60, 73, 87, 100 and 150. At intervals vials were examined (4 vials/sample for densities < 60, and 3 vials/sample for the remaining densities), larvae were removed, counted and weighed, and the remaining food was weighed. All larvae from a vial were weighed as a group.

The effect of food density on imago weight and age at emergence was investigated by preparing a series of vials (3.0 x 6.0 cm) containing 10 cm^3 of a mixture of wheat flakes and expanded mica ('vermiculite'). The proportion of wheat flakes, by volume, varied from 0.1 to 1.0, which resulted in food densities ranging from 0.04 - 3.54 g/cm^3. There were 12 food densities and 30 vials containing 1 egg for each density. The age and weight of the imagos at emergence was recorded.

In order to determine whether imago age at emergence was affected by larval numbers per container as opposed to larval density (larvae/g food), a set of containers (9.2 x 3.8 cm) was prepared containing 10, 15, 20, 25, 30, 35, and 40 g (wet weight) wheat flakes. Eggs were added to these containers (5/treatment) such that the egg:food ratio was 1.1 (10 eggs : 10 g food). The age, weight and number of imagos emerging were recorded. Imagos were weighed in groups of the equivalent sex, age, treatment and container.

Data on the effect of initial larval density on the number of imagos emerging and their age and weight at emergence were obtained by preparing a series of vials (3.0 x 6.0 cm) containing 0.9 g wheat flakes. There were 17 initial egg densities (2, 4, 6, 8, 10, 12, 14, 18, 22, 26, 30, 40,

50, 60, 80, 100, and 150 eggs/vial) and 15 vials per density. Vials were examined daily and the sex, age at emergence and number emerging per vial were determined. Imagos were not weighed individually, but pooled according to initial egg density, sex and age at emergence Once all imagos had emerged from a vial, dead pupae were removed and counted and the remaining food weighed.

Numerical analysis of the model was performed using the program SOLVER (Maas, Nisbet & Gurney 1982).

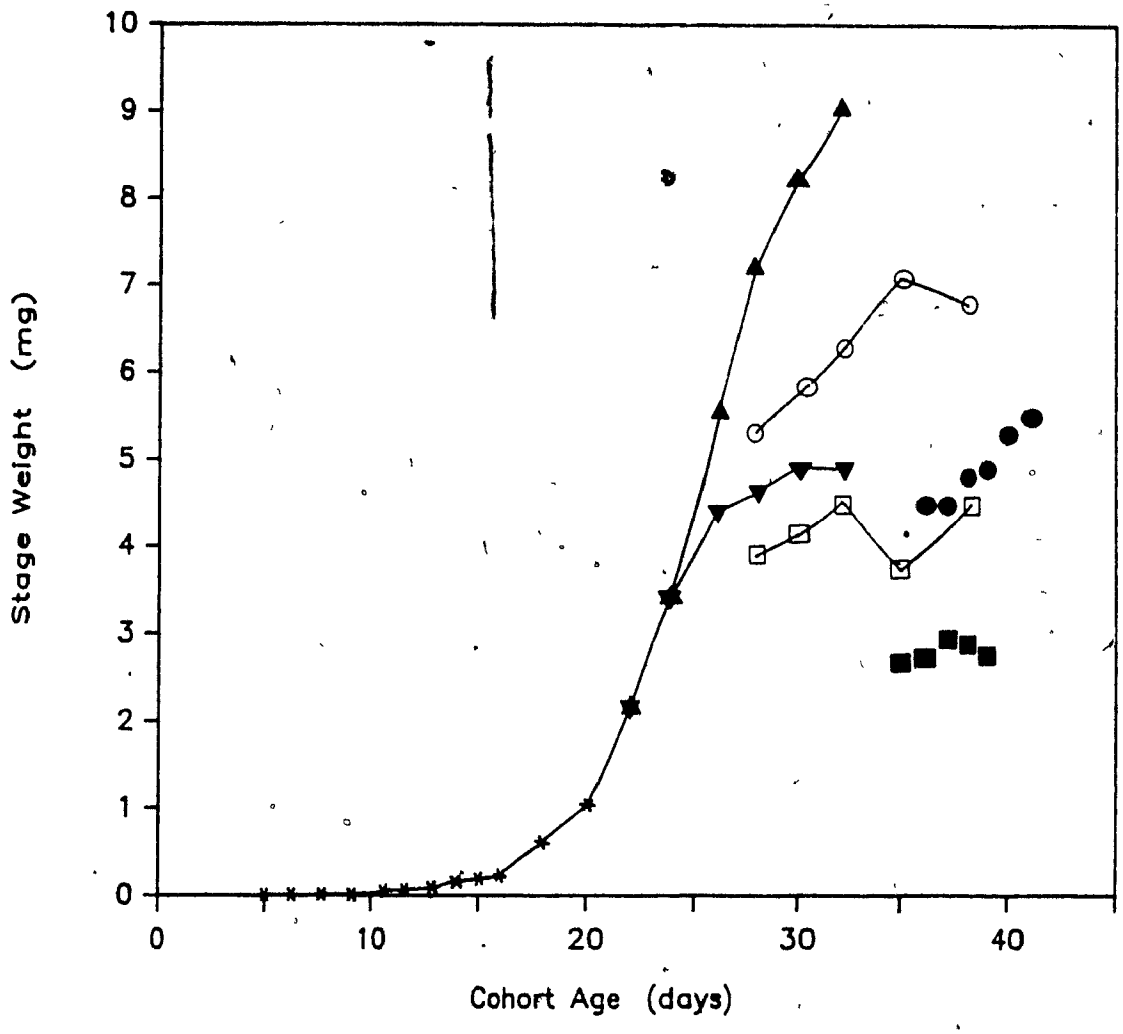
RESULTS

Figure 4.1 presents the change in C. cautella weight through time based on data obtained from rearing 25 eggs in 3.1 g food. Larval weight at hatching was 0.005±0.001 mg. At a cohort age of about 20 days 5th instar larvae could be sexed. Inspection of size frequency histograms revealed no differences between male and female weights until just prior to male pupation. These results suggest that no differences exist in the growth rate of males and females, and that the greater weight of female imagos is a result of the additional time they spent as larvae.

Due to technical constraints it was not feasible to obtain direct measures of actual initial larval density (as opposed to initial egg density), or larval survival to pupation or larval age and weight at pupation. However each of these parameters can be estimated from the data collected in this experiment.

Estimation of initial larval density involved assumptions about the proportion of eggs that hatch and the survival of larvae. Results presented in Chap. 3 show that egg hatching is independent of density and that at low densities larval survival is very high Mortality that does occur, does so soon after egg hatching. At densities between 2-12 eggs/vial (Appendix D4.2) no significant differences were detected in the proportion of eggs surviving to emergence. Therefore it was assumed that the initial larval density per vial was the sum of the number of emerging imagos plus the number of dead pupae. At higher densities, however, it was not possible to assume the lack of larval mortality. Therefore initial larval densities were estimated by multiplying the initial number

Figure 4.1. Growth of Cadra cautella when raised at a density of 8.1 eggs/g food. ✱ weight of unsexed larvae; ▼ weight of male larvae; ▲ weight of female larvae; □ weight of male pupae; ○ weight of female pupae. ■ male imago weight at emergence; ● female imago weight at emergence.


Stage Weight (mg)
Cohort Age (days)
0
1
2
3
4
5
6
7
8
9
10
0
10
20
30
40

of eggs by the average proportion (0.73) that hatch as determined using the data from densities 2-12.

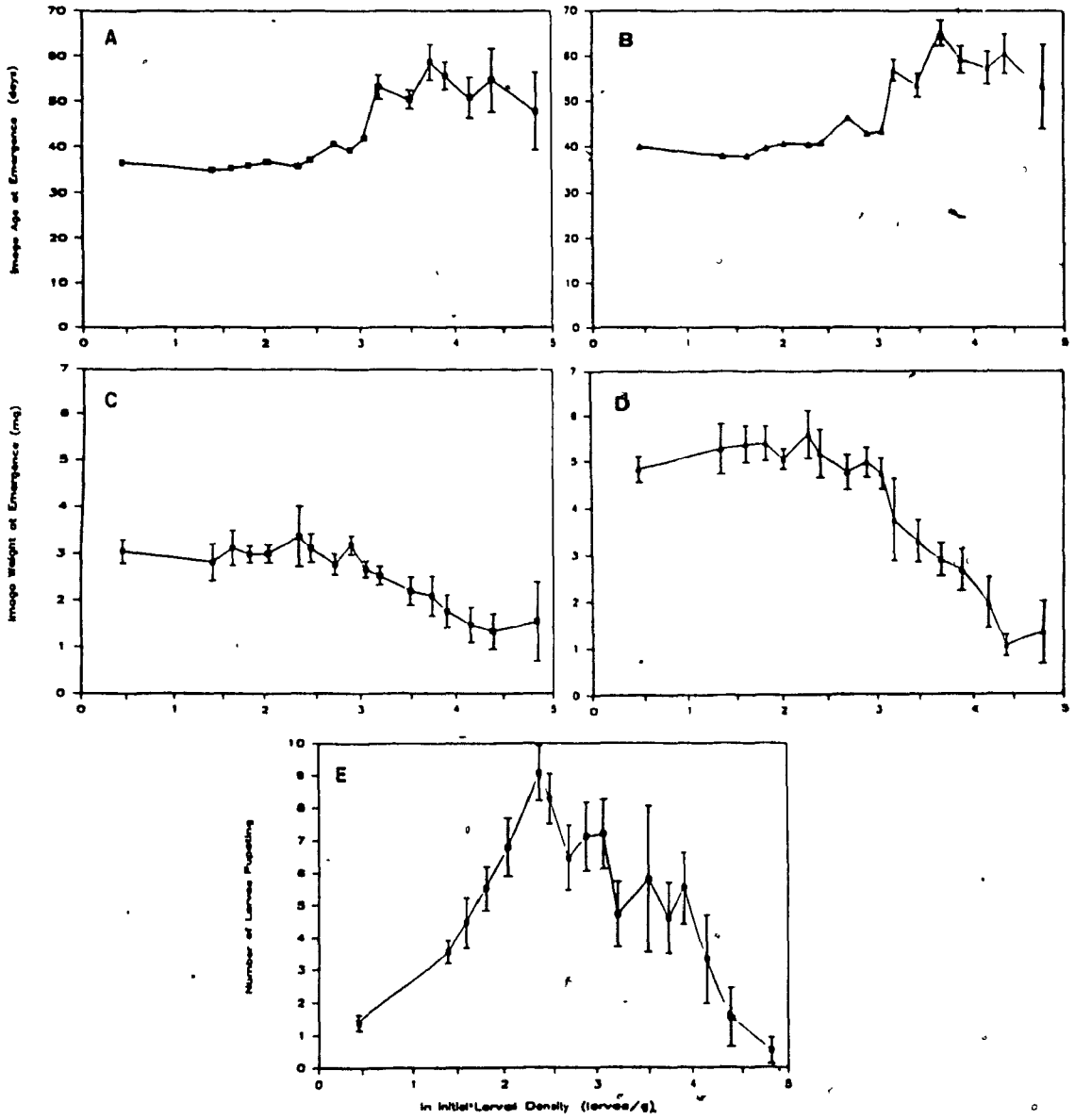
The number of larvae surviving to pupation was again estimated by adding the number of imagos emerging per vial to the number of dead pupae per vial. The assumptions concerning the estimates of number of larvae surviving until pupation requires that pupal mortality be independent of larval density. No significant differences in pupal mortality (k-values) were detected among densities ($F_{(16,225)}$=1.38, $p>0.15$).

It has been previously shown (Chap. 3) that density did not influence the duration of the egg or pupal stages, and that on average the combined duration of these stages were 11.2 days for males and 11.7 days for females. In order to estimate larval stage durations, these values were subtracted from imago age at emergence.

Larval weight at pupation was estimated using a correction factor obtained from the preliminary growth experiment (Fig. 4 1). At each day of emergence, for each sex, an estimate was made of the age at pupation (age at emergence minus pupal duration of 7.7 days males, or 8.2 days females) and the larval weight at that estimated age was assumed to represent larval weight at pupation. On average males lost 40.8±0.8% of their body weight and females lost 40.7±1.0% from pupation to emergence. The weight loss estimates are in reasonable agreement with those calculated from the data reported by Imura & Sinha (1986) for Plodia interpunctella (-30.5%) and for Anagasta kuehniella (-42.8%) by Brindley (1930). These percent weight changes were used as correction factors in order to convert imago weights at emergence to larval weights at pupation in the experiment concerning the effects of larval density on imago age and weight at emergence. It has been assumed that per cent weight loss during metamorphosis is independent of larval weight at pupation, there is no data to confirm of refute this assumption.

Figure 4.2 illustrates the effects of larval density on imago age and weight at emergence as well as the number of larvae surviving to pupate. These data show that there is an initial range of larval densities, over which survival is high and density has little effect on imago age or weight at emergence. Beyond initial larval densities of about 11/g, there is a rapid increase in mortality and decline in imago weight at emergence, while age at emergence quickly increases to new plateau over a very small

Figure 4.2. Effect of initial larval density on Cadra cautella imago age and weight at emergence and on cohort survival to pupation. A. Male imago age at emergence. B. Female imago age at emergence. C. Male imago weight at emergence. D. Female imago weight at emergence. E. Number of larvae surviving to pupation.


A
B
C
D
E
Image Age at Emergence (days)
Image Weight at Emergence (mg)
Number of Larvae Pupating
ln Initial Larval Density (larvae/g)

range of initial larval densities. This adjusted data set will be used in any further parameter estimations or comparisons with model predictions. The aim is to develop a model which reproduces these patterns and the following section presents results of the balance of the experimental data and steps taken in developing the model of larval growth and cohort survival.

The Model

The model developed in this section attempts to reduce the complex processes of insect growth and development into a simple set of mathematical equations, containing a reasonable number of parameters. The first assumption involved in simplifying larval growth and survival was that larval growth was a continuous process, commencing at egg hatching and ending at pupation, ignoring the existence of the five larval instars. Due to the substantial sex differences in imago weight (Fig. 4.1) it was decided to consider the sexes separately. The model describes the changes through time in the following basic variables:

$F(t)$ - amount of food available at time t, mg
$N_s(t)$ - number of insects alive at time t
$W_s(t)$ - weight of a larva at time t, mg
$Q_s(t)$ - larval development index at time t
s - larval sex; m male, f female.

Because the model is designed to follow a cohort through time, time also measures the age of the cohort.

The inter-relationship between these variables results, in part, from the variable describing the rate of food ingestion by a larva,

$I_s(t)$ - rate of food ingestion, mg/larva per day.

Functional responses for invertebrates typically consider the amount of food or number of prey consumed per unit time as a function of food (prey) density (Hassell 1978). The conceptual underpinning to these responses is that a 'predator' searches the environment at some rate and

encounters, at random, 'point' sources of food occurring at a particular density. Different assumptions concerning 'handling time' or the dependence of search rate on food density, give rise to the various forms of functional responses (Type I, II etc). While this conceptual basis is sound for the foraging behaviour of parasitoids and predators, it becomes less so when used as a basis to describe the feeding behaviour of insects like C. cautella, where their environment is their food source and where food 'density' therefore approaches infinity.

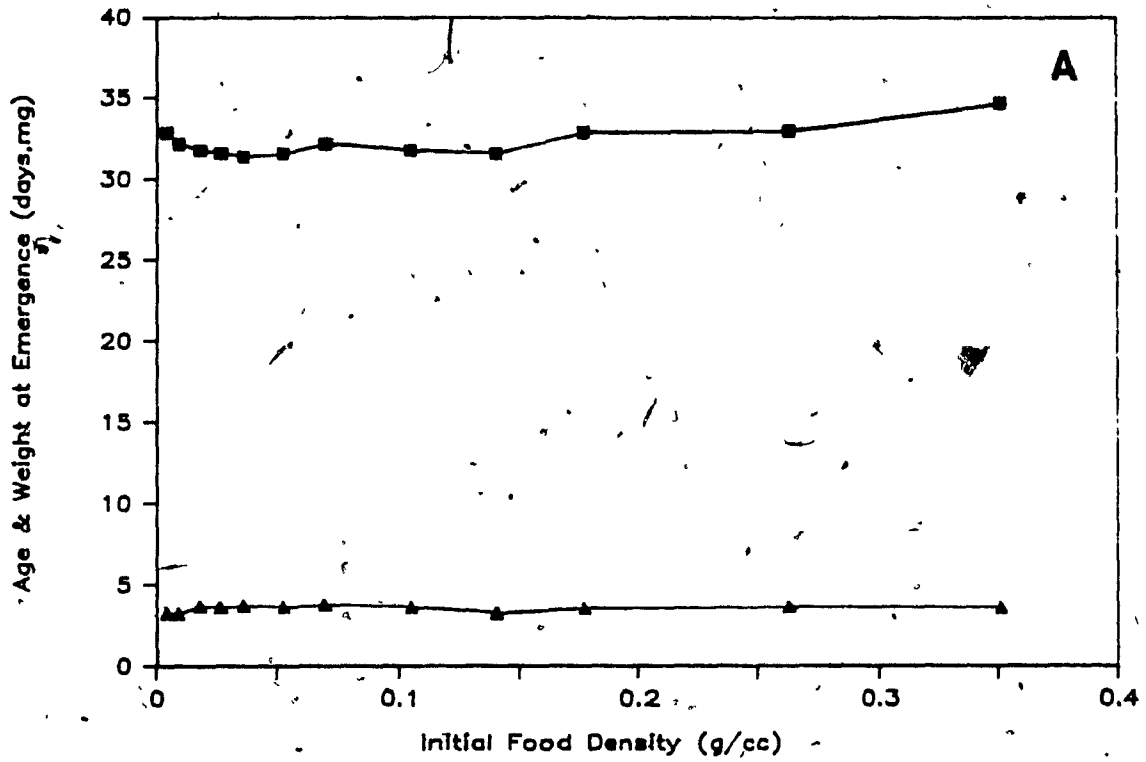
The data illustrated in Fig. 4.3 presents some evidence on the nature of the functional response of C. cautella larvae under conventional conditions of food density. Imago weight and age at emergence provide an indirect measure of larval growth and therefore the rate of food ingestion. No differences were detected in imago weight at emergence among food densities for either sex (males, $F_{(10,140)}$= 2 37, p>0 01, females, $F_{(10,126)}$=1 06, p>0 395). Age at emergence was found to depend on food density (males, $F_{(10,142)}$=6.46, p<0.001; females $F_{(10,126)}$=8.24, p<0.0001); in both sexes age at emergence was higher at low and high food densities than at intermediate food densities. The reasons for this particular pattern in age at emergence are unknown, but the data do suggest that the rate of food ingestion is essentially independent of food density.

It was assumed that the basic rate of food ingestion would be linearly proportional to larval weight and independent of the sex of the larvae. Imura & Sinha (1986), working with P. interpunctella found no sex differences in larval rates of food consumption It seems reasonable to assume that, as larvae grow and head capsule size and hence mandible size increases, the amount of food ingested per unit time increases, although the assumption of linearity is a crude first approximation. As a result of these assumptions the preliminary form of the rate of food ingestion becomes,

$$I_s(t) = 0 \qquad \text{if } F(t) = 0$$
$$I_s(t) = \omega W_s \qquad \text{if } F(t) > 0 \qquad \text{Eq. 4.1}$$

where ω = basic feeding rate, mg food per mg larval weight.

Figure 4.3. Effect of food density on Cadra cautella imago age and weight at emergence. A. Male age and weight at emergence. B. Female age and weight at emergence. ■ age at emergence; ▲ weight at emergence.


A
Age & Weight at Emergence (days,mg)
Initial Food Density (g/cc)
0
5
10
15
20
25
30
35
40
0
0.1
0.2
0.3
0.4

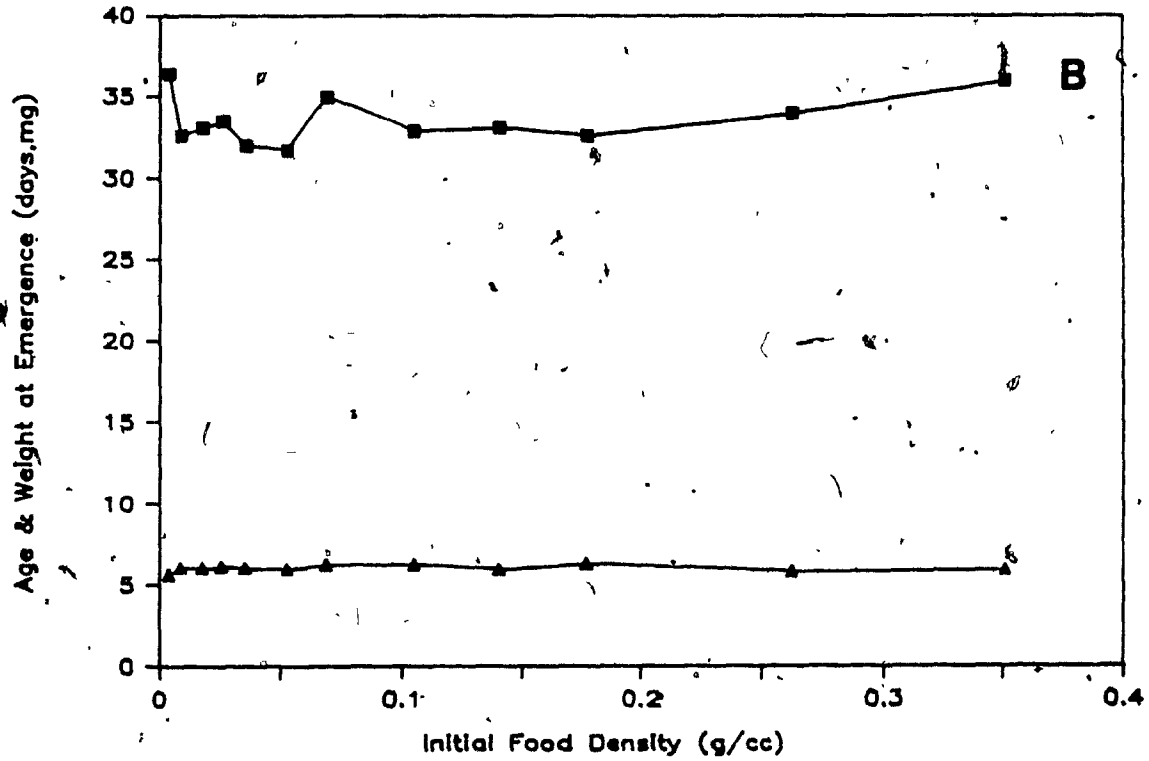
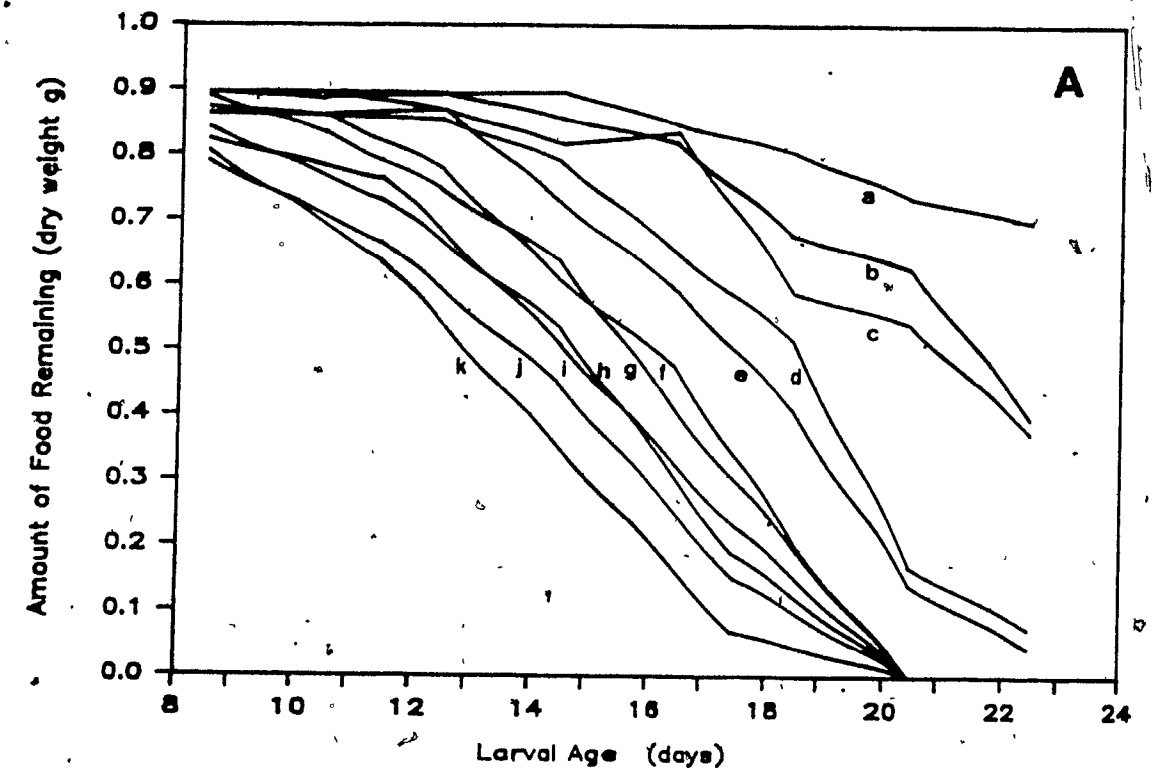

B
Age & Weight at Emergence (days,mg)
Initial Food Density (g/cc)
0
5
10
15
20
25
30
35
40
0
0.1
0.2
0.3
0.4

Figure 4.4 illustrates the observed changes in larval weight and in the amount of food remaining per vial through time. If Eq. 4.1 was a complete description of the rate of food consumption, the following patterns would occur. First, larvae would grow at the same rate regardless of larval density, and second, a doubling of larval density should half the time to food exhaustion. As can be seen by examining Fig. 4.4 neither of these patterns occur. When larval densities are sufficiently high to result in food exhaustion, the time at which this occurs is quite uniform (20 days), but substantial differences can be observed in the growth rates of the larvae well before the time of food exhaustion. These data suggest that the rate of food ingestion depends on larval density.

It has been an implicit assumption of the material presented to this point that the correct description of larval density is number of larvae per g of food. Figure 4.5 presents the age and weights of imagos at emergence, when the number of larvae per container was increased, but densities were at a 1:1 ratio of initial number of egg: g wheat flakes. No differences in female weight at emergence were detected among treatments ($F_{(6,128)}=1.37$, $p>231$), but differences in male weights among treatments were found ($F_{(6,119)}=3.35$, $p<0.005$). For both males and females age at emergence differed among treatments (males, $F_{(6,335)}=4.28$, $p<0.0005$; females, $F_{(6,326)}=3.32$, $p<0.004$). While the range in male weight was 0.57 mg, the range in age at emergence was only 1.2 days, and in neither male weight nor age at emergence was there any obvious trend with the number of larvae per container. The results of this experiment indicate that the appropriate measure of larval density is the number of larvae/g food.

There are a number of mechanisms which may be invoked to explain the dependency of larval growth (and thus food ingestion rate) on larval density. Mutual interference among searching larvae, as has been show to occur among searching parasitoids (Hassell 1978), may occur whereby larvae cease to feed as a result of contact with another larva. The act of feeding itself may inhibit food ingestion rates. Corbet (1971) showed that in late final instar larvae of Anagasta kuehniella, secretions originating in the mandibular glands and released by the larva while feeding or when in contact with another larvae resulted in increased

Figure 4.4. Cadra cautella larval growth and the amount of food remaining through time at different initial larval densities. A. Amount of food remaining. B. Larval weight. The letters indicate the average initial number of larvae per 0.9 g food: a. 3.2; b. 6.4; c. 8.7; d. 14; e. 20; f. 29; g. 44; h. 57; i. 71; j. 83; k. 122.


A
Amount of Food Remaining (dry weight g)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
8
10
12
14
16
18
20
22
24
Larval Age (days)
a
b
c
d
e
f
g
h
i
j
k

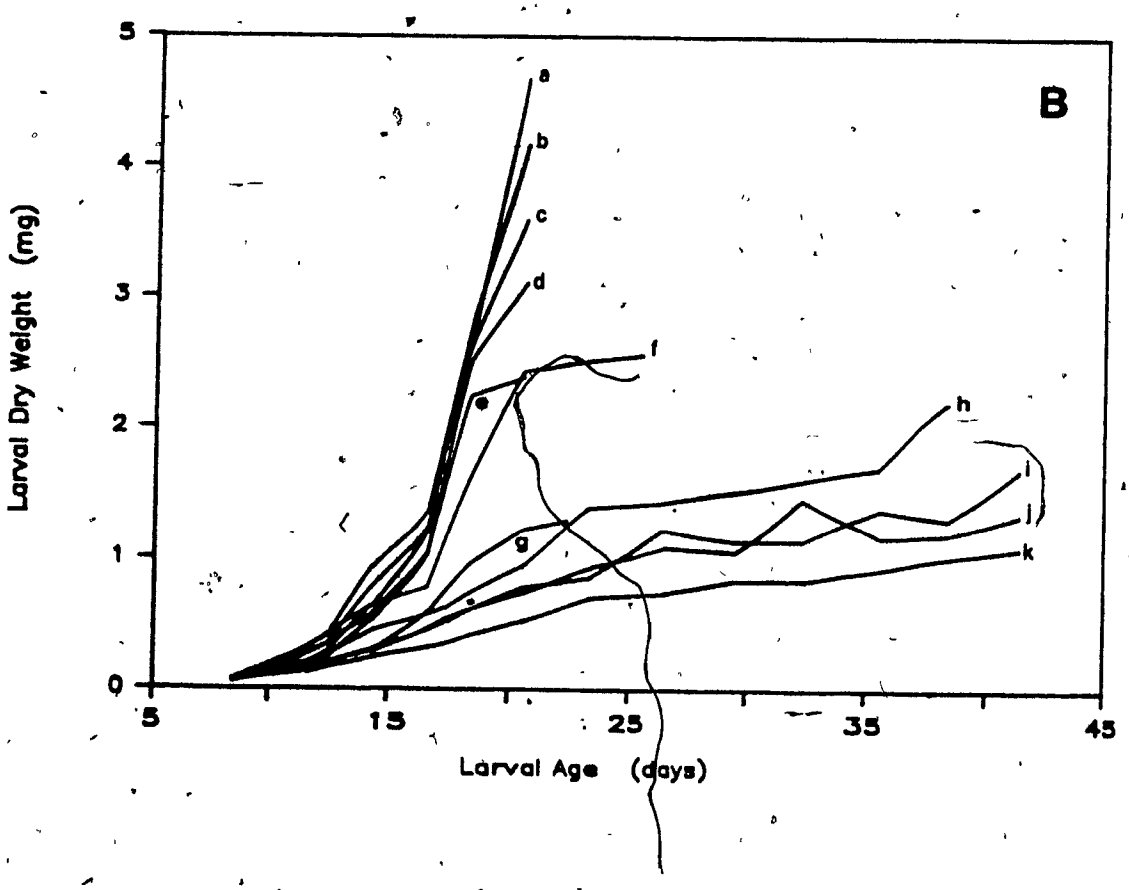
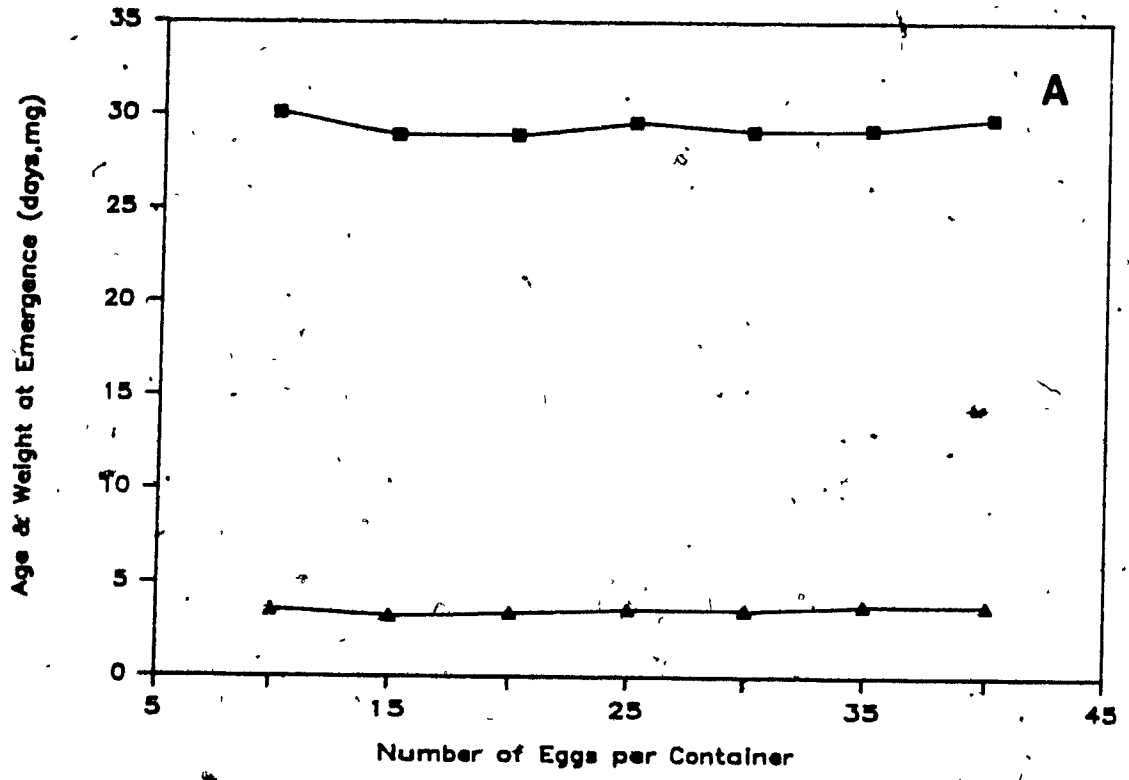
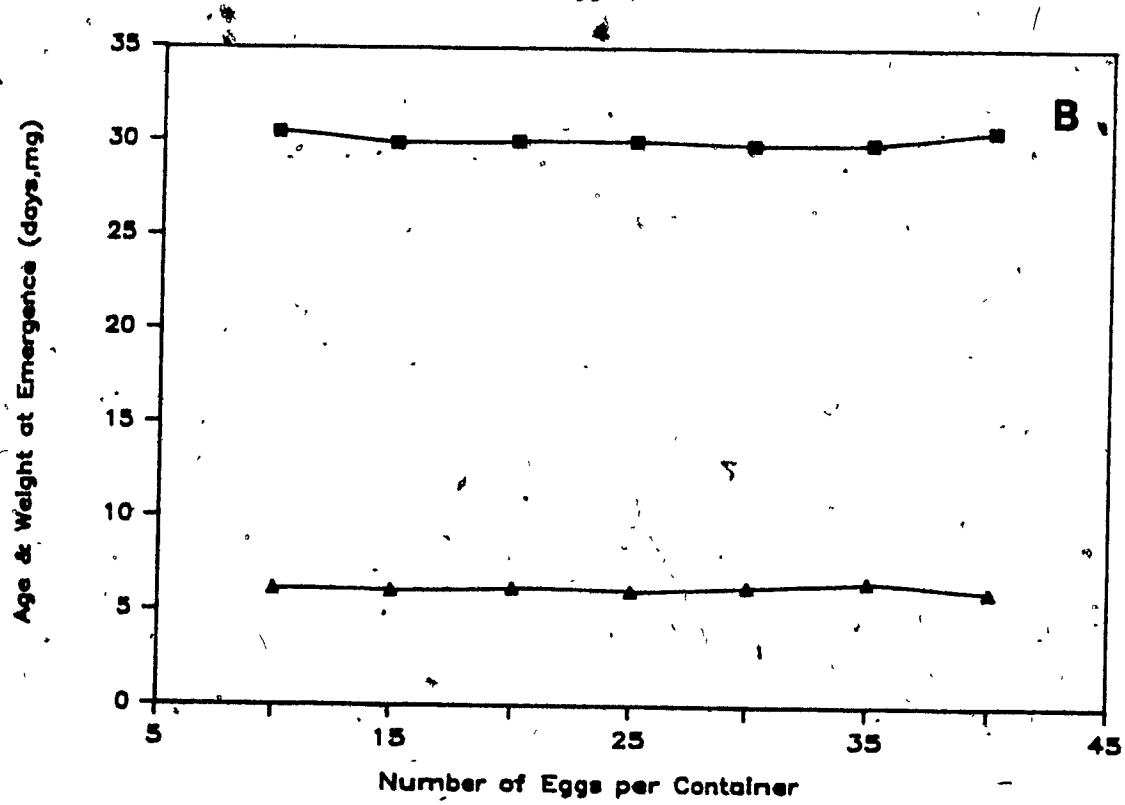

B
Larval Dry Weight (mg)
5
4
3
2
1
0
5
15
25
35
45
Larval Age (days)
a
b
c
d
e
f
g
h
i
j
k

Figure 4.5. Effect of number of larvae/container on Cadra cautella imago age and weight at emergence when initial egg density is 1 egg/g food. A. Male age and weight at emergence. B. Female age and weight at emergence. ■ age at emergence. ▲ weight at emergence.


A
Age & Weight at Emergence (days,mg)
35
30
25
20
15
10
5
0
5
15
25
35
45
Number of Eggs per Container


B
Age & Weight at Emergence (days,mg)
35
30
25
20
15
10
5
0
5
15
25
35
45
Number of Eggs per Container

larval activity ('wandering'), delayed time to pupation and decreased weight at pupation. These mandibular gland secretions are also produced by the C. cautella larvae (Mudd & Corbet 1973). Takahashi (1957) working with C. cautella found that age at emergence increased and imago size decreased in an experiment where increasing amounts of larval faeces were added to 20 g of fresh food containing 100 eggs. Whether the compound(s) present in mandibular secretions are also present in larval faeces, and thus responsible for the effects observed by Takahashi (1957), is unknown Which of these potential mechanisms might be responsible for decreased food ingestion rates is not known. However all of these mechanisms will potentially behave in a similar manner. Their inhibitory effect will increase with increasing larval weight and increasing larval numbers, and the consequences will become more severe as the amount of food remaining decreases. These arguments give rise to the final form of the expression for the rate of food ingestion,

$$I_s(t) = \omega W_s / (1+\sigma N(t) W_s(t)/F(t)) \qquad \text{Eq. 4.2}$$

where σ = interference coefficient.

The parameters ω and σ were estimated by non-linear least squares regression from the data of Fig 4.4. When the parameters were estimated using the data of each of the initial larval densities, no trend with larval density was found in the values of the parameters. The final parameter estimates were obtained by pooling the data of all initial larval densities and are presented in Table 4.1

This now leads to the need for a description of larval growth Beddington, Hassell & Lawton (1976) have shown that arthropod growth rates are typically linearly related to the amount of food consumed in excess of that needed for basic metabolic requirements. In the absence of any detailed bioenergetics data for C. cautella it has been assumed that a constant fraction of the food consumed by a larva is converted to larval biomass. The expression for the rate of weight change being,

$$dW_s/dt = \epsilon_s I_s(t) \qquad \text{Eq. 4.3}$$

where ϵ = food conversion efficiency.

Table 4.1. Parameter estimates and fixed initial conditions used in numerical solutions of the Cadra cautella model.

Parameter	Estimate ± S.E.	Description
ω	3.83±0.07	basic feeding rate
σ	2.62±0.31	interference coefficient
ϵ	8.0%	food conversion efficiency
α_m	0.01315±0.0001	D. I.[1] coefficient, Q/day
γ_m	0.1238±0.0034	D. I. coefficient, Q/mg
α_f	0.01298±0.0001	D. I. coefficient, Q/day
γ_f	0.07368±0.0016	D. I. coefficient, Q/mg
δ	0.0894±0.0062	larval death rate

Initial Conditions, at t = 0

$Q_s(t) = 0$

$W_s(t) = 0.005$ mg

$F(t) = 897$ mg

Sex-Ratio, 1:1

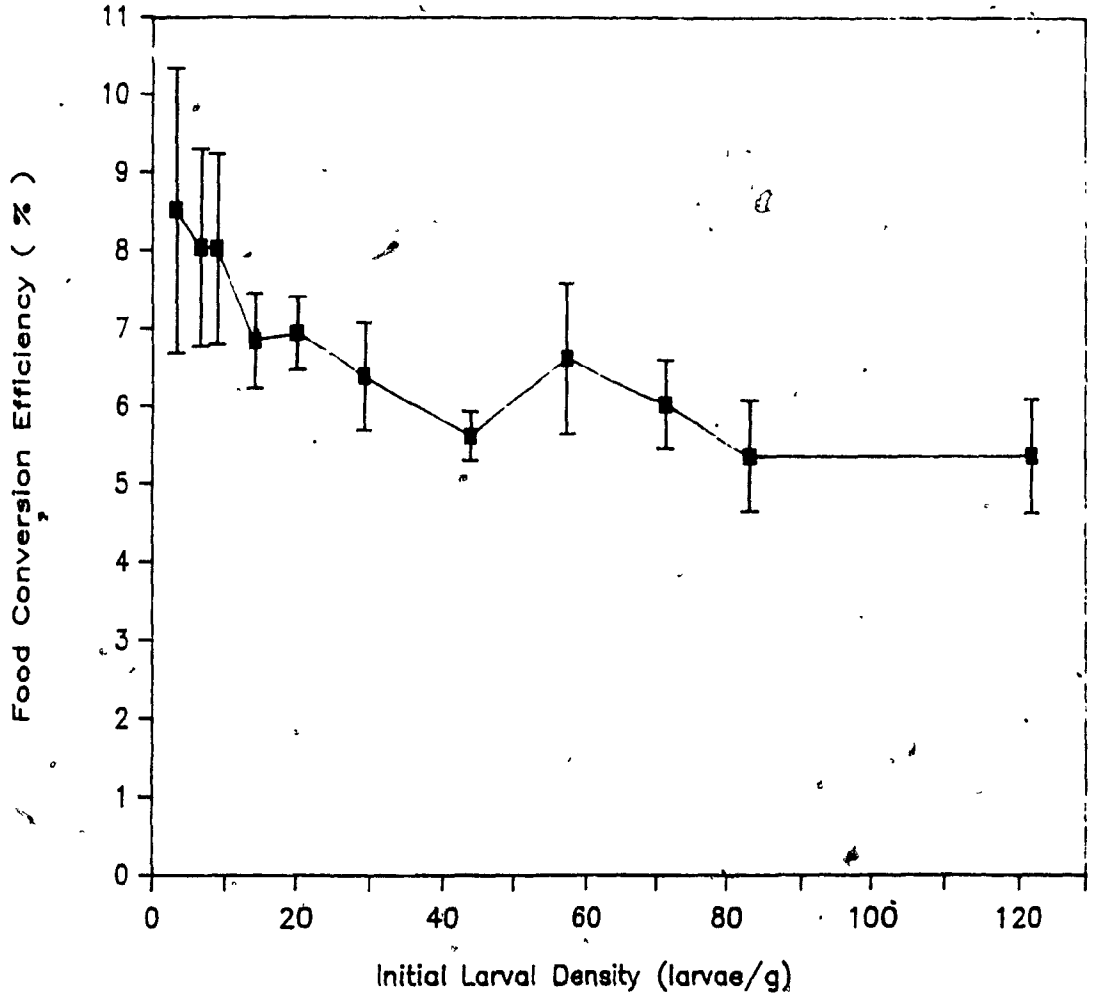
[1] Development Index.

Figure 4.6 presents the food conversion efficiencies for each initial larval density estimated from the data of Fig 4.4 by dividing the total weight of larvae per vial by the amount of food consumed for each vial and each larval density. Conversion efficiency depended on larval density ($F_{(10,117)}$=6.24, $p<0.0001$) and showed a declining trend with increasing larval density, stabilizing at about 5% at the higher larval densities. Imura & Sinha (1986) in a study of the bioenergetics of P. interpunctella presented data that, when calculated in a similar manner, suggest a gross production efficiency for larvae of about 9%. Given the crude nature of the estimates for conversion efficiency it was decided not to incorporate this phenomenon as part of the growth model. The value for food conversion efficiency was arbitrarily chosen to be 8% for both males and females. The work of Imura & Sinha (1986) supports the assumption of no sex differences in conversion efficiencies (gross production efficiencies: 12.3% males, 11.8% females).

The necessary equations for a description of larval growth through time have been developed. However larvae do not continue to grow indefinitely and some measure of larval development is required in order to decide when pupation should occur. The larval development index is a dimensionless measure of the state of development of an individual as a function of one or more other variables (eg. temperature) and is a concept that has been defined by Gurney, Nisbet and Blythe (1986). For example the development index might be related to larval age or to larval weight. The former case may be viewed as an example of a larva that pupates when it attains a certain fixed age, while the latter would be an example of an insect that pupates only after reaching some predetermined weight. Figure 4.7 presents the relationship between larval age at pupation and larval weight at pupation for males and females. The data for this figure were obtained by calculating the average larval weight at pupation for each of the observed ages at pupation, regardless of larval density. Inspection of Fig. 4.7 suggests that, as larvae do not appear to pupate at either a fixed weight or age, the most appropriate form for the development index is one that is a function of both larval age and weight, such that

$$Q_s = \alpha_s t + \gamma_s W_s(t) \qquad \text{Eq. 4.4}$$

Figure 4 6. Larval food conversion efficiency in Cadra cautella as a function of initial larval density.


Food Conversion Efficiency (%)
11
10
9
8
7
6
5
4
3
2
1
0
0
20
40
60
80
100
120
Initial Larval Density (larvae/g)

where α_s = coefficient for the change in the development index with age, Q/day

γ_s = coefficient for the change in the development index with weight, Q/(mg larval weight per day)

By definition the value of Q is 0 at egg hatching and 1 at pupation, with the result,

$$Q(p) = 1 = \alpha_s A(p) + \gamma_s W(p) \qquad \text{Eq. 4.5}$$

where, Q(p) = the value of the larval development index at pupation

A(p) = larval age at pupation, days

W(p) = larval weight at pupation, mg

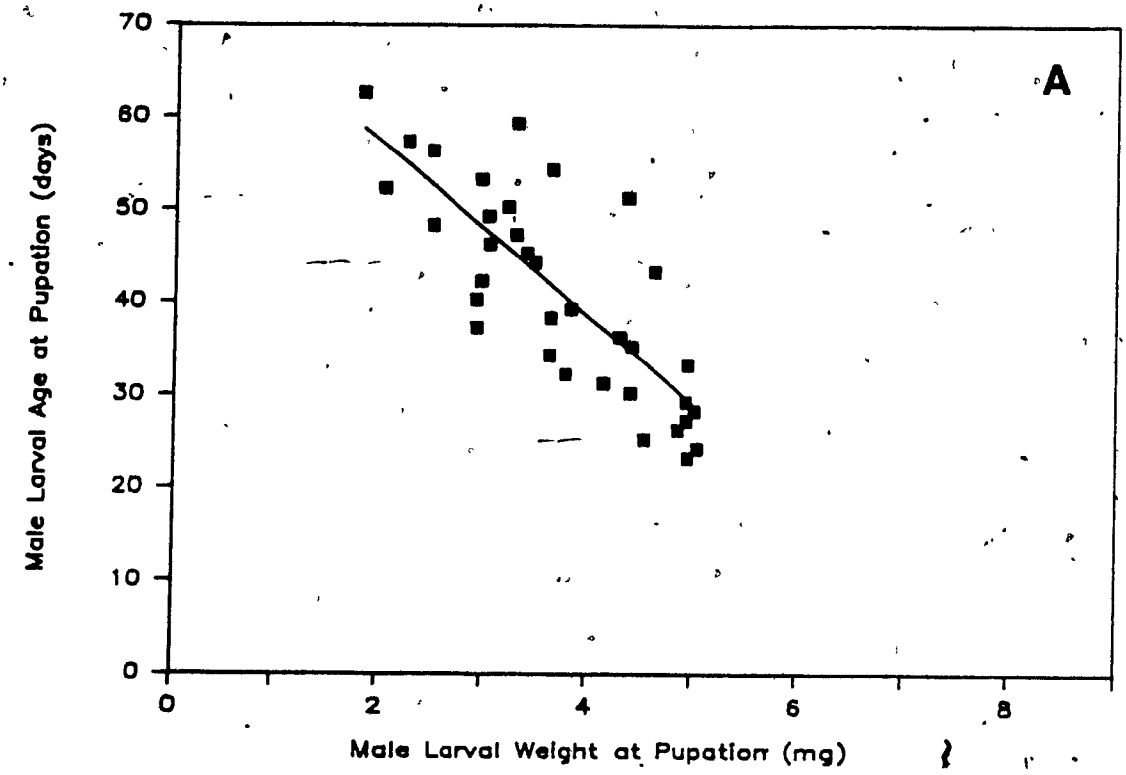
The parameters α_s and γ_s were estimated from the data of Fig. 4.7 using a non-linear least-squares procedure and are presented in Table 4.1.

The next component required for the model is a description of the change in larval numbers with time. Figure 4.8 presents the total number of insects alive through time for each of the initial larval densities. Regardless of initial larval densities, no change could be detected in the number of larvae per vial in those samples where food exhaustion had not yet occurred. For the densities for which there were sufficient data after food exhaustion (73 - 150 eggs), no significant differences could be detected in the slopes of the regression relating number of larvae surviving ($\log_e$) with time ($F_{(1,92)}$=1.60, $p>0.2$). These data suggest that only when food quantity falls to relatively low levels (about 50 mg) do larvae begin to die and that the death rate is unrelated to the influences of larval density, such that the change larval numbers with time is

$$\begin{aligned} dN_s(t)/dt &= 0 && \text{if } F(t) > 50 \text{ mg} \\ dN_s(t)/dt &= -\delta N_s(t) && \text{if } F(t) < 50 \text{ mg} \end{aligned} \qquad \text{Eq. 4.6}$$

where δ = instantaneous death rate, /larvae/day.

Figure 4.7. Relationship between larval age and weight at pupation in Cadra cautella A. Male age and weight at pupation B. Female age and weight at pupation. Regression lines depict development indices (Eq. 4.4) as a function of larval age and weight at pupation. Parameters of the regression lines are presented in Table 4.1.


A
Male Larval Age at Pupation (days)
Male Larval Weight at Pupation (mg)
0
10
20
30
40
50
60
70
0
2
4
6
8

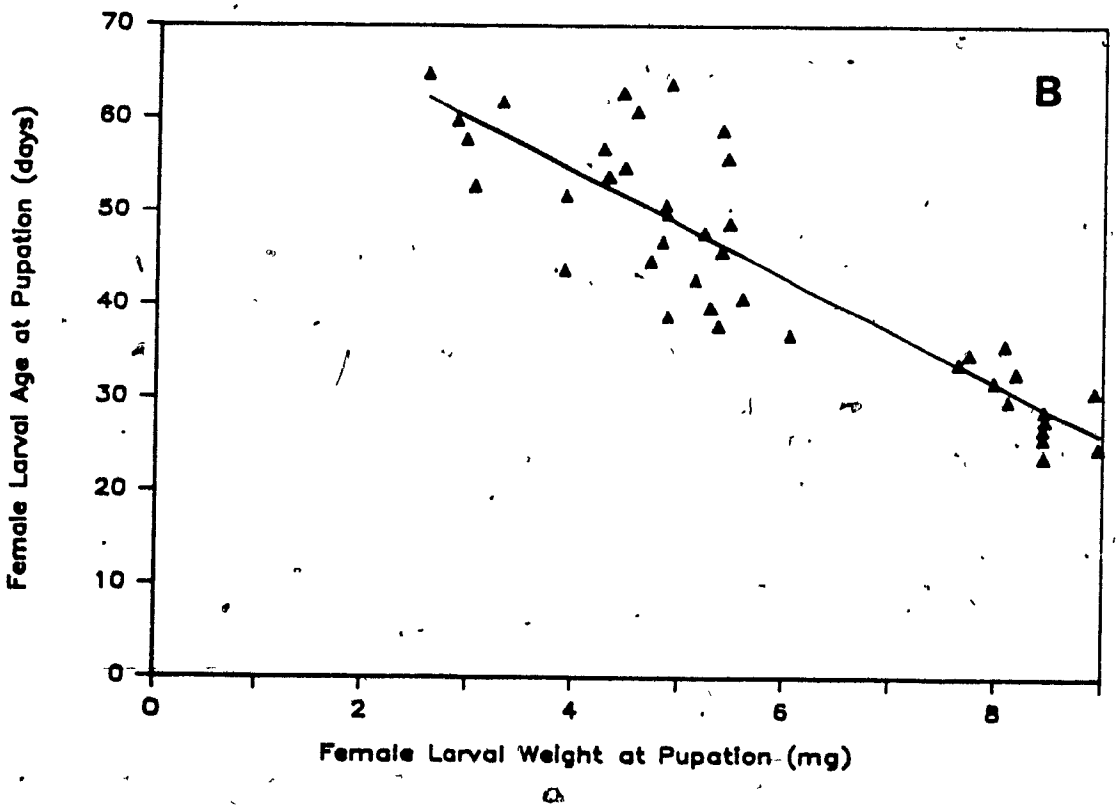
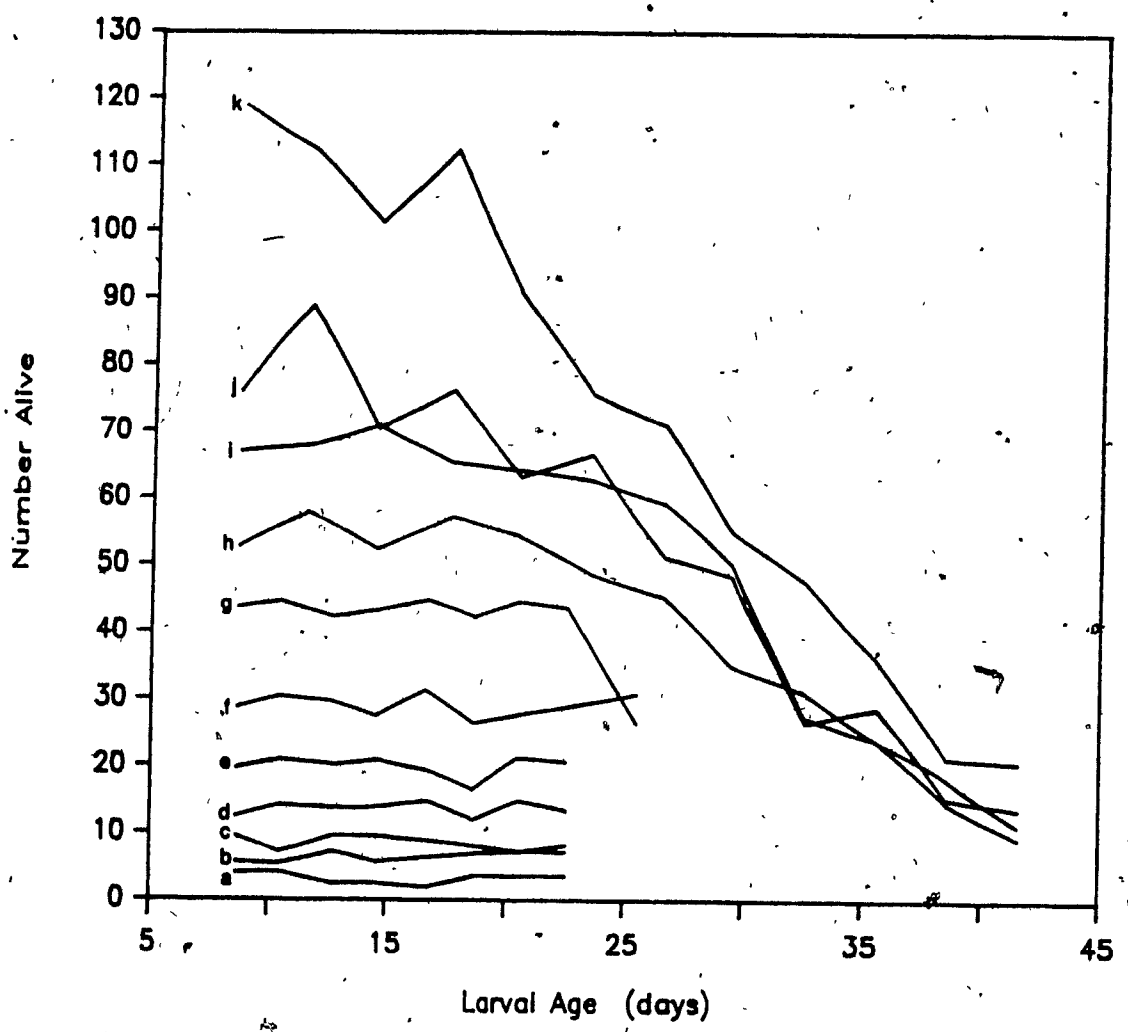

B
Female Larval Age at Pupation (days)
Female Larval Weight at Pupation (mg)
0
10
20
30
40
50
60
70
0
2
4
6
8

Figure 4.8. Cadra cautella larval survival through time at different initial larval densities. Letters indicate the average initial number of larvae per 0.9 g food: a. 3.2; b. 6.4; c. 8.7; d. 14; e. 20; f. 29; g. 44; h. 57; i. 71; j. 83; k. 122.


Number Alive
130
120
110
100
90
80
70
60
50
40
30
20
10
0
5
15
25
35
45
Larval Age (days)
k
j
i
h
g
f
e
d
c
b
a

The estimate for δ was obtained by averaging the instantaneous death rates calculated using the data of initial egg densities 73, 87, 100 and 150. A sex ratio of 1:1 has been assumed. This assumption is supported by data presented in Chap. 3. Owing to the differences in the rate of change between the sexes in development index, male larvae will tend to pupate at an earlier age than female larvae. The assumption has been made that the death rate of pupae is the same as the death rate of larvae. The validity of this assumption will be discussed later.

The final component needed for the model is a description of the change in the amount of food with time. This is simply

$$dF(t)/dt = -I_f(t) \cdot N_f(t) \qquad \text{if } Q_m > 1$$
$$dF(t)/dt = -(I_m(t) \cdot N_m(t) + I_f(t) \cdot N_f(t)) \qquad \text{if } -Q_m <= -1 \qquad \text{Eq. 4 7}$$

Equations 4.2, 4.3, 4.4, 4.6, & 4.7 constitute the model. The results of numerical solution of these equations using the parameter estimates and initial conditions presented in Table 4.1 are illustrated together with the observed data in Figs. 4.9 & 4.10.

DISCUSSION

Comparison of model predictions with observed data provides a rigorous test of the validity of a model, provided that the parameter values are estimated independently of the data used to test the model. The comparisons made in Figs 4.9 & 4.10 do not completely fulfill these requirements, as the parameters of the development index were estimated from the data set with which the predictions are compared. However, these comparisons still provide a very rigorous test of the model, owing to the number of variables which the model is describing. Furthermore the estimates involving the development indices were made independent of any considerations of larval density.

The model adequately mimics the observed patterns of larval growth and survival, as well as the pattern of food utilization, predicting the observed uniformity in larval age at food exhaustion. The model well describes the total food utilization in relation to initial larval density. The model reproduces the effects of larval density on larval

Figure 4.9. Observed data and model predictions of the amount of food remaining, larval Cadra cautella weight and larval numbers through time at different initial larval densities. A. Observed amount of food remaining through time. B. Predicted amount of food remaining. C. Observed larval weight. D. Predicted larval weight. E. Observed number of larvae alive. F. Predicted number alive. Initial larval densities are present in the captions of Figs 4.4 and 4.8. The same initial larval numbers were used to generate the predicted curves.

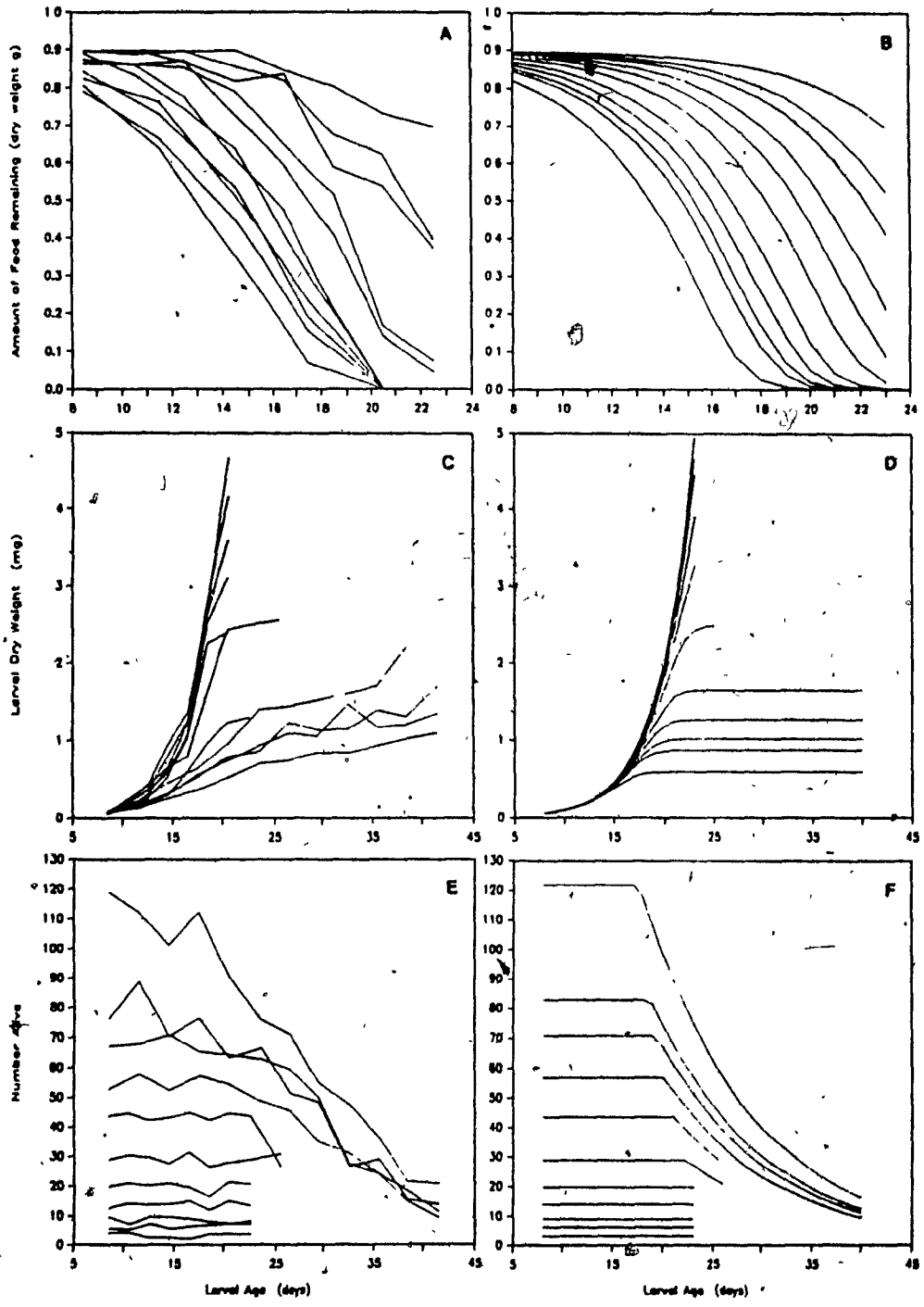
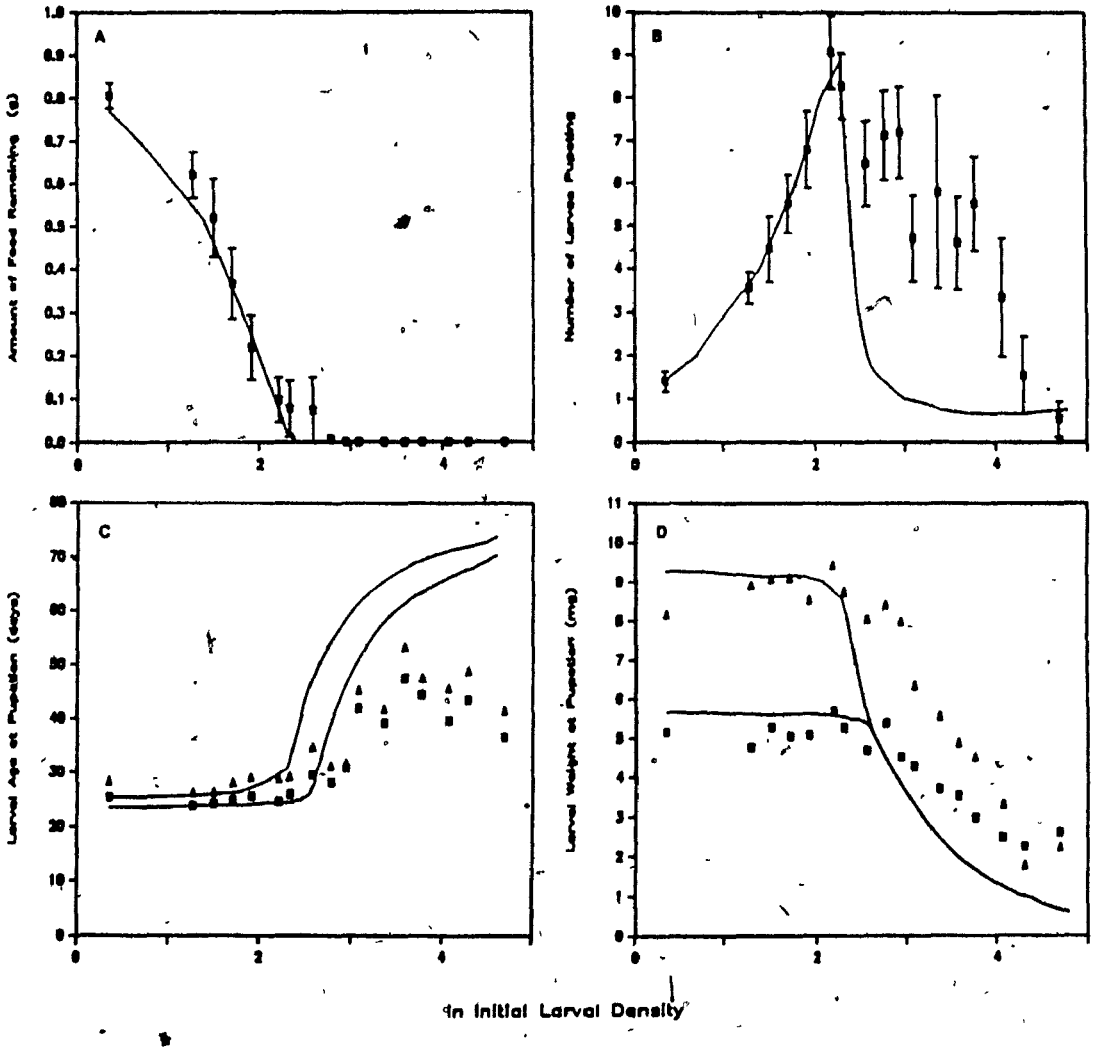

A
B
C
D
E
F
Amount of Food Remaining (dry weight g)
Larval Dry Weight (mg)
Number Alive
Larval Age (days)
Larval Age (days)

Figure 4.10. Observed data and model predictions of the amount of food not consumed (A), larval age (B) and weight at pupation (C), and the number of larvae surviving to pupation (D) at different initial larval densities. Solid curves depict the model predictions. C. D. ■ male and ▲ female larvae.


A
B
C
D
Amount of Food Remaining (g)
Number of Larvae Pupating
Larval Age at Pupation (days)
Larval Weight at Pupation (mg)
ln Initial Larval Density

duration, weight and survival. It describes the effect of a range of larval densities where no change in larval weight, duration or mortality occurs, followed by larval densities where larval duration and mortality suddenly increase, and larval weights rapidly decline.

However the model fails to adequately describe the observed data, at those larval densities at which total food utilization does occur, and overestimates the effects of larval density on larval weight and stage duration and larval mortality. The reasons for the failure over these larval densities is easily understood. The model includes the quite reasonable assumption that when food exhaustion occurs, food ingestion ceases and the larvae stop growing. However under experimental conditions once 'food' exhaustion occurs, larvae start to feed on faeces and cannibalism occurs. As a result surviving larvae will continue to feed and grow, though at a much slower rate. Coprophagy and cannibalism will also maintain food ingestion at levels sufficient to avoid or at least delay starvation. Continued larval feeding will act to decrease age at pupation by increasing the value of the development index faster than the model predicts due to further larval growth. As well, decreasing the age at pupation will also reduce the total amount of larval mortality. Observations made while carrying out these experiments suggest that larval starvation accounts for the majority of larval deaths. Intact moribund or dead larvae were often observed well before any pupation occurred. For example, in Fig. 4.6 which presents the total number of insects/ per vial, at the 4 highest larval densities, less than 10% of the larvae had pupated by day 39. Partially eaten moribund or dead larvae were never observed and cannibalism appears to have been restricted to those larvae in the late pre-pupal period (larvae which had constructed the pupal cocoon, but not yet molted) and to young pupae, prior to the complete hardening of the pupal case. These observations may refute the statement made in the previous chapter and earlier in this section that pupal mortality is independent of larval density. This conclusion was actually based on counts made on pupae that had survived cannibalism, the most likely process to account for any relationship between larval density and pupal mortality. As a result the counts reflect 'natural' pupal mortality (excluding cannibalism). However these results do suggest given the variation in larval weight at pupation as a result of the effects of

larval density, pupal mortality is independent of larval weight at pupation.

While the model that has been developed does not provide a completely satisfactory description of the growth and survival of cohorts of larvae at different initial densities, the ultimate purpose of the model is to form the basis of a population model of C cautella. There is some evidence that will be briefly presented here and more fully in a subsequent chapter, that suggests that in a large part the apparent failures of the model are due to artifacts of the experimental conditions used rather than basic conceptual failures.

In long-term population cages food is added at a fixed rate per week, and populations are limited by food availability. Larvae have been shown to move very quickly from old food to the fresh food that is added, a phenomenon that occurs even when larval densities are very low. This would result in the larvae being forced to feed on faeces for only limited periods of time, as opposed to as much as half of their life, as occurred in many of the cohort experiments. Therefore in population cages the amount of larval growth due to coprophagy would be minimal. This pattern of larval movement would also serve to reduce the degree of pupal cannibalism, by reducing the amount of time that pupae are at risk. Once the pre-pupal period occurs larvae and the subsequent pupae are immobile and remain where they are while the larvae will move onto fresh food sources when they become available. In addition larvae often move to areas of exhausted food prior to pupation, regions completely avoided by larvae.

Experiments where food was added at different rates to vials containing a fixed number of larvae and where additional pupation sites were provided would provide a very powerful test of this model.

In summary a model has been developed to describe larval growth, stage duration, and cohort survival. The model succeeds in capturing the essential effects of larval density, and evidence is presented that suggests that the failures of the model are a function of artifacts of experimental design and do not affect its appropriateness as a basis for a population model of C. cautella.

DEMOGRAPHIC CHARACTERISTICS OF VENTURIA CANESCENS IN RELATION TO ITS HOST CADRA CAUTELLA

In this chapter survival and reproductive characteristics of the wasp Venturia canescens will be presented with particular reference to effects of host larval age and density at infection, host and wasp imago density, and availability of food.

MATERIAL AND METHODS

All V. canescens used in these experiments were reared on C. cautella larvae raised at a density of 10 eggs/g wheat flakes and infected at 12-16 days of age In all infection experiments the depth of food (wheat flakes) was <5 mm, allowing all host larvae to be within reach of the imago's ovipositor. Host larval age is defined as the number of days from egg hatching.

Egg to Imago Development

The development of V. canescens was monitored in cohorts of host larvae infected at either 8.5 or 18 5 days of age. Fourteen containers (30 x 16 x 8 cm) with 50.0 g food and 450-550 host eggs were prepared and 20 adult wasps were added for 12 h to each of 7 containers. Each day, 50 insects per treatment were removed at random from a container selected at random. In drawing the sample, host larvae, pupae and empty pupal cases of host and parasitoid contributed to the sample of 50 insects. The numbers of parasitized and uninfected hosts, the numbers of host and parasitoid pupae, and the developmental stage of host and parasitoid were recorded. Empty pupal cases were considered to represent emerged adults. Only four instances of superparasitism were noted and these individuals were deleted from the analyses.

In order to more precisely quantify the effect of host age at infection on the duration of wasp development the following experiment was undertaken. A series of vials (3.0 x 6.0 cm) containing 1.7 g food and 10 host eggs was prepared. A single wasp was added to each vial for 1 day at host larval ages of 1.5 days (# of vials=133), 4.5 (88), 6.5 (78), 8.5 (86), 11.5 (49), 12.5 (60), 14.5 (59), 17.5 (60), 20.5 (58), 23.5 (59),

26.5 (40), and 29.5 (117). The total numbers and the ages of hosts and parasitoids emerging were recorded and samples of adult wasps were dried and weighed.

The effect of host density on the duration of parasitoid development was also examined. There were 7 densities (n=30) consisting of 10, 25, 50, 75, 100, 150, 200 host eggs in vials (3.6 x 6 0 cm) containing 1.7 g food. One wasp was added per vial for 1 day when the host larvae were 12 days old. The total numbers of hosts and parasitoids emerging and their ages at emergence were recorded and samples of wasp imagos were dried and weighed.

Imago Survivorship

The survival pattern of imagos was determined by monitoring cohorts as they aged. Newly emerged adults (±3 h old) were placed in glass chimneys (8.3 x 17.5 cm) resting in petri dishes (10 cm) containing 5 g food and 100-200 host larvae 12-16 days old. The petri dishes were changed daily, thus providing a new supply of naive host larvae Survivorship estimates determined for imagos provided with neither food nor water were based on 11 cohorts of 15-124 imagos (0.016-0.131 wasps/cc), for a total of 585 individuals Four cohorts totalling 110 wasps and ranging from 15 to 50 adults (0.016-0.053 wasps/cc) were monitored in order to estimate the survival of the wasp when food was available. Food for the wasps was provided daily and consisted of 2 g honey dissolved in 10 cc of distilled water. The solution was kept in a small cotton-stopped vial suspended from the top of the container.

Imago Fecundity

Estimates of the age-specific fecundity of adults were made by providing isolated individuals with uninfected host larvae daily, and recording the number of offspring produced per day as the imago aged. Wasps (±3 h old) were isolated in containers (8.3 x 17.5 cm) with 35.5±0.4 host larvae (12-16 days old) in 3.0 g food The food and host larvae were removed daily and transferred to vials containing 5.0 g food. The larvae were maintained until all host and parasitoid imagos had emerged. Imago fecundity was monitored over the life of 20 unfed wasps and 15

wasps provided with fresh food daily. The data from the last day of life were not used as the exact time of death was unknown.

Functional Response

The form of the functional response with respect to host instar was determined using naive ±12 h old imagos that had been provided with food. Wasp density was 1 per infection arena with a 24 h exposure period.

The procedure for host larvae 8 days of age or older was as follows. Larvae were raised at a density of 10 host eggs in 1.7 g food, removed from the food, added to infection arenas (30.5 x 16.0 x 8 2 cm) containing 50 g food and exposed 1 day later. For each larval age there were 6 replicates per density and host numbers per arena were 10, 20, 35, 50, 75, 100, 150, 200 for 8.5 day old larvae, and 5, 10, 20, 35, 50, 75, 100, 150 for 12.5, 17.5 and 20.5 day old larvae. The host larvae were maintained in the infection arenas for 5-10 days following exposure to the wasp, removed, fixed in 70% ethanol and subsequently dissected.

Estimation of functional responses with respect to younger larvae required a different method, because of the large numbers of larvae involved and the high mortality associated with handling. For larvae 2,5 days old, containers (9.2 x 3.8 cm) with 10.0 g food and 7 initial egg densities were prepared. There were 6 replicates of 50, 100, 200, 300, 400, 600, 800 eggs per arena. Six containers with 50 eggs served as controls and were not exposed to wasps. Following the infection period, both food and larvae were transferred to larger containers (250 ml) and additional food added until a larval density of about 5/g food resulted. A similar procedure was used for 6.5 day old larvae. The differences lay in the size of the infection arenas (4.3 x 7.0 cm) and the initial amount of food (1.0 g). There were 6 replicates of 10, 30, 75, 100, 125, 150, 200. Six additional 50 egg/g arenas served as controls. The containers containing the 1st and 2nd instars were maintained until all insects had emerged. Under these culture conditions there is minimal host and parasitoid mortality and the results obtained for the two larval age groups are completely comparable.

These experiments suggested that substantial mortality was occurring due to oviposition wounds inflicted by the parasitoid when the hosts were 6.5 days old. Vials (4.3 x 7.0 cm) containing 1.0 g food and varying

numbers of eggs were prepared. When the larvae were 6.5 days old, half of the vials were exposed to a wasp and the others left as controls. Following exposure, larval densities were adjusted to 5/g food and maintained until all hosts and parasitoids had emerged.

Parameter estimation was by non-linear regression (Sécant Method) (SAS 1982).

RESULTS

Egg to Imago Development

Figure 5.1a presents data on the course of development of V. canescens when host larvae are infected at an age of 8.5 days. Table 5.1 gives the duration of the stages as estimated by the technique of Ives and Gordon (in prep) There was no trend detected in the number of hosts infected per sample as the larvae aged ($F_{(1,36)}$=0.91, $p>0.3472$, R^2=0 025), there were 24.4±0.6 infected hosts per sample. Figure 5.1b illustrates wasp development when host larvae were infected at an age of 16.5 days; stage durations are presented in Table 5.1 The number of hosts parasitized per sample was 33.0±0.6; no trend with larval age was detected ($F_{(1,25)}$=0.03, $p>0.86$, R^2=0 001).

A more detailed examination of the effect of larval age at infection on total developmental duration of the parasitoid is shown in Fig. 5.2a. Time to imago emergence depended on host age ($F_{(11,1502)}$=116.0, $p<0.0001$).

Figure 5.2b illustrates the effect of host larval density on the age of V. canescens at emergence ($F_{(6,588)}$=111.69, $p<0.0001$).

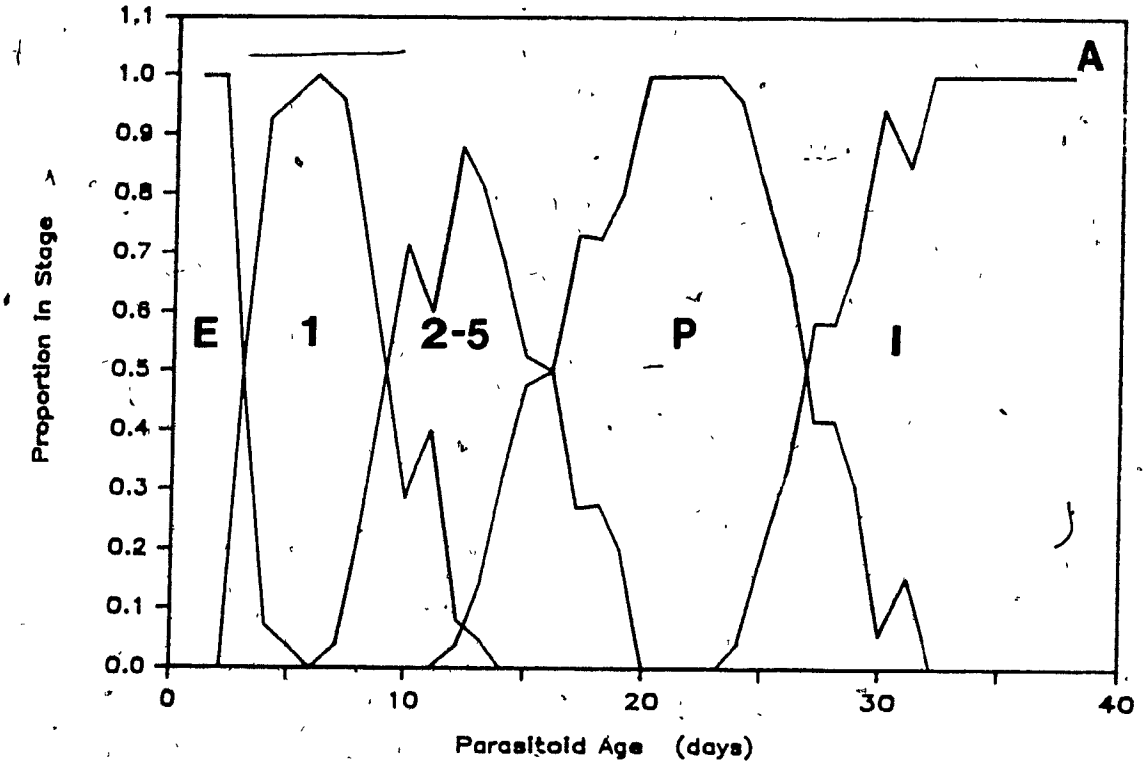
Imago Survivorship

Unfed wasps had a life span of 2.11±0.02 days. No effect of adult density on average life span was detected ($F_{(9,585)}$=2.14, $p>0.025$). Figure 5.3a presents the proportions of imagos surviving as the cohort aged. The life span of wasps provided with a honey solution was 12.4±0.4 days (Fig. 5.3b). No effect of density on average life span was detected ($F_{(2,109)}$=3.87, $p>0.024$).

Table 5.1. Stage durations in Venturia canescens when Cadra cautella larval ages at infection were 8.5 and 16.5 days old.

Host Age	Stage	Duration	
		Mean	Variance
8.5	Egg	2.55	0.383
	1st Instar	6.25	3.849
	2nd - 5th Instar	6.09	2.669
	Pupa	11.61	2.187
16.5	Egg	2.67	0.336
	1st Instar	2.64	0.221
	2nd - 5th Instar	5.77	2.828
	Pupa	10.67	0.218

Figure 5.1. Development of Venturia canescens in larvae of Cadra cautella. A. Development when host larval age at infection was 8.5 days. B. Development when host larval age at infection was 18.5 days. E corresponds to the egg stage, 1 1st instar, 2-5 instars 2 to 5, P pupal stage, I adult wasp.


A
E
1
2-5
P
I
Proportion in Stage
Parasitoid Age (days)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
0
10
20
30
40

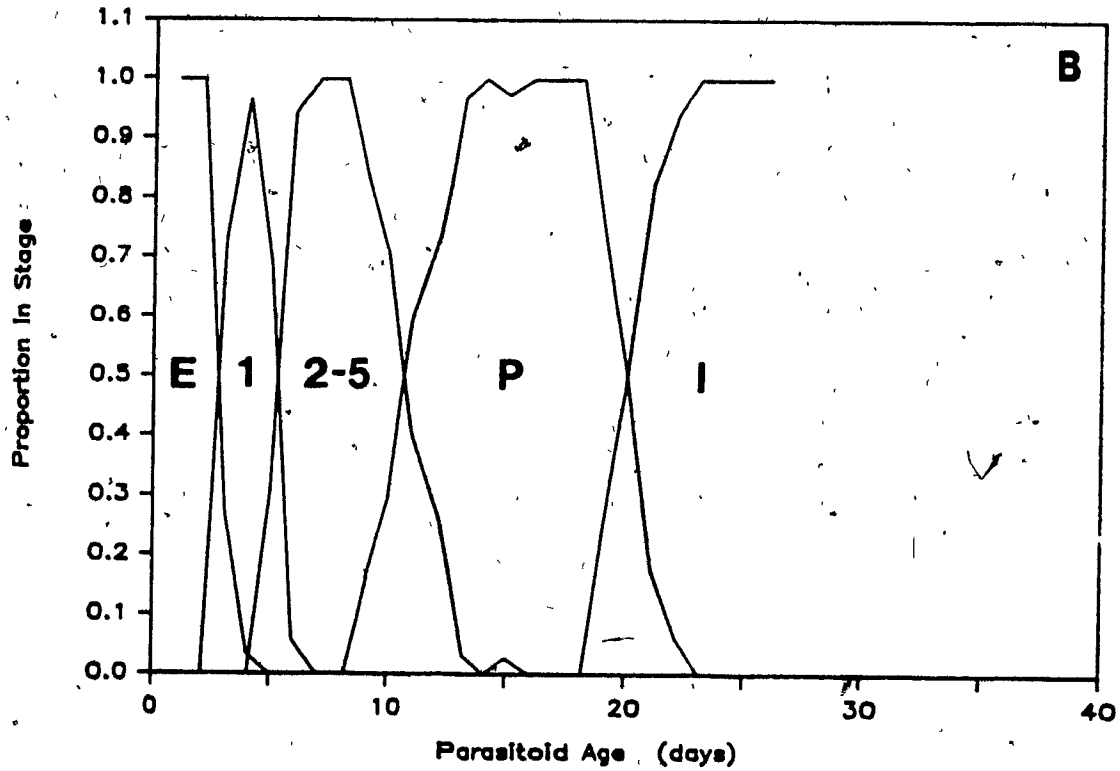
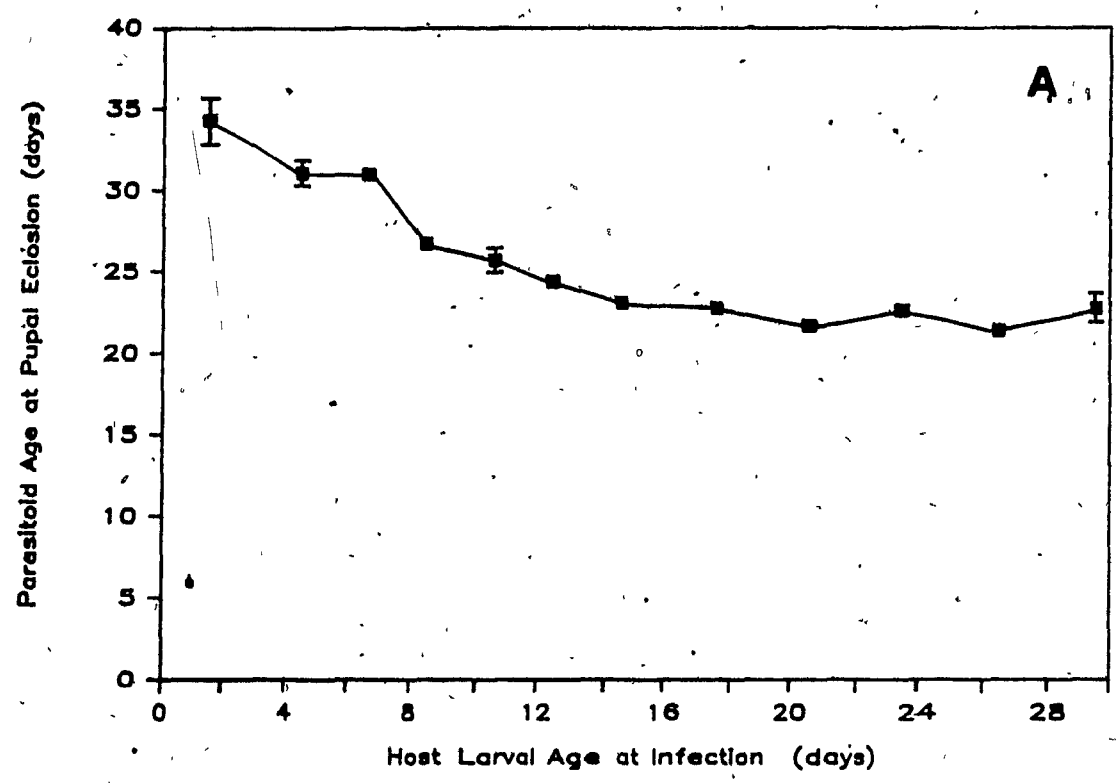

B
E
1
2-5
P
I
Proportion in Stage
Parasitoid Age (days)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
0
10
20
30
40

Figure 5.2. Age of Venturia canescens at imago emergence with respect to age and density of Cadra cautella larvae. A. Age of Cadra cautella larvae at infection. B. Density of C. cautella larvae during parasitoid development.


A
Parasitoid Age at Pupal Eclosion (days)
0
5
10
15
20
25
30
35
40
0
4
8
12
16
20
24
28
Host Larval Age at Infection (days)

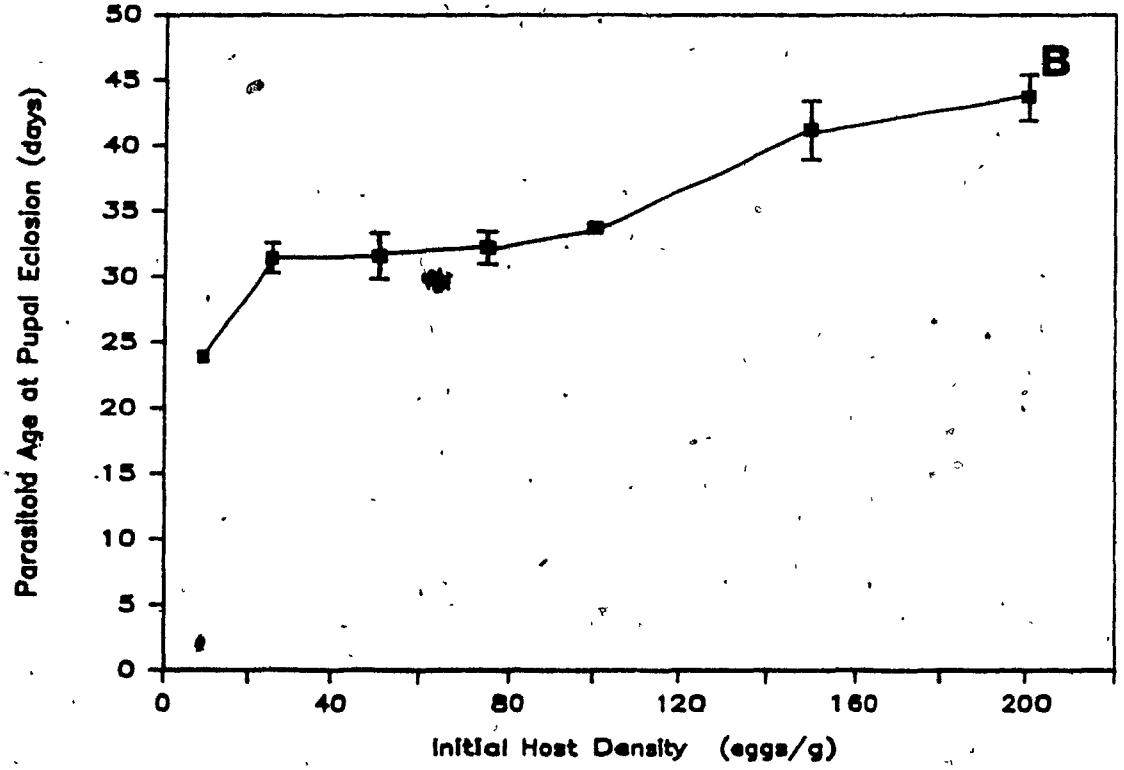
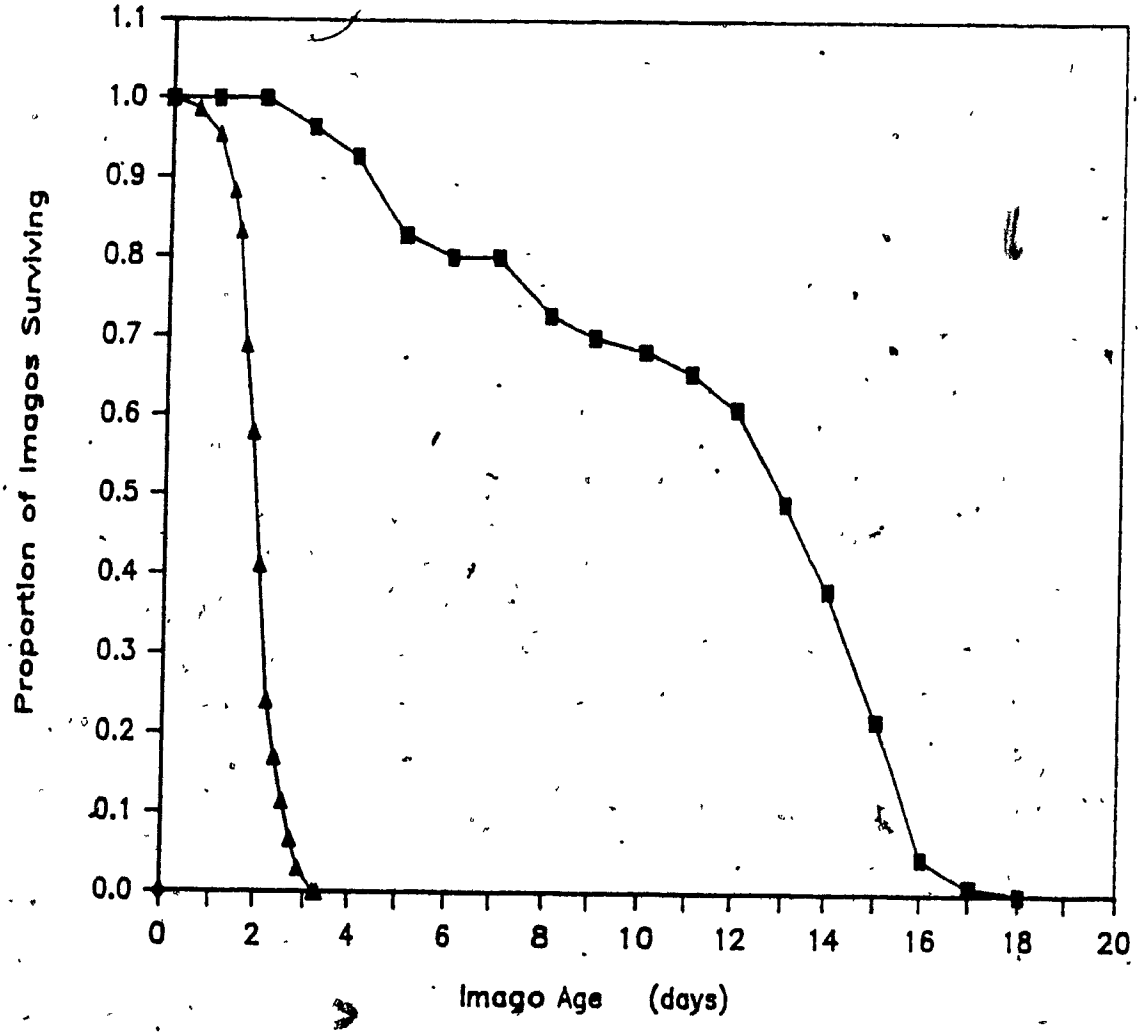

B
Parasitoid Age at Pupal Eclosion (days)
0
5
10
15
20
25
30
35
40
45
50
0
40
80
120
160
200
Initial Host Density (eggs/g)

Figure 5.3. Age-specific survival of imagos of Venturia canescens under varying conditions of food availability. ■ Survival of wasps when provided with a honey solution. ▲ Survival of wasps when no food is provided.


Proportion of Imagos Surviving
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
2
4
6
8
10
12
14
16
18
20
Imago Age (days)

Imago Fecundity

The number of progeny produced per day by unfed wasps is presented in Fig. 5.4a. Imago fecundity varied with age ($F_{(2,47)}$=6.24, $p<0.005$). The total number of progeny produced through the lifetime of an unfed wasp was 42.4±3.2. The number of progeny produced per day by wasps provided with a honey solution is illustrated in Fig. 5.4b. Wasp fecundity varied with age ($F_{(30,238)}$=15.38, $p<0.0001$). The fed wasps produced an average of 215.7±21.5 offspring.

The maximum number of progeny produced in a day was similar for unfed (19.3±1.6) and fed (20.7±1.7) imagos. Seven of the parasitoids with access to food lived between 1 and 12 days after producing their last offspring; this subset of wasps had 249.0±38.4 progeny.

Imago Weight

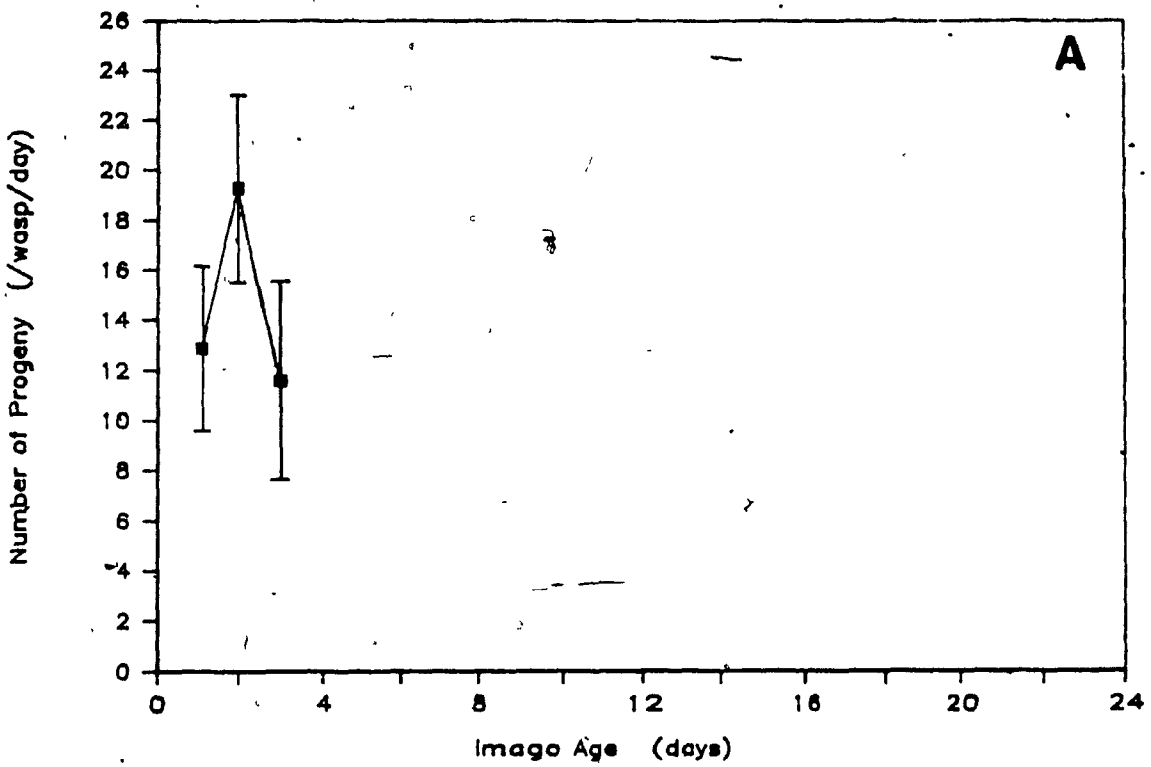
Figure 5.5a presents data on the effects of host larval age at infection on the weight of imagos at emergence. Adult weight varied with larval age at infection ($F_{(11,10)}$=6.61, $p<0.0001$). Inspection of Fig. 5.5a suggests a discontinuity in the effect of larval age, where wasps resulting from infections occurring in larvae less than 15 days old have a lower weight than those resulting from infections of larvae more than 15 days old ($F_{(1,118)}$=23.65, $p<0.0001$). Imagos resulting from infection of younger hosts weighed 1.41±0.04 mg, while those emerging from older larvae weighed 1.72±0.11 mg. Furthermore within the former group no effect of larval age on weight at emergence was detected ($F_{(1,68)}$=0.43, $p>0.5145$, R^2=0.006), while in the latter group wasp weight decreased with increasing larval age ($F_{(1,48)}$=12.65, $p<0.0009$, R^2=0.209).

Figure 5.5b illustrates the presence of a small negative effect of host larval density on imago weight at emergence ($F_{(1,98)}$=20.39, $p<0.0001$, R^2=0.172).

Functional Response

In the control arenas for larvae infected at age 2.5 days, 74.1%±5.1 of the initial number of host eggs survived to become host imagos. No difference in survival was detected between control and treatment arenas ($F_{(1,46)}$=0.01, $p>0.9148$). The pooled value from control and treatment arenas (74.2%±1.6) was used to estimate the number of larvae available for

Figure 5.4. Age-specific fecundity of Venturia canescens under varying conditions of food availability. A. No food present. B. Honey solution provided.


A
Number of Progeny (/wasp/day)
Imago Age (days)
0
2
4
6
8
10
12
14
16
18
20
22
24
0
4
8
12
16
20
24

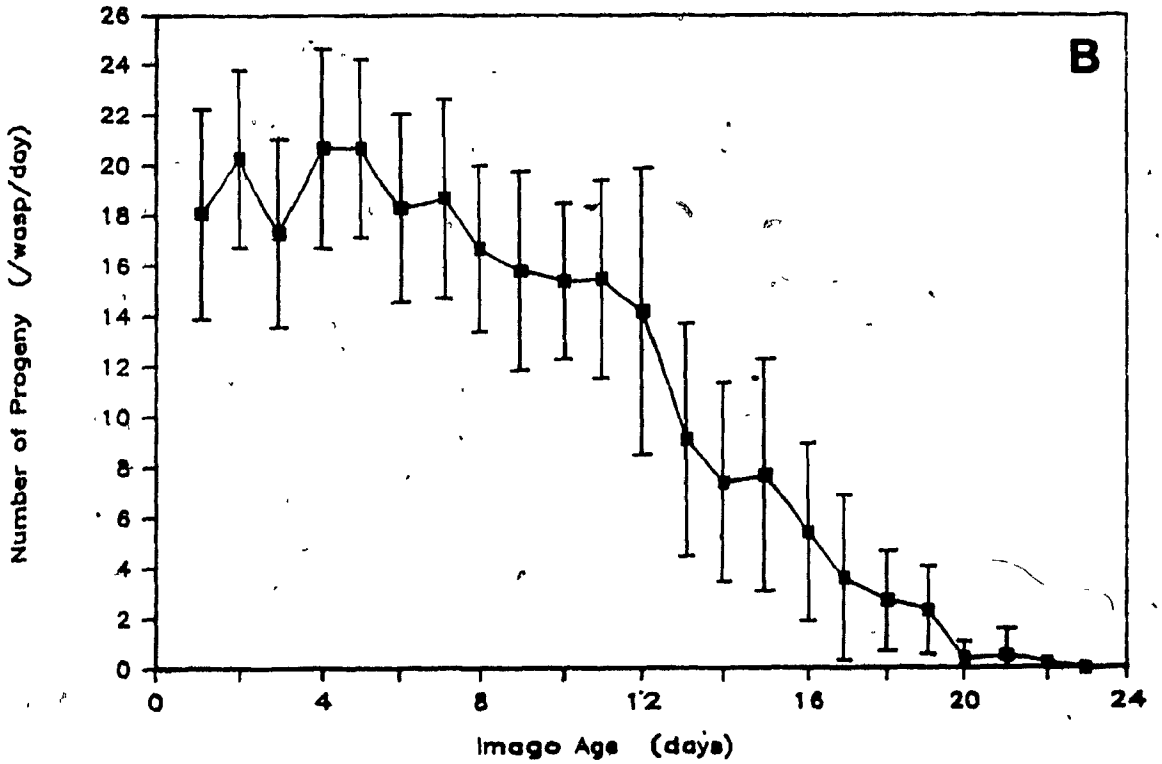
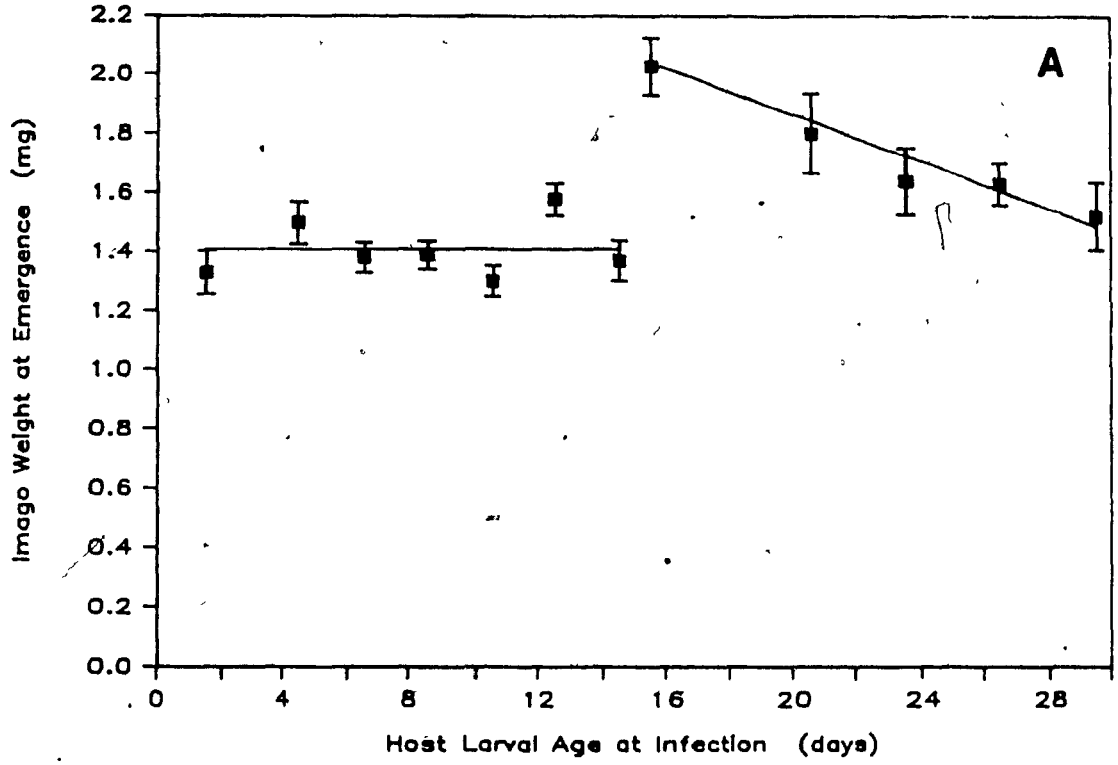
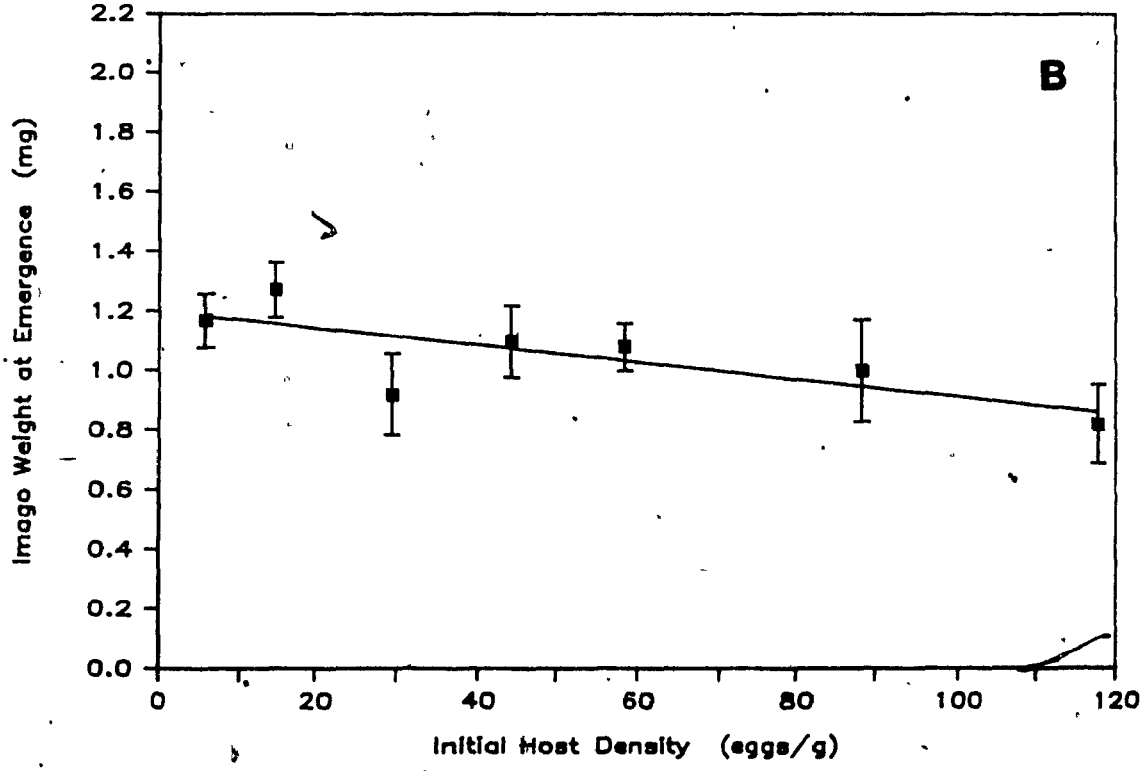

B
Number of Progeny (/wasp/day)
Imago Age (days)
0
2
4
6
8
10
12
14
16
18
20
22
24
0
4
8
12
16
20
24

Figure 5.5. Weight of Venturia canescens imagos at emergence with respect to age and density of Cadra cautella larvae. A. Age of Cadra cautella larvae at infection. Linear regression intercept=2.8 mg, slope=-0.04±0.01. B. Density of host larvae during parasitoid development. Linear regression intercept=1.2 mg, slope=-0.003±0.001.


A
Imago Weight at Emergence (mg)
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
4
8
12
16
20
24
28
Host Larval Age at Infection (days)


B
Imago Weight at Emergence (mg)
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
20
40
60
80
100
120
Initial Host Density (eggs/g)

parasitism. In the control arenas for 6.5 day old larvae, 64.7%±5.2 of the eggs became adult insects. A significant difference in the proportion surviving was found between control and treatment arenas ($F_{(1,46)}$=246.58, p<0.0001). The value from the control arenas was used to determine the number of larvae available to attack. Among the older larvae (>7 days)no differences were found in the proportion of larvae recovered among densities within an age or among ages ($F_{(31,160)}$=0.52, p>0.9838). The proportion of larvae recovered was 97.9%±0.3.

Two forms of functional response were used to describe the relationship between the number of hosts attacked and host larval density, a Type II response (Rogers 1972b),

$$N_a = N_t [1-\exp(-aTP_g/(1+aT_hN_g))] \qquad \text{Eq. 5.1}$$

and a Type III response, modified from Hassell (1978),

$$N_a = N_t [1-\exp(-a'TN_gP_g/(1+a'T_hN_g^2))] \qquad \text{Eq. 5.2}$$

where N_a - number of hosts attacked
N_t - number of hosts available
N_g - number of hosts available per g food
P_g - number of parasitoids per g food
T - time available for search, days
a - instantaneous search rate, $g/P_g \cdot T$
T_h - parasitoid handling time, $P_g \cdot T/N_g$
and a' - instantaneous search rate, $g^2/T \cdot N_g \cdot P_g$.

Table 5.2 presents the estimates for the attack rates (a, a') and handling times (T_h) for each larval age as determined by non- linear least-squares technique. The estimated values of T_h for larval ages 8.5, 12.5 and 17.5 were very similar (Table 5.2). As a result, a common handling time (T_h) was assumed for all instars and the search rates (a, a') re-estimated (Table 5.2). Figure 5.6 presents the observed data together with the Type II and Type III responses estimated assuming a common handling time.

Table 5.2. Parameter estimates for the functional responses of Venturia canescens with respect to Cadra cautella larval age.

AGE[1]	a	S.E.	T_h	S E	R.S.S [2]
Type II Response					
2.5	0.0458	0.0201	0.1042	0.2053	36.41
6.5	0.1930	0.0889	0.0246	0 0248	1324.92
8.5	98.4996	87.7598	0.0466	0.0067	2609 69
12.5	136.2934	102.1556	0.0456	0.0049	1164 38
17.5	286.0105	486.8987	0.0488	0.0057	1573 33
20.5	23.6155	7.1469	0.0436	0.0080	758.77
Type III Response					
2.5	0.0005	0.0054	0.0000	1.2313	37 36
6.5	0.0052	0.0028	0.0552	0.0139	1342 30
8.5	208.1225	169.7334	0 0496	0 0046	2512.82
12.5	403.9826	265 0697	0.0487	0.0032	1102.67
17.5	608.8035	578.7342	0.0499	0 0038	1521.76
20.5	55.9293	21.8912	0.0596	0.0052	776.18
Type II Response					
2.5	0.0458	0.0054			36.47
6.5	0.3009	0.0672			1355.02
8.5	102.5913	60.5032	(T_h fixed at 0.0470)		2609.96
12.5	162.0508	88.1076			1166.66
17.5	197.9907	147.0448			1576.97
20.5	26.3740	4.5424			761.94
Type III Response					
2.5	0.0008	0.0001			42.61
6.5	0.0043	0.0011			1347.30
8.5	205.9153	150.0432	(T_h fixed at 0.0494)		2512.92
12.5	422.8613	261.8494			1103.85
17.5	588.1767	504.7377			1522.41
20.5	31.9128	7.7993			847.71

[1] Host larval age at infection (days)

[2] Residual sum of squares

Figure 5.6. Functional responses of Venturia canescens to Cadra cautella larvae of differing ages. A. Host age=2.5 days, Type II response. B. Host age=6.5, Type II. C. Host age=8.5, Type III. D. Host age=12.5, Type III. E. Host age=17.5, Type III. F. Host age=20.5, Type II. Solid lines represent the prediction of the Type II or Type III response assuming a fixed handling time (see Table 5.2 for parameter values).

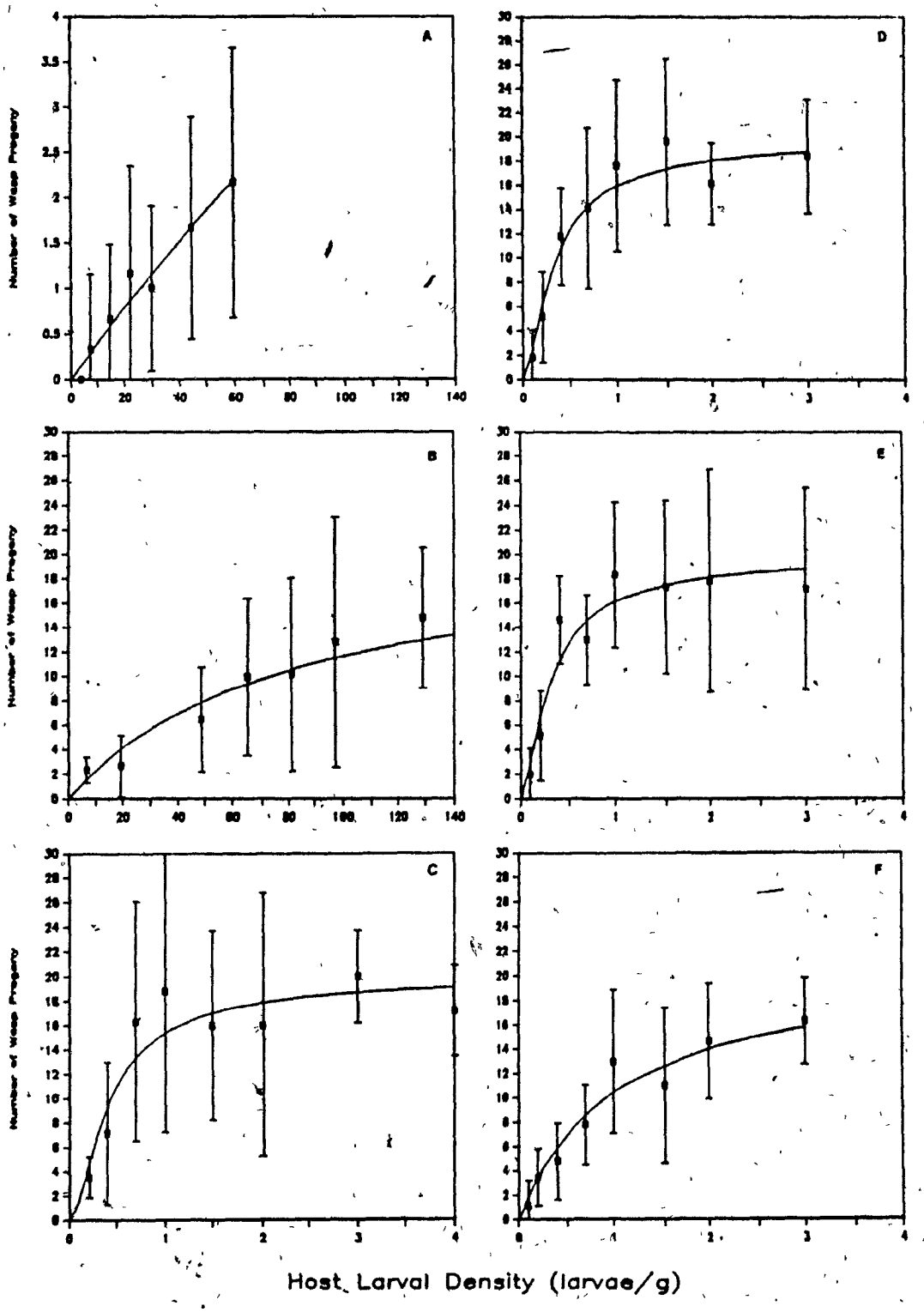
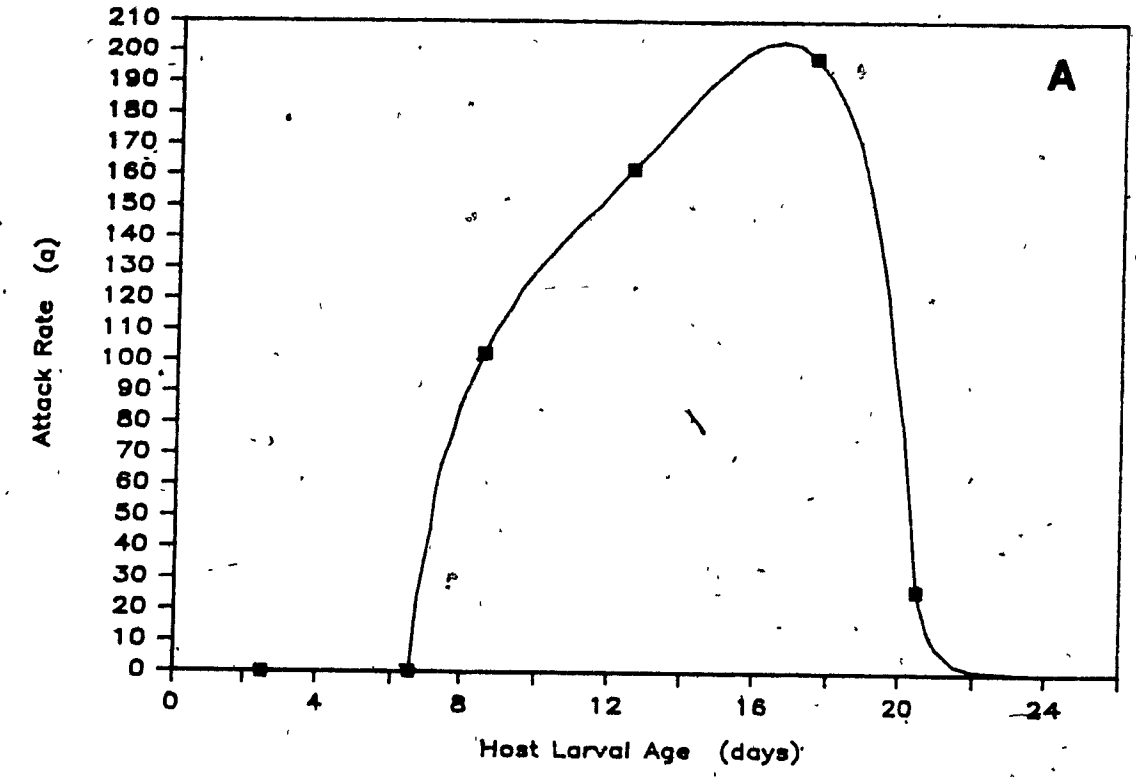
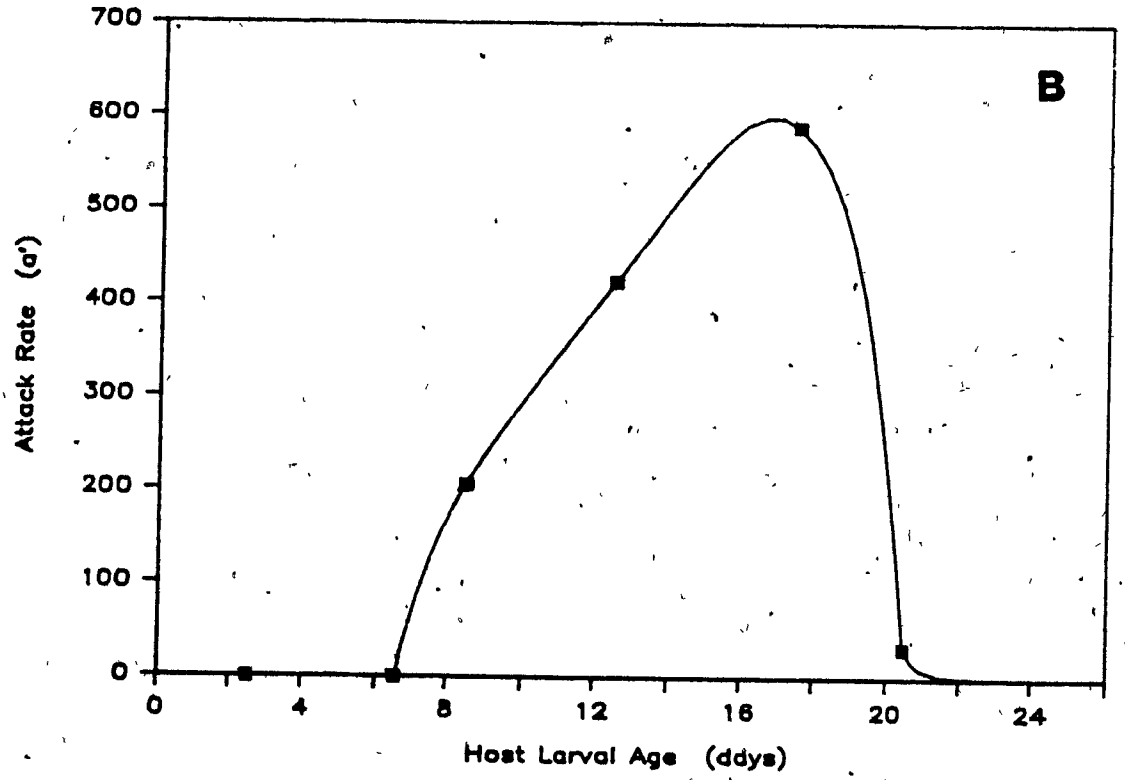

A
B
C
D
E
F
Number of Wasp Progeny
Host Larval Density (larvae/g)

Table 5.3 Parameter estimates for the functional responses of Venturia canescens with respect to the larval instars of Cadra cautella.

Instar	Search Rate	
	Type II	Type III
1	0.024	0.005
2	11.839	21.872
3	112.614	244.384
4	165.438	459.028
5	114.435	331.311
Larval Stage	88.436	237.683
T_h	0.0470	0.0494

Figure 5.7. Relationship between instantaneous attack rate of Venturia canescens and Cadra cautella larval age assuming a fixed handling time. A. Instantaneous attack rate (a) assuming a Type II functional response. B. Attack rate (a') assuming a Type III response. Symbols represent estimated parameter values from Table 5.2. Solid curves represents the observed values fitted using a cubic spline method.


A
Attack Rate (a)
210
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
0
4
8
12
16
20
24
Host Larval Age (days)


B
Attack Rate (a')
700
600
500
400
300
200
100
0
0
4
8
12
16
20
24
Host Larval Age (ddys)

The estimated attack rates, assuming a common handling time, were plotted against larval age at infection and a smooth curve fitted to the points using a cubic-spline technique (Fig. 5.7). The area under this curve gives an estimate of the average instantaneous attack rate for the larval stage. For a Type II response, a=88.4, while for a Type III response a'=237.7

The degree of parasite-induced mortality experienced when host larvae were 6.5 days of age was quantified. In the control arenas no differences among densities were detected in the proportion of eggs surviving to become imagos ($F_{(5,29)}$=0.41, p>0.8399). The pooled value of percent survival (64.2%±13.1) was used to determine the number of larvae available for attack (N_t). The number of larvae killed (N_k) in each arena was estimated by subtracting the total number of hosts and parasitoids emerging per container from the number expected (N_t). The number of larvae attacked per container (N_a) was assumed to be the number killed (N_k) plus the number of parasitoid progeny produced (N_p). No difference was detected in the proportion N_k/N_a among densities ($F_{(5,29)}$=1.04, p>0.4153). The average proportion of larvae killed was 0.63±0 27. For parasitoids the appropriate attack equation for a Type II response is Eq. 5.1, while for predators it is (Rogers 1972b),

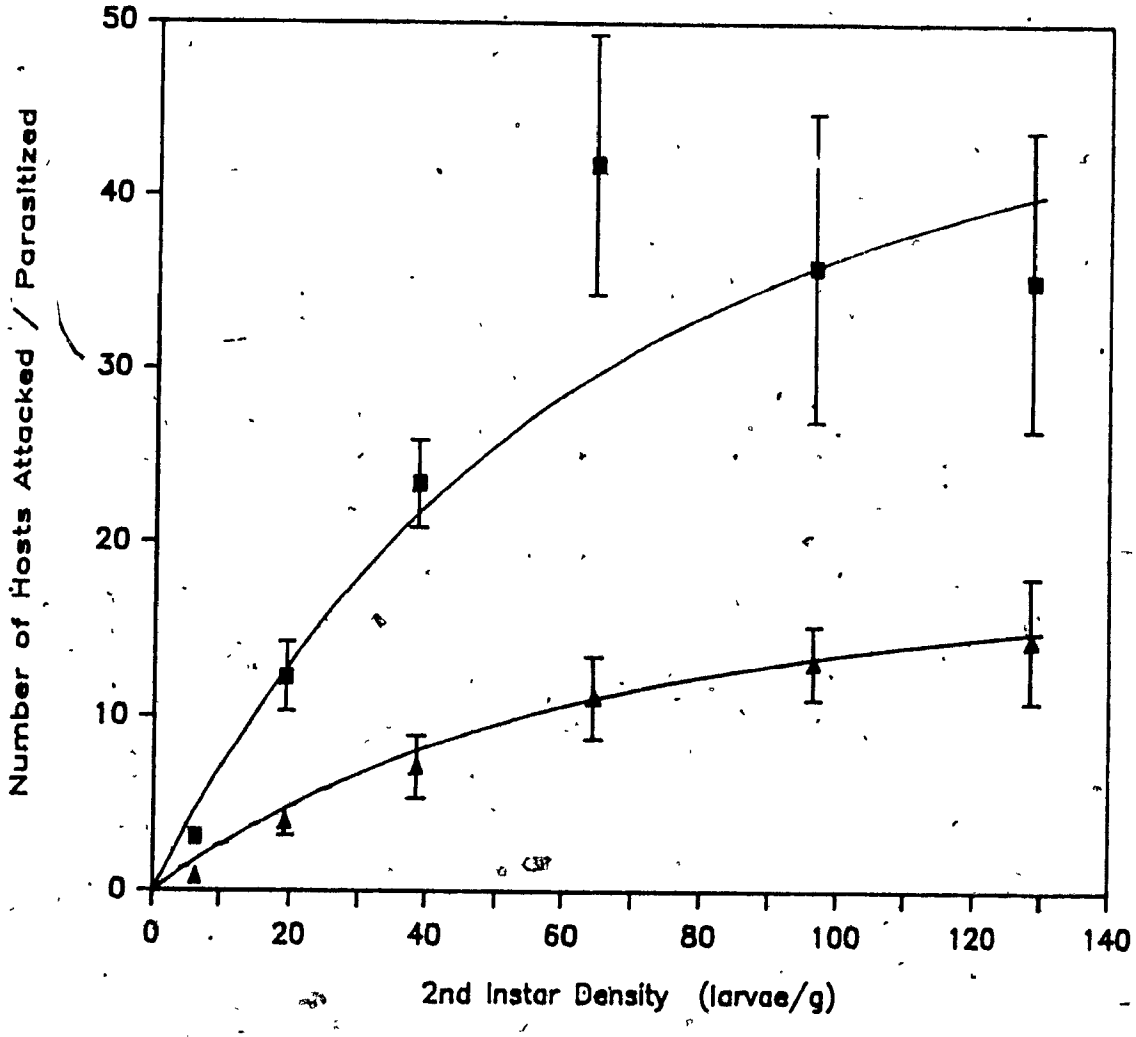
$$N_a = N_t[1-\exp(-aP_t(T-T_hN_a/P_t))] \qquad \text{Eq. 5.3}$$

The difference between the two equations is that parasitized hosts remain available for subsequent encounters, while consumed prey do not. If it is assumed that larvae wounded by the ovipositor die quickly, a situation results that is intermediate between a predator and parasitoid. Larvae that are attacked may be successfully parasitized and remain available for further encounters or they may be killed and be unavailable. The following Type II attack equation has been formulated in order to describe this situation,

$$N_a = N_t[1-\exp(-aP_t(T-T_hN_aq/P_t)/(1+aT_hN_t(1-q)))] \qquad \text{Eq. 5.4}$$

where q is the fraction of larvae killed (N_k/N_a). The derivation of Eq. 5.4 is presented in Appendix M.1. The parameter q was taken directly from

Figure 5.8. Mortality of Cadra cautella larvae (age=6.5 days) resulting from oviposition wounds inflicted by Venturia canescens as estimated by the difference between the numbers of larvae attacked and the numbers of parasitoids emerging. ■ represents the estimated mean number of host larvae attacked ±S.E.; ▲ observed mean number of parasitoid progeny produced ±S.E. The solid line represents the prediction of Eq. 5.4; a=1.514, T_h=0.018, q=0.626.


Number of Hosts Attacked / Parasitized
50
40
30
20
10
0
0
20
40
60
80
100
120
140
2nd Instar Density (larvae/g)

the data ($q=0.63\pm0.27$), while parameters a and T_h were estimated using non-linear regression ($a=1.514\pm0.5140$ and $T_h=0.0175\pm0.0068$). Figure 5.8 presents the observed data together with the predictions of Eq. 5.4.

DISCUSSION

Many species of parasitic Hymenoptera show arrested development as 1st instar larvae, where further development is dependent on the host achieving a particular stage of growth (Salt 1963). Corbet (1968) has shown this to be a feature of the larval development of Venturia canescens in its host Anagasta kuehniella, where the parasite will remain as a 1st instar larva until the host achieves its final larval instar. The same phenomenon was observed in this study and accounts for the decrease observed in imago age at emergence as the age of host larvae at infection increased (Fig. 5.2a). The duration of the other parasitoid stages was found to be independent of host age at infection (Table 5.1). Corbet (1968) showed that parasite development resumed due to increases in the feeding rate of the parasites in response to changes occurring in host haemolymph amino acid concentrations when hosts reached their final instar. The individual stage durations as well as the total developmental times observed are in close agreement with those previously reported (Ahmad 1936; Simmonds 1943; Corbet & Rotheram 1965).

The pre-imaginal period of the parasitoid was found to increase with increasing host density (Fig. 5.2b); this is a reflection of increased host larval duration with increasing larval density (Benson 1973). Simmonds (1943) reported increases in the pre-imaginal period of V. canescens in A. kuehniella when levels of superparasitism were high (>11 eggs/host).

The 2 day life span of unfed V. canescens imagos was found to be well within the 1-3 day range reported by Ahmad (1936), but longer than the maximum 1 day life span reported by Podoler (1974a). Imagos provided with a honey solution had a life span of 12 days, while average life spans of 6-72 days have been reported (Diamond 1929; Ahmad 1936). Ahmad (1936) has shown that the life span of fed imagos depends on the presence of host larvae, where the longevity is increased in the absence of host larvae. This factor, together with the unknown effects of differences in food

composition and quality between studies, likely accounts for the variation in reported life spans. Imago life span was found to be independent of parasitoid density.

The experimental conditions under which imago fecundity was studied minimize the amount of superparasitism occurring (Rogers 1975) and as such the number of progeny produced should only slightly underestimate the number of eggs produced by a wasp. Total lifetime fecundity of unfed imagos (42.4 progeny) was well within the ranges reported by Ahmad (1936) and Podoler (1974b), but less than the 60 eggs/wasp reported by Simmonds (1943). The observed total fecundity of fed imagos (215.7) was much greater than that reported by Ahmad (1936), who found no increase in fecundity when wasps were provided with food, but well within the 158-227 range reported by Narayanan (1945). An average of 249 progeny were produced by parasitoids living beyond their last day of oviposition Podoler (1974b) reported a positive association between imago weight at emergence and lifetime progeny production. However Podoler also found a positive relationship between imago weight at emergence and life span of unfed parasitoids which would be sufficient to explain the relationship between imago weight and fecundity

The maximum number of progeny produced per day is similar for fed and unfed wasps. The pattern of daily progeny production varied with age In unfed wasps the number of eggs laid was greatest in 2 day old wasps, while 1 and 3 day old wasps laid similar numbers of eggs The decline in egg production in 3 day old wasps is likely due either to declining energy reserves and the effect of this on the amount of time spent foraging, or to the rate of egg maturation. The lower level of egg production in day old imagos may be due to the time newly emerged wasps spend searching for food prior to initiating host finding behaviour (Ahmad 1936). This supposition is supported by the lack of a similar effect when imagos were provided with food. Daily progeny production in fed wasps remained relatively constant for the first 8 days and then gradually declined until the wasps died.

A positive relationship between imago weight at emergence and total egg production is a common phenomenon in insects. While not specifically investigated, the data of Fig. 5.5 suggest that imago fecundity may be dependent on both the age of the host larvae at infection and host larval

density, because these both influence imago weight at emergence. The energetic relations of host and parasitoid larvae are very closely linked (Howell & Fisher 1978) and imago weight will be affected by those factors which influence host larval weight. The decline in imago weight as the age at infection of final instars increases is likely due to the observation made in Chap. 3 that host larval weight declines with larval age in those larvae that spent an above average length of time as final instars. White & Huffaker (1969b) stated that infected A. kuehniella host larvae consume less food than uninfected larvae. Whether this is due to an inhibition of host feeding rates or a decrease in the time available for feeding is unknown, but either would explain the observation that when larvae are infected as pre-final instars, imago weight is less than when hosts are infected as final instars. Most host growth occurs in the final instar. As a result any parasitoid inhibition of host growth would operate throughout the entire final instar of hosts infected prior to the final instar. When the host is infected while in its final instar, there will have been a longer period of uninhibited host growth, during the development of the parasitoid egg and 1st instar. The decline in imago weight with increasing host density (Fig. 5.5b) is a result of the negative relationship between host larval density and host larval weight (Benson 1973).

The increased searching efficiency of the wasp with increasing host age (Fig. 5.6) is largely a function of increasing host size. The effect of host size operates in two ways. First the probability of the ovipositor contacting a host is dependent on host size. Second, the size and rough texture of the wheat flakes used as a host food medium will provide a relatively greater refuge effect as host size decreases The decline observed in imago searching efficiency in the presence of late final instar larvae (Fig. 5.6f), may relate to the physiological state of the larvae. Larvae at these ages are generally in a relatively immobile, non-feeding pre-pupal period, attributes which may cause significant reductions in the level of mandibular gland secretion and as a consequence, reductions in parasitoid probing behaviour. A Type II functional response provided a better description of the data for 2.5, 6.5 and 20.5 day old larvae than did the Type III response equation. In the case of 8.5, 12.5 and 17.5 day old larvae, the opposite was true, with the

Type III response providing a slightly better description of the data, primarily at low host densities. The form and the shape of the functional responses to 3rd, 4th and mid-5th instars are characterized by very high searching efficiencies.

The attack rates observed in this study are comparable to those estimated using the data of Matsumoto & Huffaker (1974), once experimental conditions have been standardized by converting larval densities to number/cm^2. The numbers of host larvae in both studies ranged from 10-200, wasp density was 1 per arena and the infection period was 1 day. The surface area of the arenas used in this study was 488 cm^2, while those used by Matsumoto & Huffaker (1974) were 9604 cm^2. The estimated attack rates assuming a Type II response were 8201 (this study, Fig 5 6c), 7055 (M & H, Fig. 2), and 8727 (M & H, Fig 3) for the data of Matsumoto & Huffaker (1974)

However substantial differences exist between the results of this study and those of Takahashi (1968) working with V. canescens and C cautella. Takahashi (1968, Fig. 1) added 1 wasp imago for 24 hours to a container 4.5 cm in diameter containing 2.5 g rice bran and varying numbers of host larvae. After converting his data to the same units as used in this study, inspection of the data suggested that a Type III functional response would provide the most appropriate description of Takahashi's results. Non-linear curve fitting produced the following results for his 2nd instar data; $a'=0.019\pm0.002$, $T_h=0.00\pm0\ 017$; 3rd instars, $a'=0.084\pm0.007$, $T_h=0.032\pm0.003$; 4th instars, $a'=0.119\pm0.006$, $T_h=0.020\pm0.001$. Comparison of the estimates based on Takahashi's data with those of this study (Table 5.2), show that while handling times (T_h) are broadly comparable, with the exception of 2nd instars, the search rates (a') are substantially lower. The reasons for the differences between the data of this study and that of Takahashi (1968) are unknown.

The estimated values of handling time (T_h) (Table 5.2) do not reflect combined time required not only for a parasitoid to oviposit once a host is located but also for it to be able to recommence searching. This has been estimated by direct observation to be about 45 seconds (Cook & Hubbard 1980) and 21 seconds (Hassell & Rogers 1972). The estimated maximum numbers of hosts attacked per day for larvae older than 8 days (T/T_h) were 21.3 (Type II) and 20.2 (Type III). Taylor (1974) and

Huffaker & Matsumoto (1982a) reported that the maximum number of eggs laid by V. canescens in a 24 h period was about 25, while Matsumoto & Huffaker (1973b, 1974) and Stinner (1976) found that V. canescens laid a maximum of ~~about~~ 40-50 eggs per day. Dissection of the ovaries of newly emerged imagos reveals that the number of mature eggs is a fraction of the total number of eggs present (Diamond 1929; Taylor 1974). Taylor (1974) reported a decline in the oviposition rate of V. canescens over a period of 7 h and concluded that this decline was due to the effects of egg limitation. It appears that under experimental conditions the number of eggs laid or the number of hosts attacked per day by the parasitoid is determined by the number of mature eggs available and the rate of egg maturation and this explains the discrepancy between the handling times estimated from the functional response equations and actual handling times.

Oviposition wounds accounted for substantial mortality (63%) of young (6.5 days old) host larvae. This was undoubtedly related to the small size of the host (Fig 5.8). Younger hosts are probably even more susceptible to this mortality; however owing to the very low probability of the parasitoid encountering these very young (2.5 days) larvae, no mortality was detected. Nor was any mortality due to oviposition wounds detected in older host larvae (> 8 days old). These results are in agreement with those reported by Simmonds (1943) and Williams (1951) working with V. canescens and A. kuehniella.

Rogers (1970) reported that the 5th and to a lesser extent the 4th instar larvae of C. cautella were able to mount a strong haemocytic response and eliminate the eggs of V. canescens, while 3rd instars were unable to mount an effective response. The present study does not support this observation. ~~No~~ change in the fraction of hosts infected over the course of wasp development was detected when hosts were infected at 18.5 days of age (5th instar; data from Fig. 5.1b). The lack of any substantial differences in the functional response curves for larval ages 8.5, 12.5 and 17.5 (Figs 5.6c,d,e) also suggests that there is no effect of age on ability to mount an effective defense response. While the functional response curve with respect to old final instar hosts (Fig. 5.6f) was different, the differences are not in accordance with the presence of an effective host defense response. Rogers (1970) suggested

that hosts were able to recognize the parasitoid egg as a foreign body (Salt 1968) because the egg capsule was often damaged when the host moved in response to being stabbed by the ovipositor. Perhaps the food medium (wheat flakes) used in this study restricts the movement of the host in response to an ovipositional attempt by the wasp. Encapsulation of supernumary eggs and larvae was observed during this study.

The results of the parasitoid development experiments suggest that very little mortality occurred in established infections and that any pre-imaginal mortality was due to host mortality.

The dependence of parasitoid larval developmental rates on the age of the host larvae results in a synchronization of the life cycles of V. canescens and Cadra cautella. For example, under the experimental conditions used to obtain the data illustrated in Fig. 5 2, a cohort of female host eggs will emerge as host imagos in about 37 days, while parasitoid infection of the host cohort will result in wasp imagos emerging on average in 42 days from the start of the host cohort The arrestment of parasitoid development until the host achieves its final larval instar results in the parasitoid pupating slightly later than the host. In addition to this there appears to be another period of arrested development shown by the parasitoid. Pupal stage duration is 10-12 days, however, apparently fully developed imagos are present within the pupal case 3-4 days prior to imago emergence (this study; Corbet & Rotheram 1965).

While not a subject of experimental investigation in this study two more phenomena related to the biology of the wasp need to be discussed mutual interference and superparasitism.

Mutual interference between searching wasps may arise in two ways The first results from physical interference between searching wasps, where a foraging wasp stops searching due to contact with or the close proximity of another wasp. Interference also arises when the parasitoid attempts to avoid superparasitism, resulting in time being spent determining whether a host has previously been infected. The time spent in these sorts of encounters reduces the total searching time available to the wasp. Mutual interference between searching V. canescens has been documented (Hassell 1971) and has been estimated to result in about 25 seconds being wasted per encounter (Hassell & Rogers 1972; Rogers &

Hassel 1974), while Cook & Hubbard (1980) have estimated the time wasted in avoiding superparasitism to be about 25 seconds. However, opinions concerning the importance of this phenomenon under other experimental conditions are varied. Simmonds (1943) and Stinner (1976) found no effect of V. canescens density on the number of eggs laid per parasitoid, while Huffaker & Matsumoto (1982) found a more than a 50% reduction in the number of eggs laid per female when wasp density was 10 as compared to 1. There are considerable differences in the experimental protocols of the studies cited above, in terms of parasitoid:host ratios, arena volume and host spatial distribution and these differences make interpretation of the results difficult.

V. canescens has been found to be up to 80% efficient in avoiding superparasitism, with the degree of avoidance increasing with the age of the primary infection (Rogers 1972a). However the tendency to avoid superparasitism is lost when the ratio of parasitoids to hosts is high (Simmonds 1943; Rogers 1975; Stinner 1976).

A possible explanation for the breakdown in avoidance of superparasitism and the apparent lack of any mutual interference when parasitoid:host ratios are high is proposed. Superparasitism in V. canescens results in egg wastage as only one parasitoid can successfully develop in one host, with the older parasitoid killing the eggs and younger 1st instars present. However, this is not a strictly deterministic process, but a stochastic one particularly when the parasitoids are similar in age. Stochasticity results in two ways, due to variability in the time to egg hatching, and due to chance effects determining the winner of larval-larval encounters, where the probability of winning approaches 50% when the larvae are the same age (weight). When parasitoid:host ratios are high, the probability that an individual wasp will encounter an already infected host will increase very rapidly given the high searching efficiencies of these parasitoids. Under experimental conditions where the wasp is unable to search out sources of uninfected larvae the best 'tactic' for an individual wasp may be to lay eggs as rapidly as possible. Under these conditions any time spent avoiding superparasitism or responding to the presence of other wasps would not only detract from the time it could spend ovipositing, but would also increase the age differential between the eggs it lays and the eggs

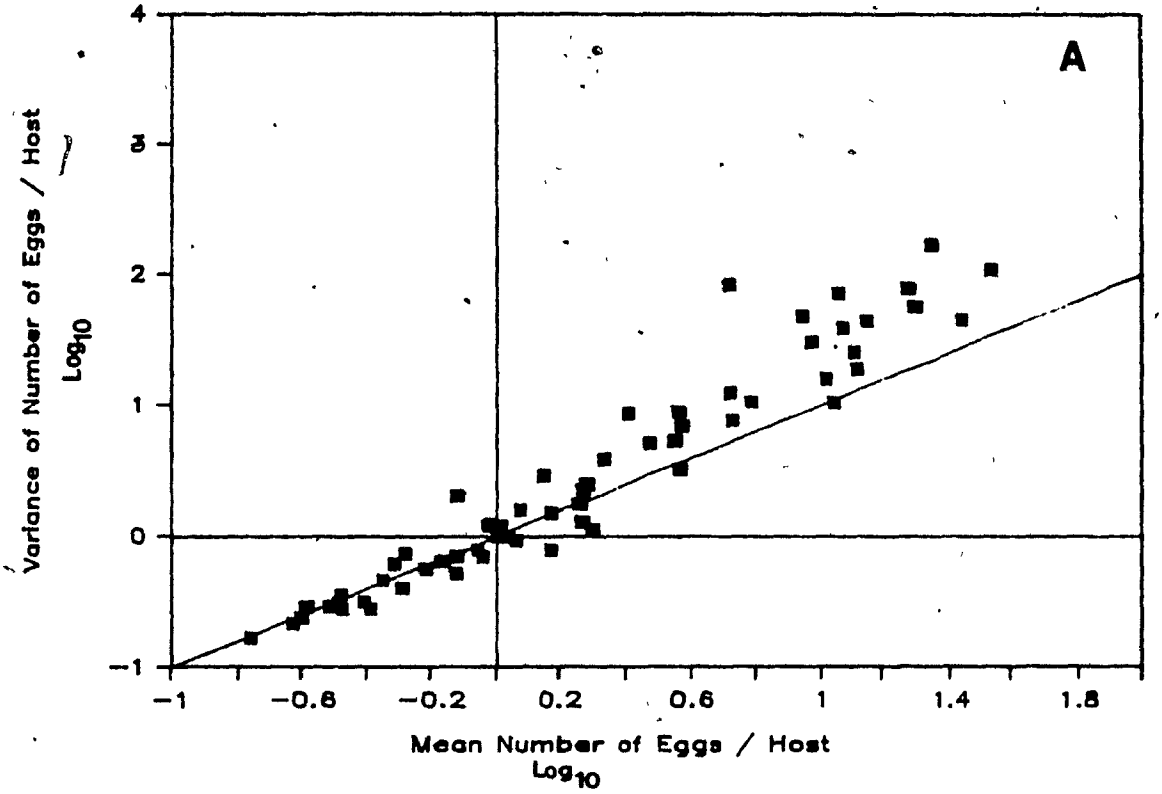
already present in the host population. The element of 'chance' involved in winning a host, also suggests that any individual who 'cheats' in a population that avoids superparasitism, will increase its reproductive fitness relative to the 'non-cheaters', a situation that will result in the trait completely invading the population. It would be interesting to contrast the degree to which superparasitism is avoided in 'wild' populations of V. canescens, semi-feral populations associated with stored products and laboratory populations.

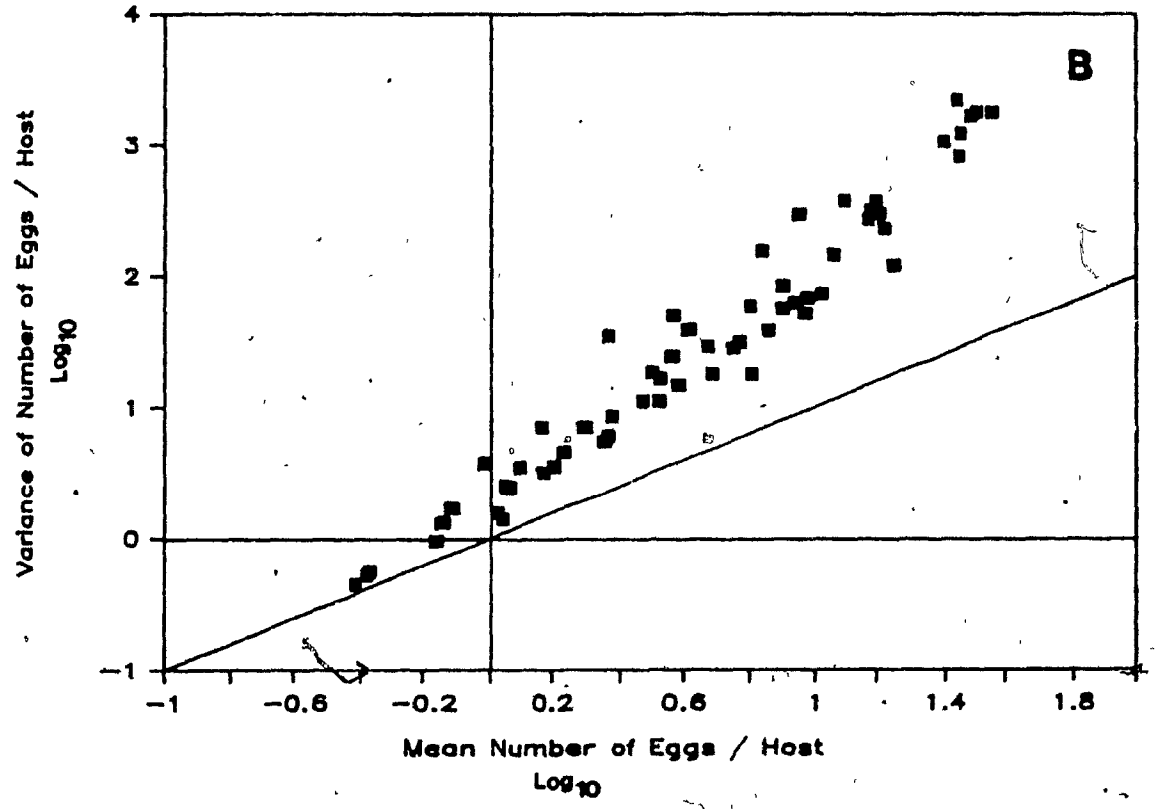
When superparasitism occurs, the number of wasp progeny produced will depend on the frequency distribution of parasite eggs per host. It is generally assumed that when parasitoids search at random the number of encounters per host will also be random (Rogers 1972b; Hassell 1978); if an egg is laid at each encounter the resulting frequency distribution of eggs per host will also be random. Figure 5.9 presents two sets of data on the frequency distribution of V. canescens eggs in its host A. kuehniella (Simmonds 1943; Stinner 1976). The majority of the data shows that observed frequency distributions are aggregated (variance/mean ratio > 1). While a random distribution of eggs per host is an appropriate null hypothesis many factors will contribute to creating observed egg distributions (Anderson & Gordon 1982). The avoidance of superparasitism will tend to generate uniform egg distributions, while the most likely factor responsible for generating aggregated egg distributions is heterogeneity in host susceptibility (Anderson & Gordon 1982) Many factors may ~~create differences~~ in host susceptibility, and it is not possible at present to identify all the factors responsible for creating the heterogeneity between hosts that accounts for the egg distribution patterns observed in Fig. 5.9.

A considerable number of demographic factors and interactions have been identified in V. canescens in relation to its host. These are summarized in relation to a number of processes which contribute to the parasitoid's intrinsic rate of increase.

The rate at which imagos encounter host larvae is strongly dependent on host larval age (Fig. 5.7). As larvae age the searching efficiency increases as a result of larval growth, and the form of the functional response becomes increasingly less dependent on the attack rate (a, a') and more dependent on handling time, a reflection of parasitoid egg

Figure 5.9. Variance-mean relationships for the frequency distributions of eggs of Venturia canescens in Anagasta kuehniella larvae (Simmonds 1943; Stinner 1976). The solid diagonal line represents random distribution (variance=mean), points above this line represent aggregated distributions while points below the line represent uniform distributions. A. Data from Simmonds (1943). B. Data from Stinner (1976).


A
Variance of Number of Eggs / Host
Log10
Mean Number of Eggs / Host
Log10
4
3
2
1
0
−1
−1
−0.6
−0.2
0.2
0.6
1
1.4
1.8


B
Variance of Number of Eggs / Host
Log10
Mean Number of Eggs / Host
Log10
4
3
2
1
0
−1
−1
−0.6
−0.2
0.2
0.6
1
1.4
1.8

limitation. Instantaneous search rates may also depend on host density (Figs 5.6c,d,e). One of the factors determining host density will be the amount of mortality occurring due to oviposition wounds (Fig. 5.8); which will be a function of host age and host encounter rates. Parasitoid density may also play an important role in determining the encounter rate, as a result of the effects of mutual interference (Hassell 1971). While it has not been discussed, non-random parasitoid search, resulting from patchily distributed hosts, will also have important effects on net host encounter rates (Hassell 1978).

The dominant factor influencing the potential fecundity of imagos is the availability of food (Fig. 5.4). The increase in potential fecundity is primarily a result of the increased life span of fed wasps (Fig. 5.3), rather than any change in the daily egg production of fed and unfed imagos. Imago weight at emergence also influences the potential fecundity of imagos. Imago weight is influenced by the age of the host larva at infection, and by host larval densities during parasitoid development. Imago weight may influence imago fecundity through its effects on the death rate of unfed imagos, or through its effects on the total number of eggs present in the ovaries of fed imagos.

Realized imago fecundity or the number of progeny produced by an imago will depend on potential imago fecundity as well as host density and parasitoid density. Host density will determine the absolute number of hosts available for infection, while the interaction between host density and imago density will determine the degree to which superparasitism is avoided. The form of the frequency distribution of parasitoid eggs/hosts (Fig. 5.9) will be an important factor in determining the number of parasitoid progeny. One of the critical factors shaping the frequency distribution of eggs/host will be the level of superparasitism. Once supernumary larvae are eliminated rates of parasitoid larval mortality are extremely low and any parasite larval mortality occurring will be due to host mortality.

Parasitoid pre-imaginal period depends on host larval age at infection (Fig. 5.2a) and host density (Fig. 5.2b). The dependence of parasitoid development on host development serves to synchronize the life cycle of the parasitoid with the life cycle of its host. V. canescens is a larval parasitoid. As a result a substantial portion of

the host life cycle is invulnerable to parasitism: eggs, 1st instar larvae, pupae and adults. Therefore for only 44% of the total life span of the host is it susceptible to attack by the parasitoid.

Any attempt to formulate a population model which incorporates the relationships summarized above would result in a very complex model. Although it may be difficult to identify those factors which are most important in determining the behaviour of this host-parasitoid system, the experimental evidence does allow for some simplification and a prior elimination of effects that are thought to be of lesser importance.

LONG-TERM POPULATION CAGES

This chapter presents the results of 'long-term' experiments dealing with single-species populations of the moth Cadra cautella and two-species populations of the host and its parasitoid Venturia canescens carried out in large cages where the host or host-parasitoid populations were allowed to reproduce, die and interact with minimal interference.

The purpose of these experiments was two fold. First the results presented in previous chapters were based on short-term experiments designed to identify and quantify the demographic characteristics of uniform-aged host and parasitoid cohorts under restricted conditions. In other experiments, such as inter-stage cannibalism, implicit assumptions concerning the spatial and temporal overlap of the stages were involved. Results from 'free-running' population experiments will provide data allowing the validity of the results and assumptions of the short-term experiments to be assessed.

The second purpose of the population-cage experiments was to provide a set of data with which the predictions of a mathematical population model could be compared. When the predictions of a population model are based on parameters estimated independently of the data with which the model is compared, such a comparison provides an excellent test of the power of the model. An even more powerful test of the model is obtained when long-term population cages are experimentally manipulated in order to produce a quantifiable change in the biological attributes of the specie(s) involved.

This is the reason that experiments concerned with the survival and fecundity of host and parasitoid have been carried out under conditions of varying food availability, conditions that produce predictable changes in imago fecundity and survival which may be easily incorporated into a population model.

MATERIALS AND METHODS

Two sizes of cage were used for the long-term experiments. The larger cages were 43 cm wide, 61 cm deep, and 61 cm high at the back of the cage and 40 cm high at the front (volume = 0.13 m^3). The bottom,

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week. Neither host nor parasitoid imagos were provided with food or water.

Once a week, at the time of food addition, all dead moth and parasitoid imagos were removed from the cages and counted. The amount of work involved in determining larval population sizes only allowed for detailed sampling of 1 host population cage and 1 host- parasitoid cage. In these cages, food units which had been removed were examined and the number, stage or instar of the moth and the number of parasitoid pupae present in each food unit determined. In cages containing both host and parasitoid a sample of the larvae was removed and dissected in order to determine the level of parasitism for each host larval instar. In addition, at the time of food replacement, counts were made of the number of imagos alive in the population cage.

In the host population cage selected for detailed sampling, egg distribution in relation to the age of the food units was determined. One day prior to the replacement of the food units a small piece of screening (60 μm mesh) supported by a thin plastic ring was placed in each of the 37 food units to be removed. The circle of screening fit within the petri dishes and rested directly on the food. When the food units were removed the number of eggs per dish was determined. This procedure was done every 4 weeks starting on week 12.

Series L2

In the series L1 cages, host-parasitoid populations became extinct after about 25 weeks. In these cages no protective cover was provided for the host larvae; as a result all host larvae were susceptible to infection by the parasitoid. In the L2 series of cages refuges were provided for the host larvae. The refuges consisted of round glass cover slips placed in the center of each food unit and resting on top of the food. Three diameters of cover slips were used: 1, 1.5 and 2.0 cm. These covered 11%, 25% and 44% of the surface area in each food unit. It was felt that the effects of providing host refuges in this way could be more easily quantified, than would be the case if a refuge effect was created by increasing the depth of the food. Two host population cages and 8 host-parasitoid cages were established, 2 each of 0%, 11%, 25% and 44% protective cover. No protective cover was provided in the single-species

population cages. Neither host nor parasitoid imagos were provided with food or water.

The food replacement procedure was identical to that described above, as was the sampling procedure for dead adults. No estimates were made of larval population densities. Host populations were established by adding 50 eggs/day to each cage for 6 weeks; parasitoid populations were initiated by adding 2 wasps per cage at the beginning of the fifth week.

The cages had been slightly modified by replacing the coarse 0.5 mm mesh screening with 60 μm mesh screening

Series L3

As a result of the extinctions which occurred in the L2 series of experiments, regardless of the level of protective cover, a number of changes were made in the experimental protocol The basic change was in the food replacement regime. The food was no longer contained in petri dishes but was placed directly on the floor of the cage. The bottom of the cage was divided into produce 32 rectangular areas (11 x 7.5 cm) or food units. There were 8 food ages and 4 food units per food age. The food units were located in such a manner that new food was placed adjacent to the youngest food units in the cage. The cages were established by adding food to 4 food units each week, so that at the end of eight weeks food units ranged in age from 1 to 8 weeks. The oldest (8 week) food units were removed each week to provide room for the addition of new food. The rate of food replacement was 56 g/week, 14 g per food unit

Protective cover was provided by covering 1, 2, or 3 units per age with a piece of black non-corrugated cardboard, thereby providing 25%, 50% or 75% cover. The cages were established by adding 50 host eggs/day for 6 weeks. Five wasp imagos were introduced at the start of week 5. There were 2 cages of the host alone and 2 cages each of 0%, 25%, 50% and 75% cover. The single-species cages were not provided with protective cover Neither host nor parasitoid imagos were provided with food or water. Dead imagos were removed and counted at the time of food replacement.

Series S

This series of experiments used the small size of cage. The protocol for food replacement was similar to that described for the L3 series of

experiments. Food was placed directly on the bottom of the cage and added to the cage weekly but there were only 6 food ages and 2 food units per age, a total of 12 food units (5 x 8 cm). Food units were removed at the end of six weeks. The rate of food addition was 20 g/week, 10 g per food unit. Protective cover was provided by covering 1 set (50%) of food units (food ages 1-8) with a 1.5 cm thick layer of expanded mica ('vermiculite'). Weekly counts were made of the number of dead imagos in each cage. Owing to the small size of these cages, imagos had to be lightly anaesthetized with CO_2 in order to remove the dead imagos.

Moth populations were established by adding 10 host eggs/day for 6 weeks; 2 wasp imagos were added at the start of the fifth week. Five cages of the host alone were established with no protective cover, food nor water provided. Ten host-parasitoid cages with 50% cover were established In half of the cages the wasp and host imagos were without food or water, while in the other half food and water were provided in the form of a 20% honey solution in water which was changed daily.

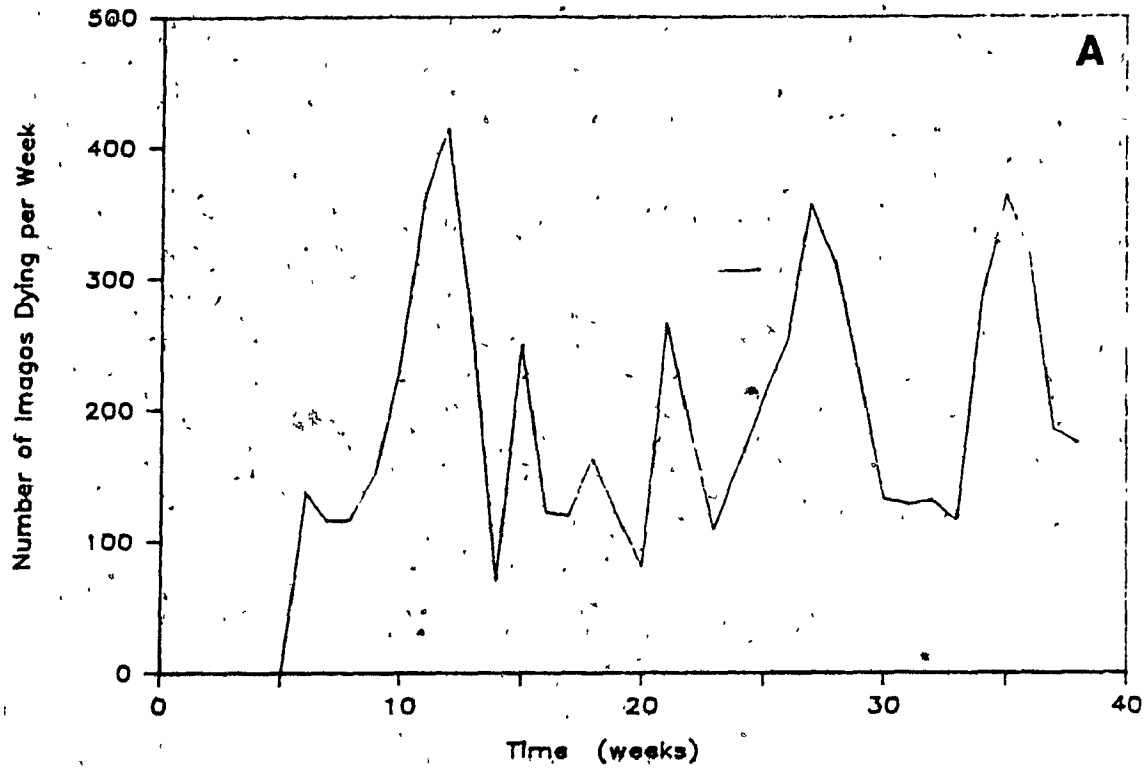
RESULTS

Figure 6.1 illustrates the number of C. cautella imagos dying per week for two of the series L1 replicates for the host population in isolation. While there was insufficient data for statistical analyses, there does appear to be a distinct cyclical pattern in the number of imagos dying/week. When averaged over all replicates the period of these oscillations is about 44 days. Figure 6.2 presents the sex ratio of the imagos found dead each week. There was no trend in the sex ratio with time, nor was there a departure from a 1:1 sex ratio.

Figure 6.3 presents the estimated population sizes for the different host stages through time (this data corresponds to the data of Fig. 6 1a). As was seen in the graphs depicting the number of dead adults, there was a distinct cyclical pattern in larval and pupal population sizes. Figure 6.4 presents the average stage structure of the host population estimated from the data of weeks 15-38.

Figure 6.5 illustrates the average distribution of eggs, larvae and pupae in relation to the age of the food units. Figure 6.5a depicts the proportion of various food ages in the population cages. If egg, larval,

Figure 6.1. Weekly counts of dead imagos in single-species long-term population cages of Cadra cautella. A. Data from series L1, replicate 1. B. Data from replicate 2.


A
Number of Imagos Dying per Week
500
400
300
200
100
0
0
10
20
30
40
Time (weeks)

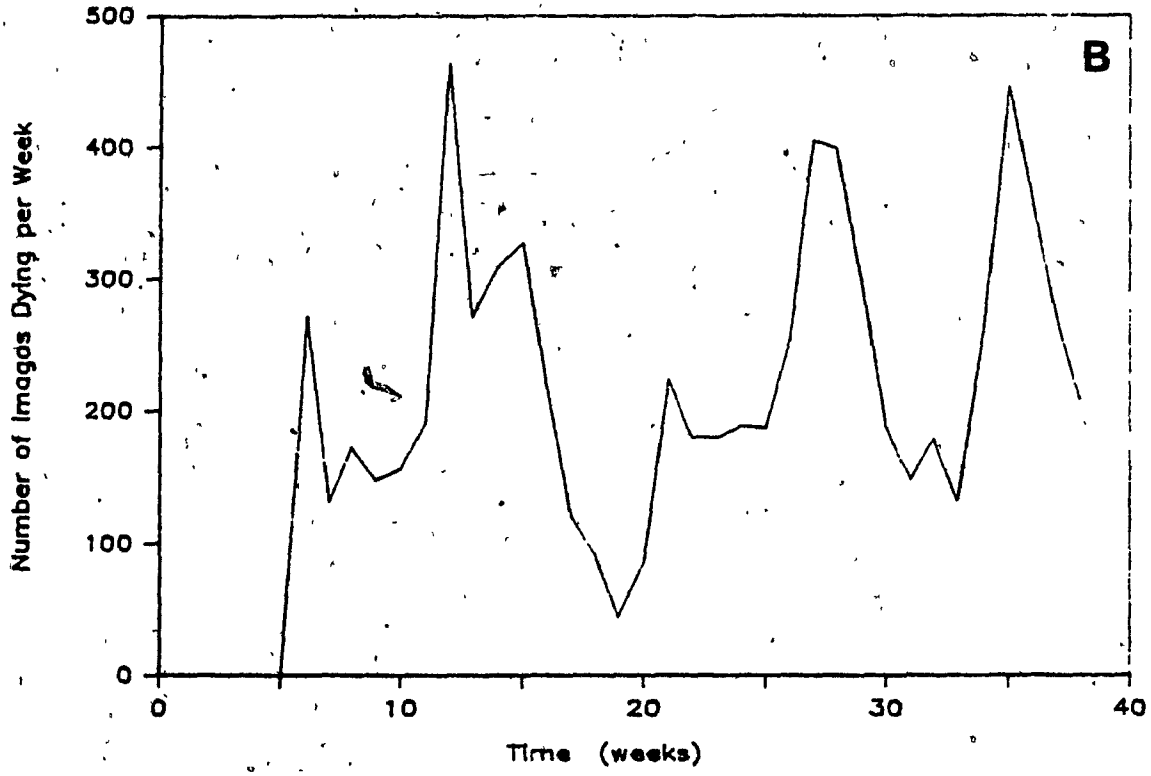
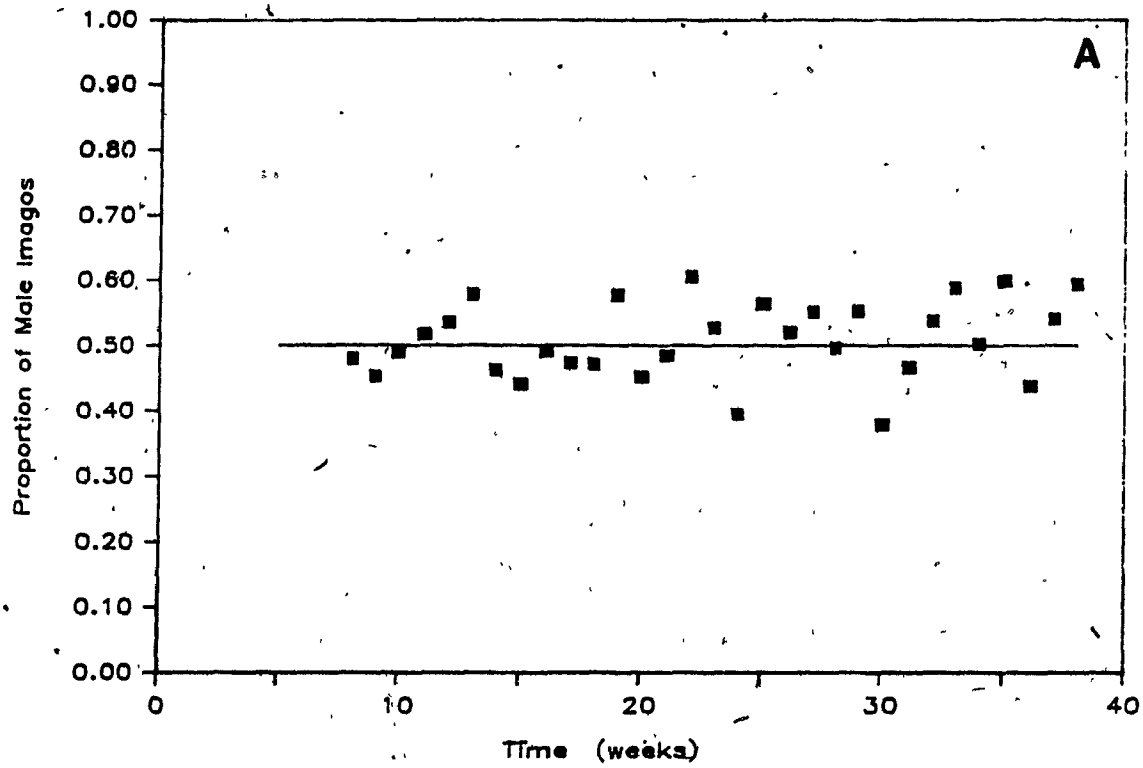

B
Number of Imagos Dying per Week
500
400
300
200
100
0
0
10
20
30
40
Time (weeks)

Figure 6.2. Changes in the proportion of males in the weekly counts of dead imagos in single-species long-term population cages of Cadra cautella. A. Data from series L1, replicate 1. B. Data from replicate 2.


A
Proportion of Male Imagos
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0
10
20
30
40
Time (weeks)

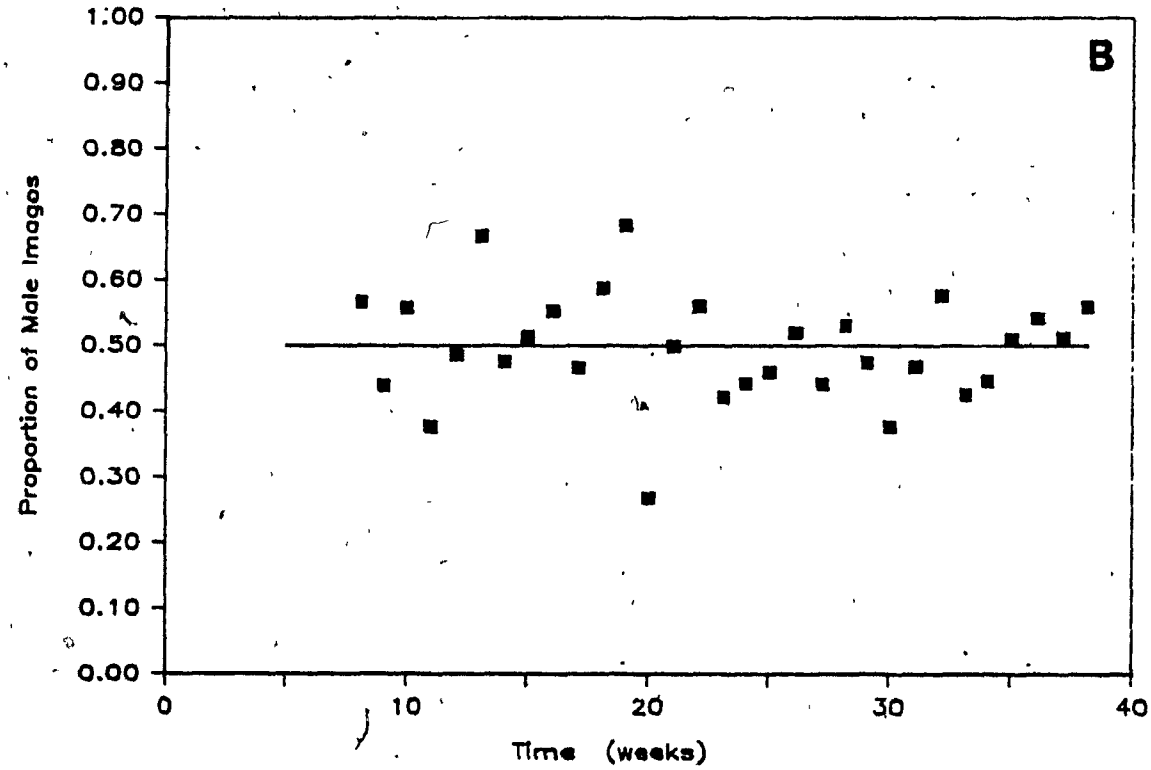

B
Proportion of Male Imagos
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
0
10
20
30
40
Time (weeks)

Figure 6.3. Changes in the estimated population sizes of larvae and pupae in a single-species population cage of Cadra cautella. Changes in population numbers of 1st instars A, 2nd instars B, 3rd instars C, 4th instars D, 5th instars E, and pupae F. Data from series L1, replicate 1.

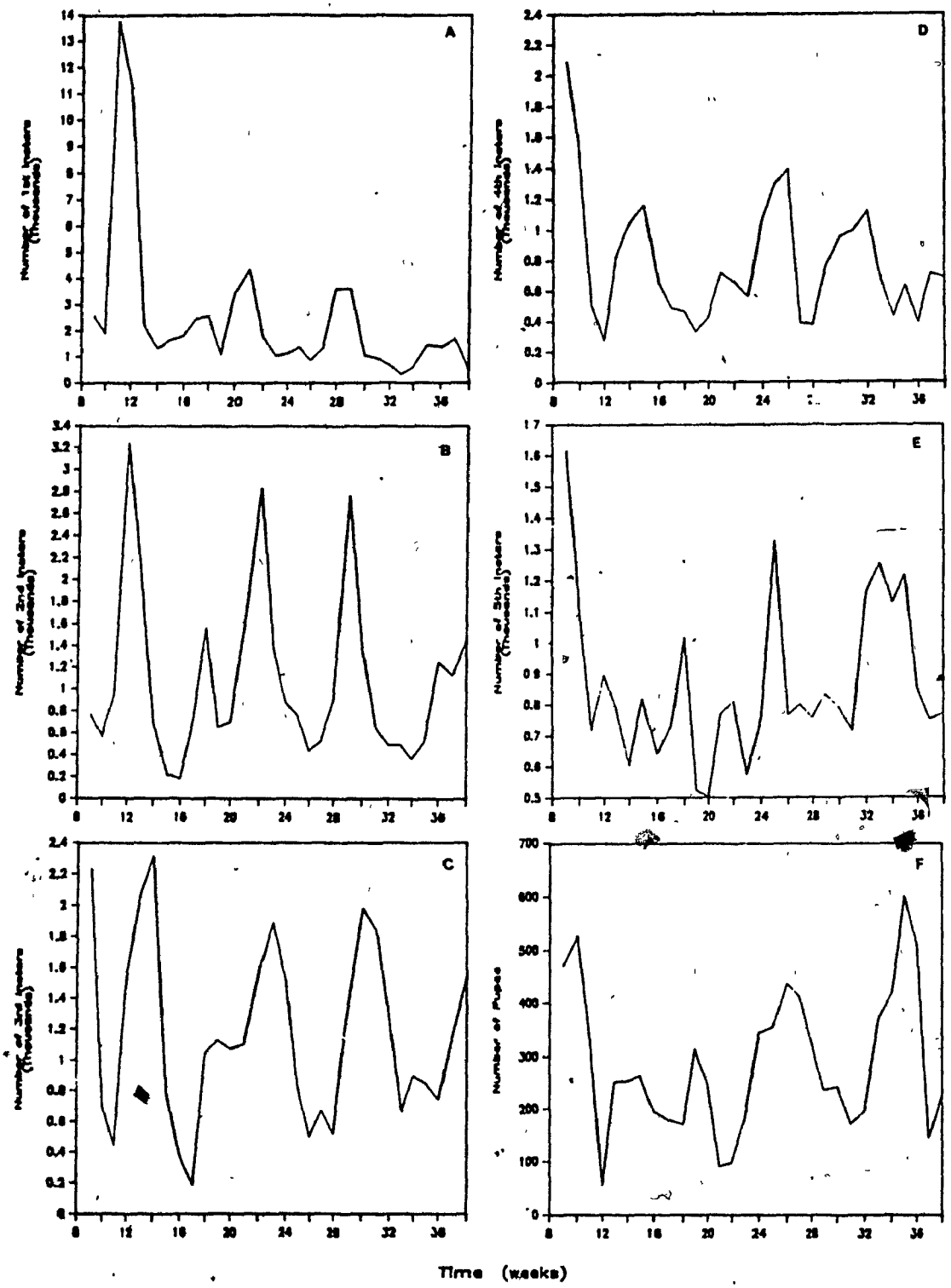

A
B
C
D
E
F
Number of 1st Instars (Thousands)
Number of 2nd Instars (Thousands)
Number of 3rd Instars (Thousands)
Number of 4th Instars (Thousands)
Number of 5th Instars (Thousands)
Number of Pupae
Time (weeks)

Figure 6.4. Age-structure of Cadra cautella in a single-species population cage. Depicts the average age-structure calculated using the data of weeks 15-38 from replicate 1, series L1.

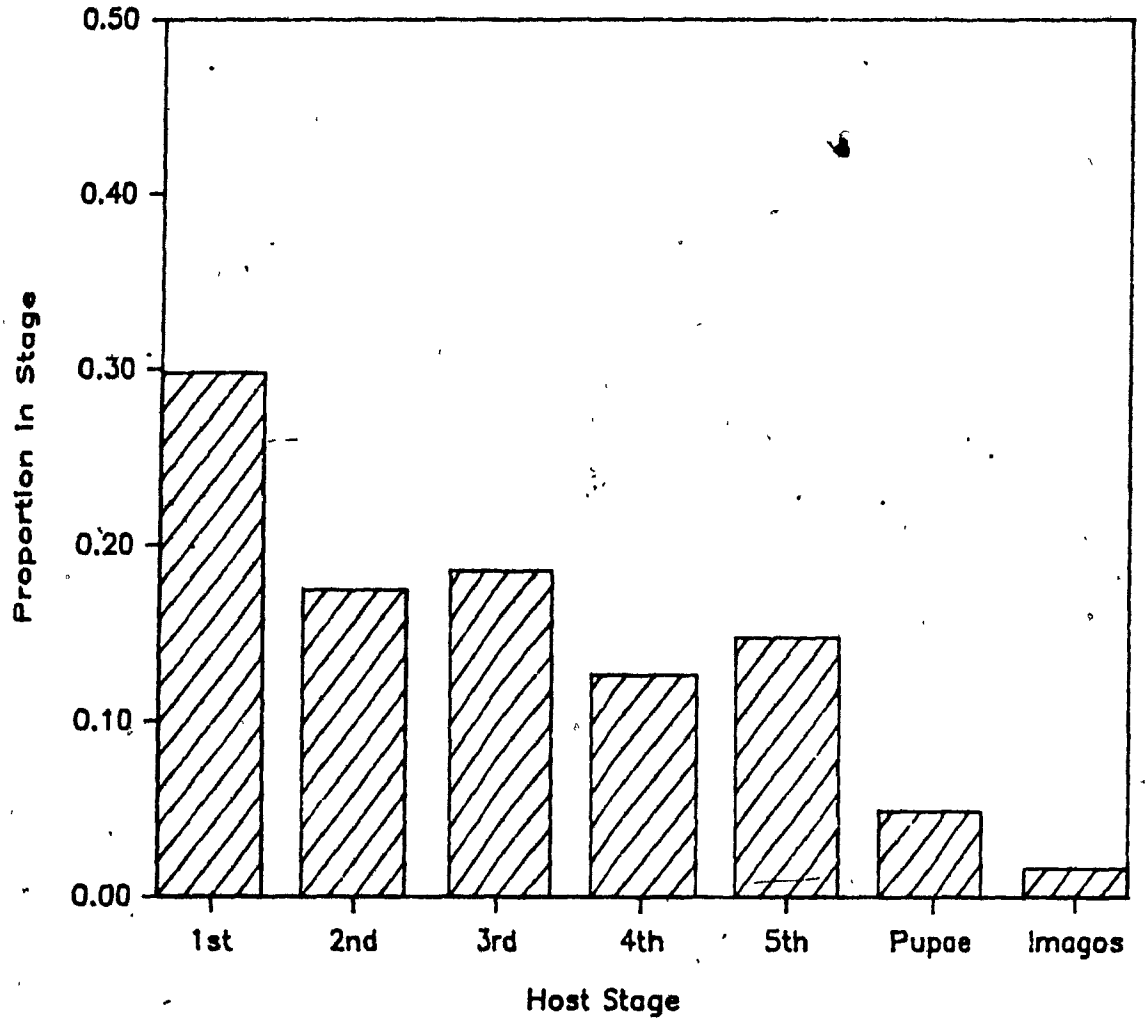
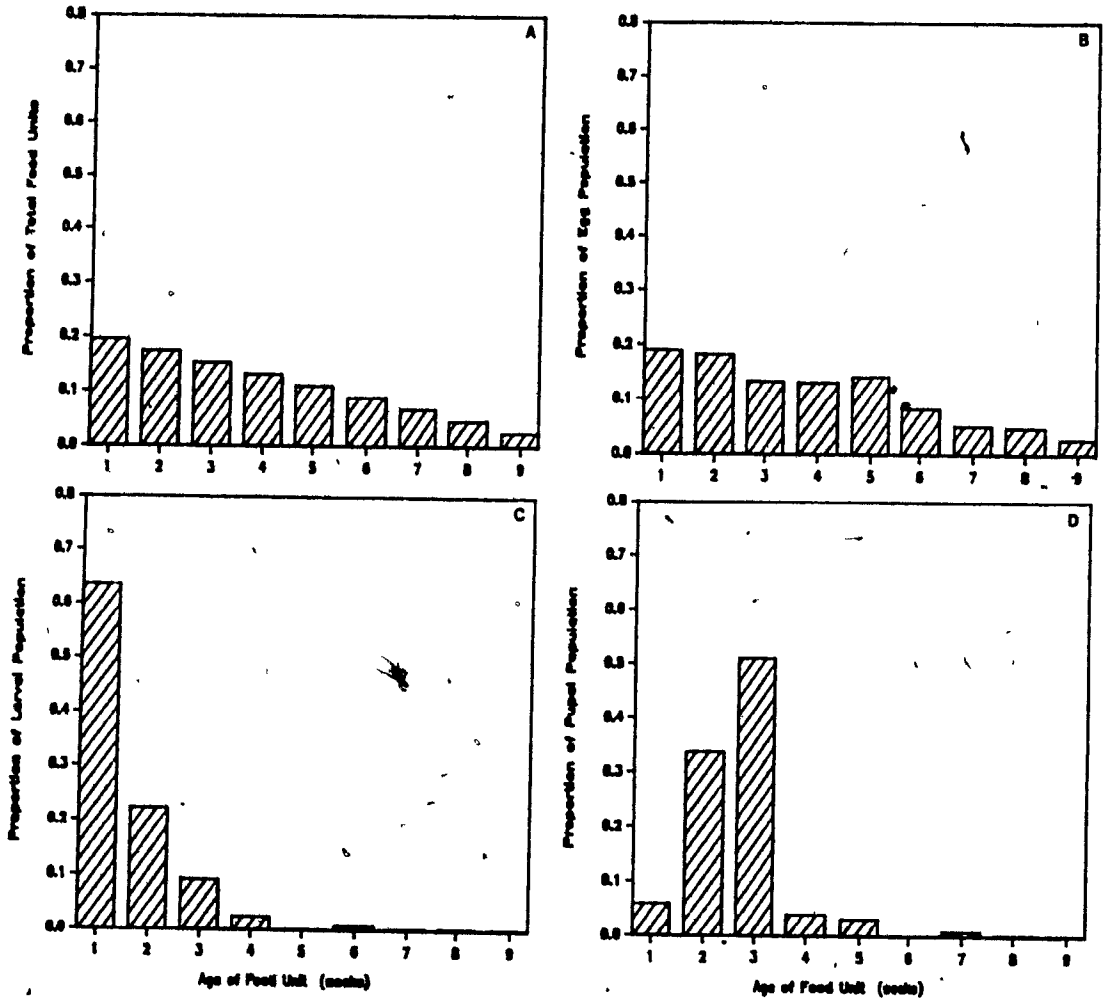

0.50
0.40
0.30
0.20
0.10
0.00
Proportion in Stage
1st
2nd
3rd
4th
5th
Pupae
Imagos
Host Stage

Figure 6.5. Distribution of Cadra cautella stages among the different ages of food units in a single-species population cage. A. Presents the proportion of total food units of different ages. The distribution of stages among the various food unit ages; eggs B, larvae C, and pupae D. Depicts the average distribution using the data of weeks 15-38 from replicate 1, series L1.


A
B
C
D
Proportion of Total Food Units
Proportion of Egg Population
Proportion of Larval Population
Proportion of Pupal Population
Age of Food Unit (units)
Age of Food Unit (units)

or pupal distribution was independent of the age of the food unit, the proportion of the total population in each age of food unit should be the same as proportion of food unit ages (expected frequency 37:34:29:25:21:17:13:9:5). The proportion of total eggs in each age of food unit (Fig. 6.5b) was not significantly different from expected ($X^2_{(8)}$=2.5, p>0.975). Larval distributions (Fig. 6 5c) were however significantly different from expected ($X^2_{(8)}$=8359 1, p<0.0001), with larvae occurring in the youngest food units (1 week old) with much greater frequency than expected. Pupal distributions (Fig. 6.5d) were also significantly different than expected ($X^2_{(8)}$=124 6, p,0 0001), with pupae being infrequent in the 1 week old food units and more common than expected in the oldest food units.

Figure 6.6 presents the results of 2 replicates of the host-parasitoid systems from series L1 Extinction of the host and parasitoid occurred within 22-25 weeks, in all 5 replicates. Larval population sizes have not been presented due to the small size of the data set. The percentage of larvae infected (data corresponds to Fig. 6.6a) for each of the larval instars through time is presented in Table 6.1. Infection levels of 1st and 2nd instar host larvae were uniformly very low, while the infection levels in 3rd, 4th and 5th instars were high and reached 100% by the end of the experiment.

Figure 6.7 illustrates the distributions of host larvae and host and parasitoid pupae among the various food unit ages. The distribution of both larvae and pupae were significantly different from expected values (larvae, $X^2_{(8)}$=6059.1, p<0.0001; pupae, $X^2_{(8)}$=82.2, p<0.0001). The distribution of larvae and pupae among the different age food units was similar to the patterns observed in the single species population cage.

Three of the replicates of the host population became accidentally infected by the wasp, probably due to between cage movement of small larvae, or oviposition by wasps which occasionally escaped through the mesh of the cages. This problem was completely corrected by replacing the ventilation and sleeve screening with a much smaller mesh size (60 μm). Due to the extinction of the host population by the parasitoid, further series of the large cages were established, which provided various levels of protective cover for the larvae.

Figure 6.6. Weekly counts of dead imagos in long-term population cages of Cadra cautella and Venturia canescens where no host refuges were provided. A. Data from series L1, replicate 3. B. Data from replicate 2. Black line denotes the host and the red line the parasitoid.

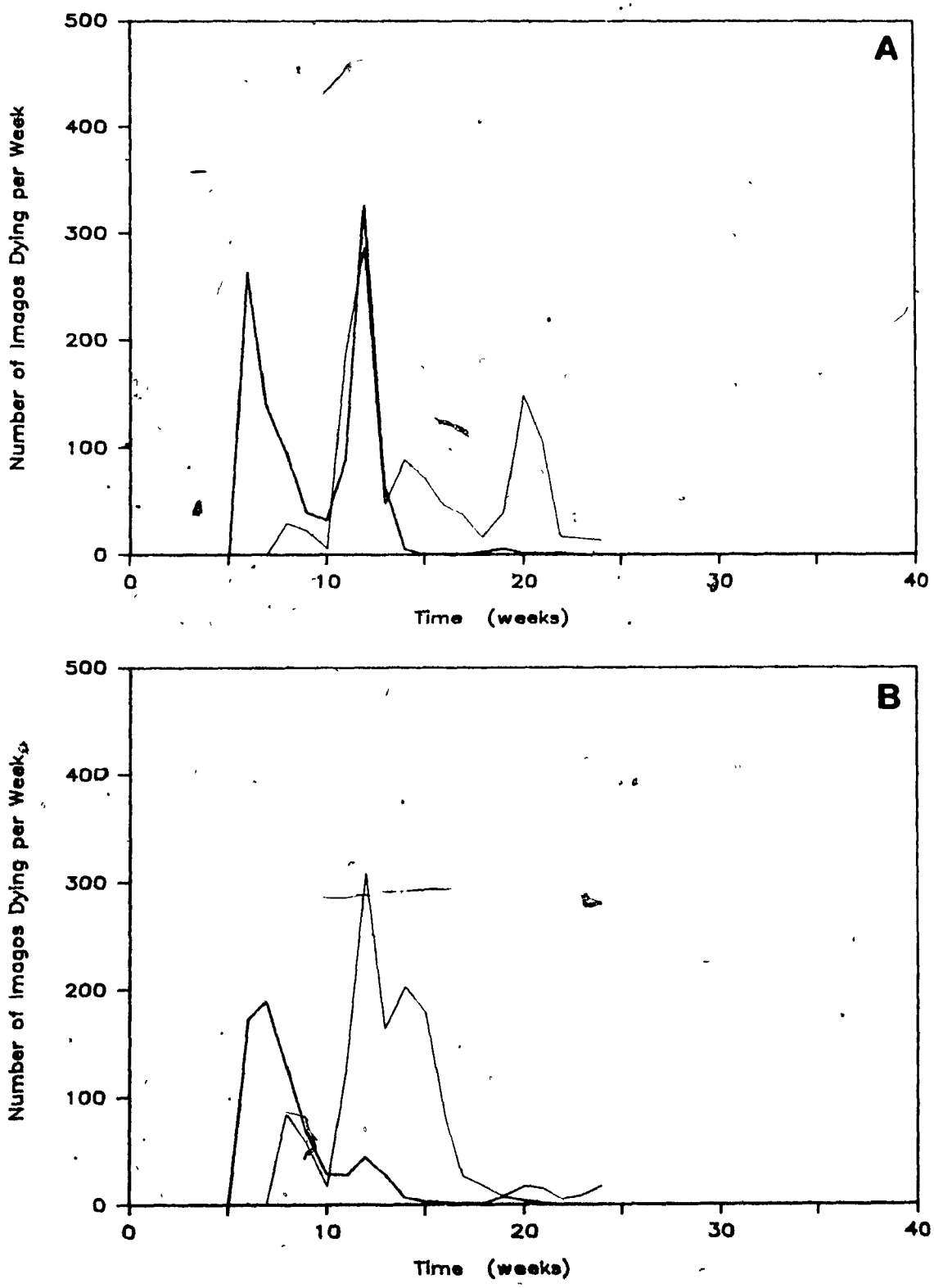
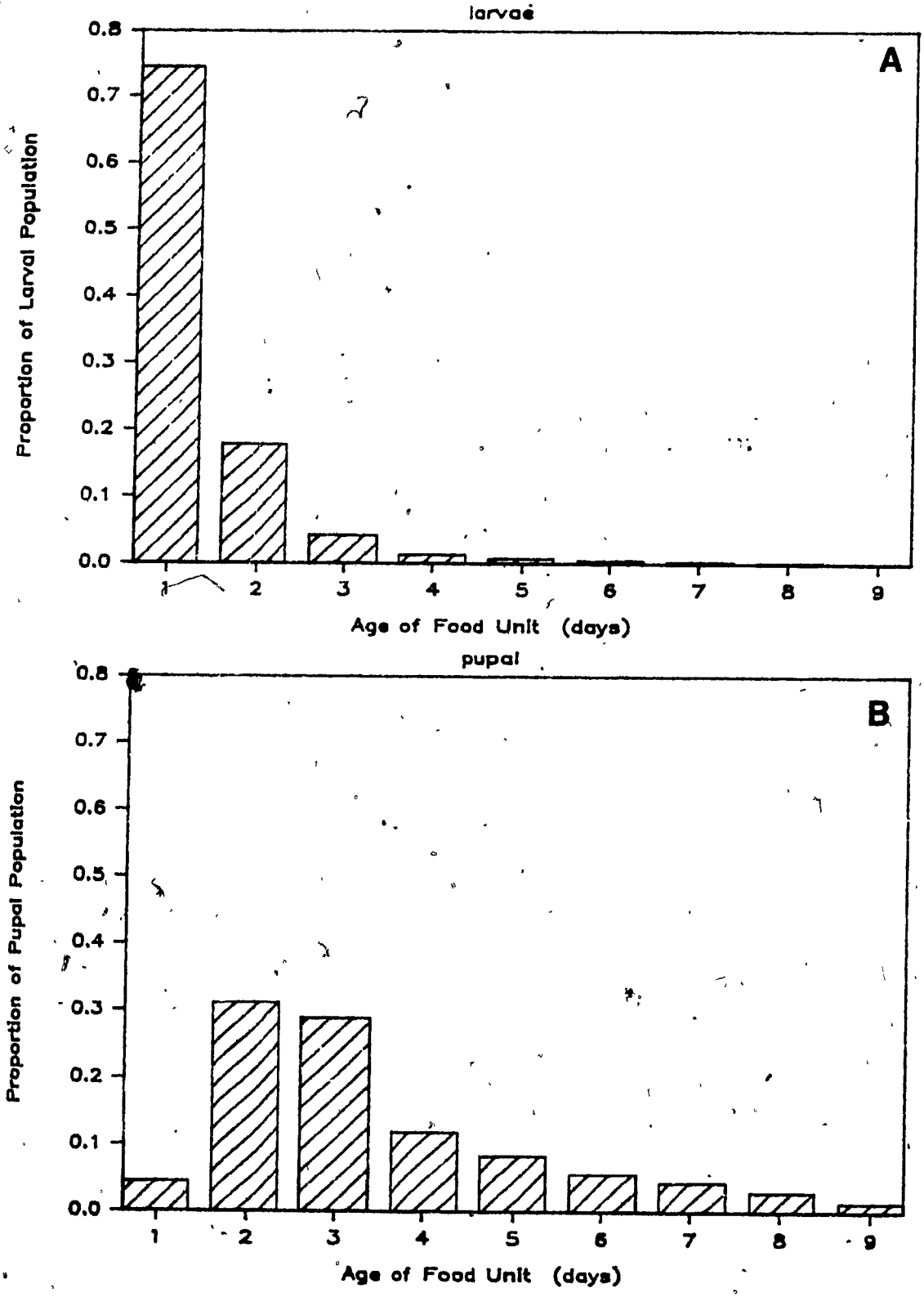

A
Number of Imagos Dying per Week
500
400
300
200
100
0
0
10
20
30
40
Time (weeks)
B
Number of Imagos Dying per Week
500
400
300
200
100
0
0
10
20
30
40
Time (weeks)

Table 6.1. The percentage of Cadra cautella larvae parasitized by Venturia canescens in a long-term population cage. Data from replicate 3 series L1.

	Percentage of Host Larval Instars Infected					
Time[1]	1st	2nd	3rd	4th	5th	N[2]
10	0%	0%	0%	12%	26%	4,8,59,84,104.
11	0%	0%	24%	95%	76%	150,1,17,20,50
12	0%	8%	45%	95%	90%	53,75,40,22,40
13	0%	0%	42%	65%	91%	38,41,38,26,22
14	0%	7%	15%	54%	93%	5,30,55,41,41
15	0%	0%	65%	84%	91%	8,7,43,32,11
16	-	0%	71%	100%	100%	0,12,21,20,12
17	0%	-	77%	78%	86%	3,0,13,32,28
18	-	-	40%	86%	94%	0,0,5,14,35
19	7%	9%	67%	67%	95%	29,11,3,12,19
20	0%	0%	100%	100%	100%	9,3,4,3,7
21	0%	0%	89%	100%	100%	2,2,9,5,5
22	-	-	100%	100%	100%	0,0,2,1,14
23	-	-	100%	100%	100%	0,0,2,3,11

[1] Age of the population cage, weeks
[2] Number of larvae dissected

Figure 6.7. Distribution of host and parasitoid stages among the different ages of food units in a population cage of Cadra cautella and Venturia canescens. A. Distribution of host larvae among the various food unit ages. B. Distribution of host and parasitoid pupae. Data of weeks 15-23, replicate 3, series L1.


larvae
A
Proportion of Larval Population
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1
2
3
4
5
6
7
8
9
Age of Food Unit (days)
pupal
B
Proportion of Pupal Population
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1
2
3
4
5
6
7
8
9
Age of Food Unit (days)

Figures 6.8 and 6.9 present the results of 1 replicate of each of the various levels of protective cover employed in the L2 and L3 population cages respectively. In all experiments regardless of the level of protective cover employed, the populations became extinct within 22-25 weeks. The differences in the initial pattern of parasitoid population growth among the three series of experiments (L2 vs L1 and L3) are due to the smaller number of parasitoid imagos (2 vs 5) used to establish the parasitoid populations resulting in a longer lag prior to the build-up of parasitoid populations in L2 cages.

In spite of extensive and exhaustive (as technically possible) precautions invasions by the mite Blattisocius tarsalis (Berlese) (Acarina: Blattisociidae), an egg predator, caused the extinction of all host population cages. Examination of the dead imagos removed from the cage at each census allowed fairly accurate track of the mite populations to be kept. Mites were first found (<1 per 200 host imagos) by 20-25 weeks following establishment of the cages. Mite populations increased very rapidly, and within 5 weeks had greatly reduced the size of the host larval populations or eliminated the host. The experiments were terminated 3-5 weeks after mites were found in the system. It is unlikely that mite invasions were responsible or contributed to the extinction of the host-parasitoid populations. When cages were terminated, all food units in the system were carefully examined. No uninfected host larvae were found, suggesting that the timing of the mite invasions was such that these populations had already reached the point of extinction (100% of host larvae infected).

In the course of carrying out the censuses on the population cages provided with 50% and 75% protective cover (cardboard cover) there was some (unquantified) host imago mortality due to the failure of newly eclosed imagos to escape from beneath the cardboard. For this reason it was decided to provide larval refuges by covering food units with a layer of expanded mica ('vermiculite') in the final set of experiments (S1).

Figure 6.10 presents the results from experiments using small cages of 1 replicate of the host population alone, and 1 replicate of the host-parasitoid populations where imagos were either with or without a food source. Results are comparable to those of the larger cages. Low initial host populations sizes are due to the low rate of egg inoculation

Figure 6.8. Weekly counts of dead imagos in long-term population cages of Cadra cautella and Venturia canescens where host refuges provided 0%, 11%, 26% or 44% cover. Data from series L2. A. No protective cover provided, replicate 1. B. 11% cover, replicate 2. C. 26% cover, replicate 1. D. 44% cover, replicate 1. Black line denotes the host and the red line the parasitoid.

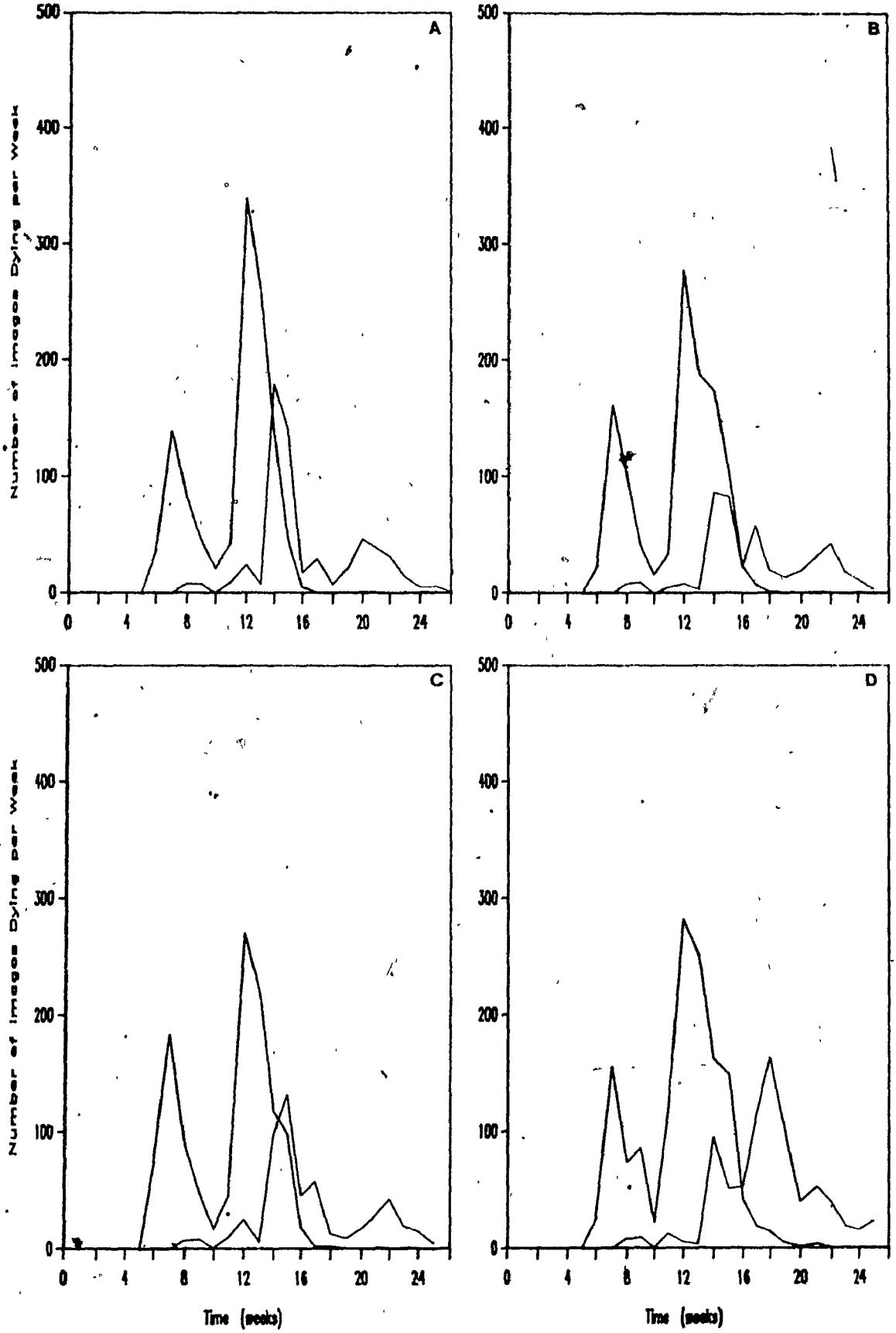

A
B
C
D
Number of Imagos Dying per Week
Time (weeks)
0
100
200
300
400
500
0
4
8
12
16
20
24

Figure 6.9. Weekly counts of dead imagos in long-term population cages of Cadra cautella and Venturia canescens where host refuges provided 0%, 25%, 50% or 75% cover.. Data from series 1.1 replicate 1. A. No protective cover provided. B. 25% cover. C. 50% cover. D. 75% cover. Black line denotes the host and the red line the parasitoid.

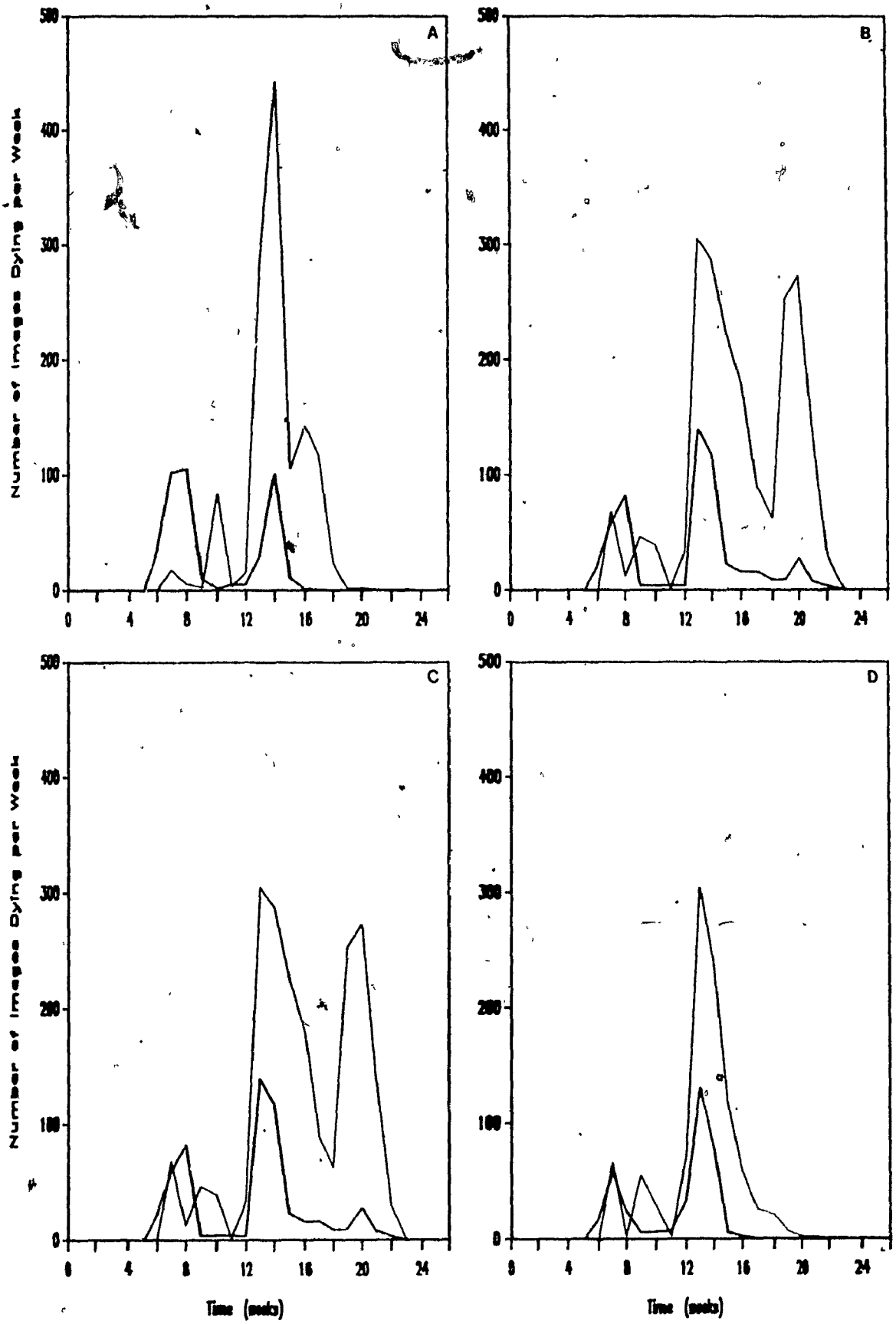
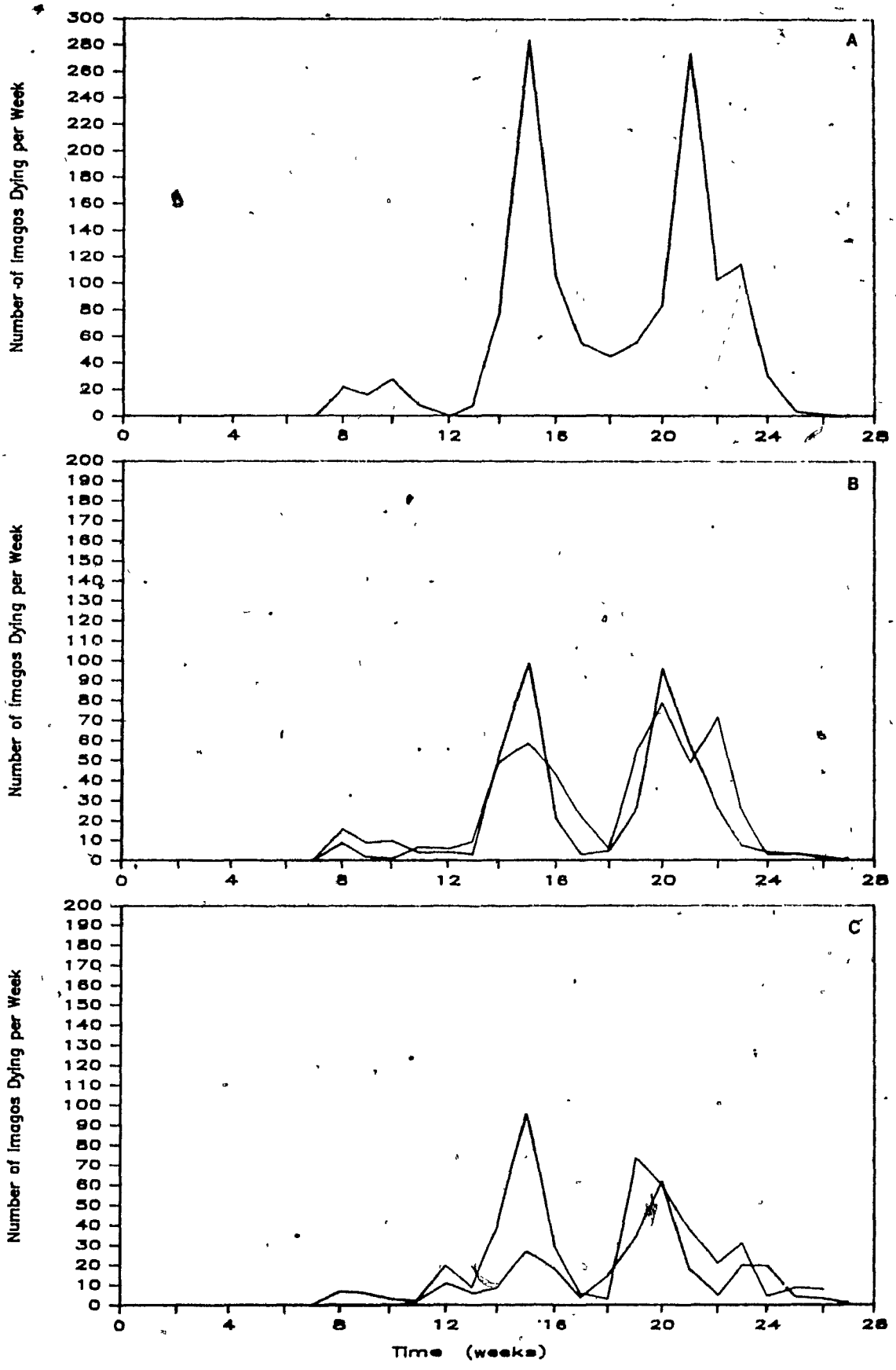

A
B
C
D
Number of Imagos Dying per Week
Time (weeks)
0
100
200
300
400
500
0
4
8
12
16
20
24

Figure 6.10. Weekly counts of dead imagos in long-term population experiments of Cadra cautella and Venturia canescens using the small cages. A. Single-species populations of Cadra cautella, replicate 3. Populations of the C. cautella and Venturia canescens, 50% protective cover provided; B. No food nor water provided for imagos, replicate 8. C. Imagos provided with food and water, replicate 1. Black line denotes the host and the red line the parasitoid.


A
B
C
Number of Imagos Dying per Week
Number of Imagos Dying per Week
Number of Imagos Dying per Week
Time (weeks)
0
4
8
12
16
20
24
28

used to establish the small population cages. Invasion by the predatory mite B. tarsalis resulted in the premature termination of this entire series of experiments. There was however some indication that protecting 50% of the food units using a covering of vermiculite may have provided a degree of host refuge sufficient to allow continued co-existence of host and parasitoid.

DISCUSSION

The results of the single-species population cages (Figs 6.1 and 6.10) suggest that C. cautella populations do exhibit quasi-cyclic behaviour where the period of the cycles is approximately 40 days. Very similar results have been obtained for C. cautella by Takahashi (1973) (40 days) and for Plodia interpunctella (39 days) by Gurney, Nisbet & Lawton (1983).

The distribution of C. cautella eggs among the various food units (Fig 6.5b) shows that female imagos distributed eggs among the food units independent of the age of the unit. This suggests that eggs were scattered at random throughout the population cage.

Host larvae were found far more frequently in the youngest food units (Fig. 6.5c) and rarely in the older food units. In the single-species population cages, this pattern of larval distribution is in part explained by the rapid depletion of food units, such that in food units greater than 2 weeks of age, no uneaten food remains. However, a very similar pattern of larval distribution (Fig. 6.7a) occurs in the host-parasitoid population cages where larval densities are an order of magnitude lower, and large amounts of unconsumed food are found in even the oldest food units. C. cautella larvae apparently prefer feeding in food uncontaminated by larval by-products (faeces) and actively seek out these uncontaminated food sources. The effect is quite dramatic, and larvae can be observed moving into new food units immediately after introduction. This results in many new food units being fully colonized in less than a day. The effects of this behaviour are discussed more fully in Chaps. 3 and 4.

The distribution of host and parasitoid pupae (Fig. 6.5d and 6.7b) is the opposite of that observed for host larvae; pupae are found in the

youngest food units less often than expected. The low numbers of pupae in 1 week old food units might be due to cannibalism by host larvae, as it is in these units that larval densities are greatest, a similar pupal distribution is also observed under conditions of much lower larval densities in the two-species population cages (Fig. 6.7b). These results suggest that the distribution of pupae among food units is a result of larvae seeking out regions of low host larval density in order to pupate.

The migratory behaviour of C. cautella larvae among food units also explains why large proportions of the food units must be provided with protective cover, in order to create a refuge for the host larvae from the parasitoid. Results of population cage series L2, L3, and S1 indicate that more than 50% of the food units must be provided with protective cover in order to allow the long-term co-existence of host and parasitoid. The effect of refuges is generally to protect a fraction of the susceptible host population from infection by the parasitoid over the duration of the stage of host susceptibility. The migratory behaviour of the host larvae has the following effect. While at one instant in time a particular larva may be under an area of protective cover, when the larva moves into a new food unit there is a probability that it will not be under cover in the new food unit. For example, assuming that the larva moves at random, and that on average a larva will move 3 times (food added once per week, larval duration >21 days), in a population cage with 50% of the food units protected, the probability that a larva will be under protective cover for its entire larval period could be as low as 0.125.

A number of other studies have investigated the behaviour of populations of V. canescens and stored-products moths: Flanders (1968), White & Huffaker (1969a,b) worked with E. kuehniella; Takahashi (1973) used C. cautella and Podoler (1974) used P. interpunctella. In all cases they have shown that long-term, co-existence of host and parasitoid can be achieved with little or no protective cover. The reasons for the difference between the results of this study and those of other workers regarding the stable co-existence of the two species are essentially unknown and may simply be due to the different experimental conditions, species differences or differences among the strains of wasp used. Podoler (1974) used a population cage about 5 times larger than was used in this study. The searching efficiency of the parasitoid appears to

have been much lower under the experimental conditions employed by Takahashi (1968) compared with the searching efficiency of the wasp in these experiments (see Chap. 5). Both Flanders (1968) and White & Huffaker (1969a,b) made the observation that there is very little larval movement between food units. This could potentially have produced aggregated larval distributions, and hence could have contributed to a more stable host-parasitoid system (Hassell 1978).

The results of this and previous studies (see Chap. 1) suggest that most single-species laboratory populations of stored-products Lepidoptera tend to exhibit discrete generations. The one exception to this observation appears to be the work with A. kuehniella by White & Huffaker (1969a). The differences between C. cautella and A. kuehniella may be due to the differences in larval behaviour. C. cautella migrates extensively among the food units, while A. kuehniella does not. White & Huffaker (1969a,b) suggested that the colonization of a food unit depends upon the female host imagos depositing eggs in new food units. This and the lack of larval movement between food units would create a series of larval sub-populations, behaving essentially independently of one another. This situation would greatly obscure any tendency for the total imago population to exhibit discrete populations, even if larval competition was expressed in a manner conducive to the creation of discrete generations. The behaviour of C. cautella populations results in a much more homogeneous larval population. It is not known if the larvae of P. interpunctella exhibit similar movement patterns.

Providing host and parasitoid imagos with food resulted in no difference in the total number of wasp imagos produced when compared to the cages where imagos were unfed (Fig. 6.10). There was however about a 32% reduction in the numbers of host imagos produced when imagos were provided with food. This result suggests that there may have been increased host larval mortality due to parasite-inflicted oviposition wounds. While wasp fecundity increases substantially when food is provided, realized wasp reproductive success will be limited by host availability. As a result while there may be no difference between population cages with or without food in the number of wasps produced, in cages with food, average wasp population densities would in theory be

substantially higher, a situation which would produce a greater degree of larval mortality due to oviposition wounds.

As a result of repeated problems with predatory mite invasions these long-term population cage experiments failed to produce a completely adequate set of data with which a future population model could be compared. The experimental results of population cages with no host refuges are complete, and a substantial number of replicates are available. In addition the results have provided some indication of the degree of host refuge necessary to achieve the stable co-existence of host and parasitoid. Furthermore the detailed data collected on larval populations provide extremely important insights toward the formulation of future population models.

The interrelation of the experiments presented in this and the preceding chapters will be discussed in the next and closing chapter.

OVERVIEW

This study of laboratory populations of the stored-products moth, C cautella and the parasitoid V canescens has identified and quantified the density- and age-dependent demographic characteristics of this host-parasitoid system This chapter summarizes the results obtained, and discusses their implications in terms of the population dynamics of the single-species populations and host-parasitoid populations In addition it presents areas in which further work is needed

The short-term C cautella cohort experiments showed that there are two primary density-dependent processes occurring in the host population The first is larval competition for food This is a 'scramble' form of competition which is expressed as decreased larval survival and increased larval stage duration with increasing larval density. In addition, larval competition decreases larval weight at pupation resulting in reduced imago fecundity and longevity While affecting the adult stage, larval competition does not appear to influence pupal survival or pupal mortality. The second density-dependent effect is the inter-stage interactions occurring as a result of egg, larval, and pupal cannibalism by larvae. First instar larvae were found to be the only larval instar vulnerable to cannibalism

Age-dependency in a number of the rate processes was found and included age-dependent imago survival and fecundity, as well as age-dependent rates of egg and larval cannibalism by larvae, a dependency which was likely a reflection of larval weight

The long-term single-species population experiments confirmed the importance of food limitation as a factor regulating population growth, and provided important data on the way in which larvae are distributed among the food units in the population cages The results suggested that C cautella eggs are scattered at random throughout the cage, while larvae are concentrated in the youngest food units. This pattern occurs because of larval movement into recently added food units This movement behaviour is independent of larval instar, and suggests that 1st instar cannibalism by older larvae maybe an important factor in the regulation of host populations. The different distribution patterns of these two stages result in a partial spatial separation of eggs and larvae, and therefore,

depending on the actual age-distribution of the food units, the impact of egg cannibalism by larvae will be substantially reduced. A similar partial spatial separation of pupae and larvae was also observed. The similarity of pupal distributions between the single-species and host-parasitoid population cages, even under very different larval population densities, suggests that the observed distribution patterns are not a product of pupal cannibalism, but a result of larval migration to regions of low larval density just prior to pupation

The theoretical work of Gurney & Nisbet (1985) predicted that when larval competition is expressed as density-dependent larval mortality or larval stage duration, populations should show limit cycles with periods slightly in excess of the species maturation period, while if larval competition is expressed as reduced adult fecundity, populations should cycle with periods greater than twice the maturation delay Mertz (1969) and Bellows (1982) showed that discrete-generation population cycles (limit cycles with periods close to the maturation period) may be produced when strongly asymmetric inter-stage cannibalism is present.

Thus, three density-dependent processes occurring in single-species populations of C cautella are predicted to separate generations, and therefore produce discrete generations: cannibalism, density-dependent larval mortality and larval stage duration. It appears that only one delayed density-dependent process is occurring that would be predicted to counter-act the appearance of discrete generations: reduced adult fecundity and longevity as a result of larval competition for food. The results of the long-term single-species population experiments suggest that the dominant regulatory factors are the direct density-dependent processes of larval mortality, stage duration and cannibalism Assessment of the relative importance of cannibalism versus larval mortality and stage duration, as well as the effects of larval competition on adult fecundity, as determinants of the observed behaviour of these single-species populations requires further experimental and theoretical work. Given the technical difficulties that would arise in undertaking further empirical investigations, it would be more advantageous to formulate a mathematical population model which incorporates the observed density-dependent processes.

The mathematical model formulated in Chap. 4 to describe the observed effects of larval competition represents a major step in the construction of such a population model. The cohort model of larval competition succeeded in capturing the essential effects of larval density on the rate of food utilization, larval survival, stage duration and weight at pupation for both sexes. The main features of the model were a food ingestion rate that was independent of food density, but decreased as a function of larval biomass density (mg larvae/mg food) and a development index that was a linear function of larval weight and age The dependency of larval food ingestion rates on larval biomass density is thought to reflect responses by the larvae to by-products released while feeding. It is unknown whether these by-products are specific compounds released in order to promote larval dispersal, as has been suggested for the compounds released from larval mandibular glands (Corbet 1971) or are specific or non-specific compounds released with the faeces It is thought that the same phenomena account for the movement behaviour of C cautella larvae observed in the long-term population cages.

One the most significant demographic characteristics of V. canescens is the dependence of parasitoid larval developmental rate on host larval age. The arrested development of parasitoid larvae in non-final instar hosts is the most important factor operating to synchronize parasitoid development with that of its host Parasitoid attack rates were found to depend on host larval age, and probably reflect the way in which parasitoid searching efficiency depends on host size Parasitoid oviposition was found to cause substantial mortality of 2nd instar hosts, this mortality is probably due to physical damage resulting from attempted oviposition by the wasp Further experimental work is needed to more precisely quantify this mortality. It is likely that all larval instars are susceptible to oviposition-induced mortality (Simmonds 1943) and that the actual rates of mortality are a function of larval size (weight) and the number of wounds received, where the probability of a larvae being attacked increases as it grows, as does the number of wounds required to kill the larva. This parasitoid-induced host mortality may have a greater impact on parasitoid populations than on host populations, representing an important source of parasitoid larval mortality as a result of the deaths of infected larvae.

The theoretical work of Auslander, Oster & Huffaker (1974) has shown how a parasitoid with the appropriate characteristics may alter the age structure of the host population to an extent sufficient to produce total generation separation (discrete generations) of the host population This effect is caused and reinforced by the parasitoid infecting either very early or very late larvae in a given host generation. While not in any way detracting from this important finding, the applicability of the model's predictions to host-parasitoid systems involving a stored-products moth and V. canescens cannot be adequately assessed. Although the model was inspired by the A kuehniella - V. canescens host-parasitoid system, it is a complicated simulation model incorporating a number of density-dependent factors such as density-dependent host larval mortality, stage duration and imago fecundity as well as variable developmental times. The model was formulated in a very ad hoc manner, and is far more complicated than is justified from the very incomplete knowledge of the host's biology. In addition while recognizing the dependence of parasitoid larval development on host larval age, it is not at all clear that this age dependency was incorporated in a manner that would result in the sychronization of host and parasitoid life cycles that is known to occur.

Given that it has been shown that discrete generations may result from events occurring within the host population itself, independent of any outside influences, it is impossible to determine the exact influence of the parasitoid on the behaviour of stored-products Lepidoptera laboratory populations. Further empirical and theoretical work is needed to clarify the impact of the parasitoid on the age structure of host populations. Formulation of mathematical models describing this host-parasitoid system could proceed in two directions. The first course would be to follow convention and develop a simulation model which assumes that the parasitoid is the only potential regulating factor present; that is, in the absence of the parasitoid the host population grows exponentially. The results of the long-term host-parasitoid experiments, with their low larval densities, together with the predictions of the cohort model of larval competition, suggest that this would be a reasonable first approximation. Such a model would enable assessment of the impact of the parasitoid on the age structure of the host

population in the absence of the significant effects of host larval competition on the age structure of the host populations. However, an assumption of no density dependence would be unrealistic for populations where host refuges are provided. The experimental results suggest that large areas of host refuge are required to achieve stable host-parasitoid co-existence, and that the inclusion of a refuge will result in higher equilibrium larval population densities, thereby increasing the effects of larval competition.

The second course would be the inclusion of the parasitoid in a population model of host population growth based on the cohort model of larval competition Such a model would allow the assessment of the relative contributions of larval competition and the parasitoid in modifying the age structure of the host population

While the empirical work presented in this study has provided the base and illustrated the need for population models of a more 'tactical' nature (May 1974) it has also suggested two more general 'strategic' models that appear to be worthy of future investigation. The first of these 'strategic' models is illustrated by means of a flow chart in Fig. 7.1 and presented in slightly more detail in Appendix M7.1. The model is inspired by the observed dependency of parasitoid developmental rates on host larval age, which serves to synchronize the life cycles of host and parasitoid. Such life cycle synchronization is implicit in the Nicholson-Bailey type discrete-time host-parasitoid models (see Hassell 1978 for details of the N-B models and their properties). The model illustrated in Fig. 7.1 captures the synchronization of host-parasitoid life cycles in a continuous-time model formulated using a delay-differential equation approach and is very similar to the N-B model. While this model is amenable to more formal analysis, preliminary numerical investigations suggest that the model is capable of showing stable limit-cycle behaviour (Fig. 7.2), a property entirely absent from the Nicholson-Bailey model.

The second more general model was suggested by the interaction between the refuge effect and larval movement behaviour observed in the long-term host-parasitoid population experiments. Most models concerning the 'host refuge' phenomenon have investigated the effect of protecting a fixed fraction or a fixed number of hosts in of the host population

Figure 7.1. A flow chart illustrating a continuous-time model of a host-parasitoid association with synchronous host and parasitoid life cycles. Further details of the model are presented in App. M7.1.

R_L - rate of recruitment of host larvae

R_{DP} - rate of recruitment of developing parasitoids

R_{HP} - rate of recruitment of host pupae

R_P - rate of recruitment of adult parasitoids

R_H - rate of recruitment of adult hosts

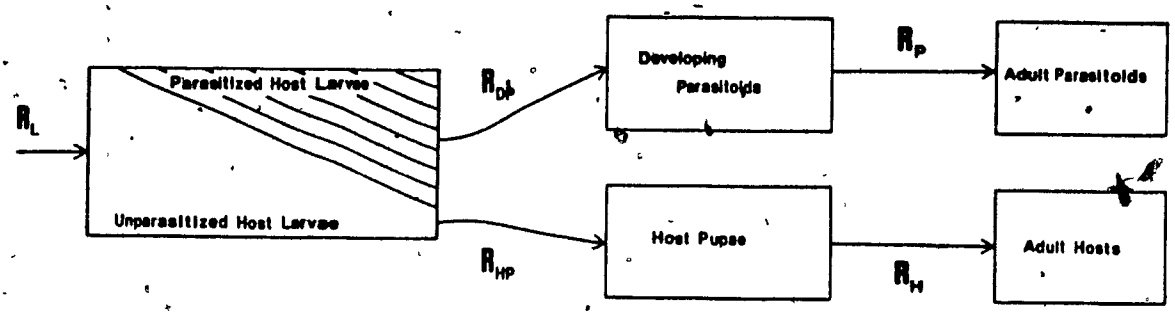
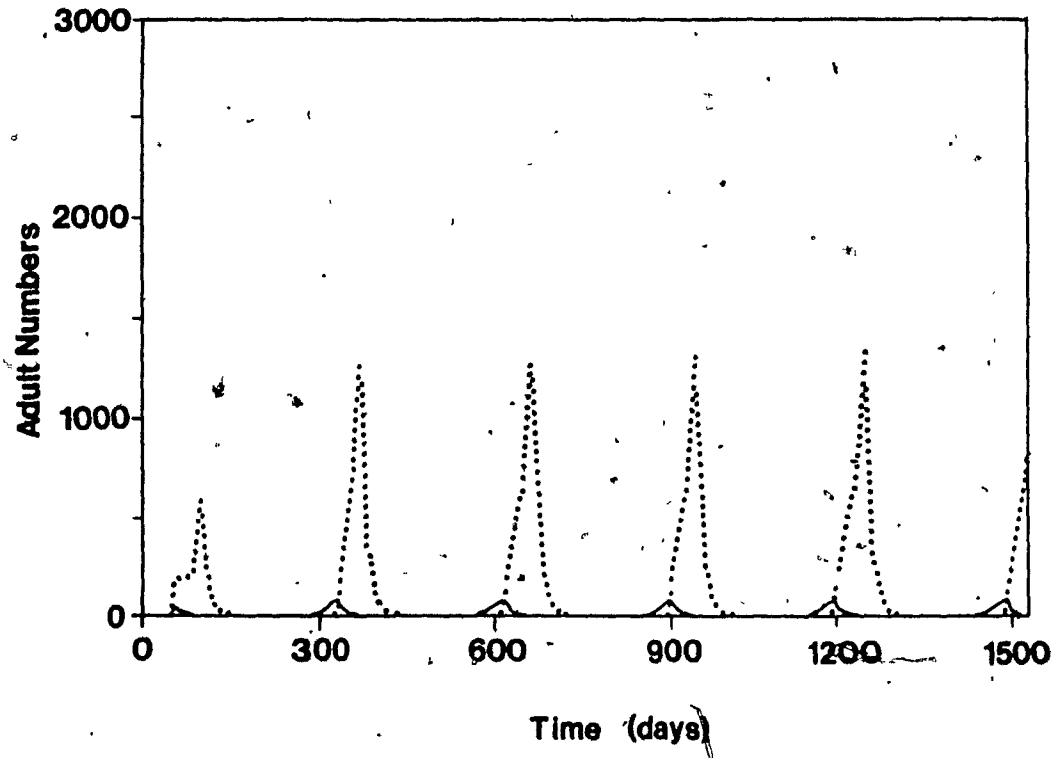

R_L
Parasitized Host Larvae
Unparasitized Host Larvae
R_{DP}
R_{HP}
Developing Parasitoids
Host Pupae
R_P
R_H
Adult Parasitoids
Adult Hosts

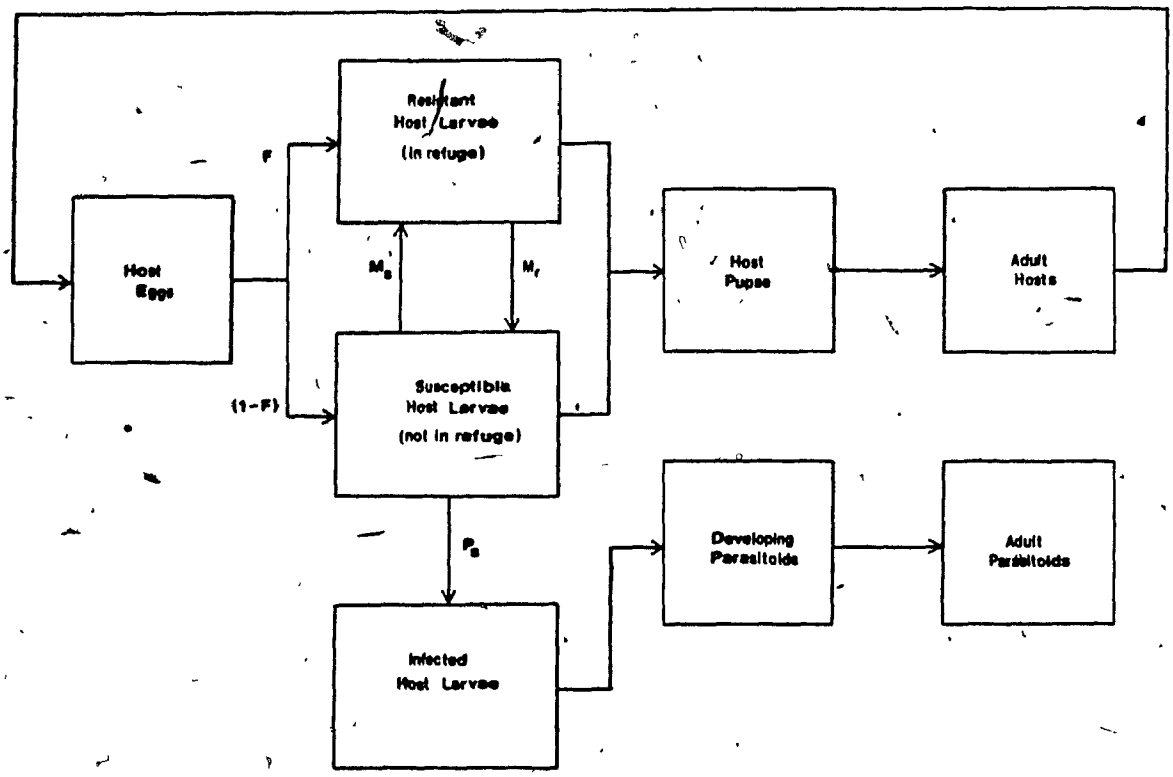
Figure 7.2. An example of a numerical solution of the model presented in Fig. 7.1. Parameter values are presented in App. M7.1. Solid line represents the host population and dotted line represents the parasitoid population.


3000
2000
1000
0
Adult Numbers
0
300
600
900
1200
1500
Time (days)

(Hassell 1978). The model illustrated by means of a flow chart in Fig. 7.3 describes the refuge effect in a more dynamic manner, where individuals of the susceptible host stage are protected from infection depending upon their movement behaviour. Using the C. cautella-V. canescens system as an example, there is a population cage where a certain fraction of the food units are provided with protective cover Host eggs are laid in the refuge areas or non-refuge areas, with the proportion of eggs (F) laid in these two areas being the same as the fraction of food units provided with protective cover. These eggs hatch and three class of host larvae exist, uninfected larvae either in the refuge (resistant larvae), or not in a refuge (susceptible larvae), and infected larvae. The critical rates determining the numbers of larvae in each of these classes are the rate of parasitism (P_s), and the rates of diffusion of the larvae between susceptible and resistant classes (M_s and M_r) as determined by the movement behaviour of the host larvae. While this model has some similarities to the microparasite models of Anderson & May (1980), in their models susceptible hosts can only become resistant following recovery from infection. In the model presented in Fig. 7.3 infected hosts never recover from infection, but susceptible hosts can become resistant by moving into a refuge area.

In conclusion the experimental work and the cohort model of larval competition presented in this thesis provides a very sound empirical basis for the development of population models describing the single-species dynamics and host-parasitoid dynamics of the C. cautella-V. canescens host-parasitoid association.

Figure 7.3. A flow chart illustrating a host-parasitoid system which incorporates a dynamic host-refuge effect. The critical rates are those describing the movement of host larvae between the various classes of larvae. These are the rates of diffusion between the susceptible and resistant classes (M_s and M_r) and the rate of larval parasitism (P_s).


Resistant
Host Larvae
(in refuge)
F
Host
Eggs
M_s
M_r
Host
Pupae
Adult
Hosts
Susceptible
Host Larvae
(not in refuge)
(1-F)
P_s
Developing
Parasitoids
Adult
Parasitoids
Infected
Host Larvae

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APPENDICES

APPENDIX D3.1

Egg hatching in Cadra cautella. Age-dependent egg hatching (A), and effect of imago age (B) and density (C) on proportion of viable C. cautella eggs produced.

A	AGE	PROPORTION OF UNHATCHED EGGS[1]
	0.00	1.000
	0.19	1.000
	0.69	1.000
	1.19	1.000
	1.69	1.000
	2.19	1.000
	2.72	0.982
	3.15	0.893
	3.31	0.689
	3.45	0.424
	3.56	0.212
	3.82	0.033
	4.17	0.000

B	AGE	N^2	PROPORTION HATCHING	S.D.
	1	30	0.822	0.278
	2	106	0.797	0.214
	3	87	0.734	0.237
	4	61	0.627	0.333
	5	52	0.561	0.298
	6	33	0.594	0.317
	7	24	0.438	0.273
	8	11	0.250	0.209

C	DENSITY	N^2	PROPORTION HATCHING	S.D.
	1	58	0.645	0.273
	10	63	0.593	0.321
	25	59	0.658	0.298
	50	52	0.655	0.310
	75	58	0.660	0.326
	100	59	0.786	0.215
	150	31	0.753	0.315
	200	31	0.634	0.328

[1] N = 1676 eggs

[2] Number of samples with 20 eggs per sample

APPENDIX D3.2

Effect of initial egg density on Cadra cautella age at imaginal emergence (days).

DENSITY[1]	FEMALES			MALES		
	N	MEAN	S.D.	N	MEAN	S.D.
1	131	34.3	2.2	115	35 4	2.3
10	195	44.1	5.7	209	47.3	6.1
25	294	50.4	6.8	354	52.5	6.5
50	262	52.6	8.2	288	52.9	8-3
75	250	52.9	9.0	275	52.5	7.5
100	202	57.1	7.1	327	58.2	5 9
150	136	59.4	9.9	138	60.9	9.2
200	130	59.1	10.3	114	61.5	9.3

[1] Number of eggs per 1.7 g food

APPENDIX D3.3

Effect of initial egg density on number of Cadra cautella imagos emerging

DENSITY[1]	MALES			FEMALES		
	N	MEAN	S.D.	N	MEAN	S.D.
1	288	0.45	-	288	0.40	-
10	60	3.15	2.05	60	3.58	1.81
25	60	4.90	2.76	60	5.90	2.98
50	90	2.90	2.86	90	3.31	3.50
75	90	2.63	2.33	90	2.90	3.00
100	90	2.27	2.21	90	3.67	3.62
150	149	0.89	1.44	149	0.94	1.66
200	135	0.96	1 43	135	0.87	1.40

[1] Number of eggs per 1.7 g food

APPENDIX D3.5

Effect of initial egg density on stage duration of Cadra cautella.

Development of Cadra cautella from initial egg density of 1 egg per 1.7 g food.

AGE	EGGS	L_1	L_2	L_3	L_4	L_5	PUPAE	ADULTS
1	57							
2	57							
3	57	0						
4	9	48						
5	0	57						
6		56	0					
7		54	1					
8		15	38					
9		1	55	0				
10		1	47	5				
11		0	9	48				
12			1	56	0			
13			0	34	21			
14				9	47			
15				2	49	0		
16				2	33	18		
17				0	13	40		
18					8	46		
19					3	52	0	
21					0	36	19	
23						12	43	
25						2	53	0
27						2	50	2
29						0	17	38
31							8	46
33							1	56
35							0	55

... continued ...

APPENDIX D3.5 (continued)

Development of *Cadra cautella* from initial egg density of 10 eggs per 1 7 g food.

AGE	EGGS	L_1	L_2	L_3	L_4	L_5	PUPAE	ADULTS
1	93							
2	93							
3	93	0						
4	15	78						
5	0	93	0					
6		93	1					
7		91	2					
8		47	36					
9		5	80	0				
10		1	79	2				
11		0	55	27	0			
12			11	71	1			
13			3	76	4			
14			0	42	40			
15				21	64	0		
16				1	80	2		
17				1	61	19		
19				1	23	60		
21				0	6	78	0	
23					0	69	11	
25						61	27	
27						20	61	0
29						9	72	3
31						6	68	13
33						2	42	39
35						0	27	53
37							4	75
39							0	80

... continued ...

APPENDIX D3.5 (continued)

Development of *Cadra cautella* from initial egg density of 25 eggs per 1.7 g food.

AGE	EGGS	L_1	L_2	L_3	L_4	L_5	PUPAE	ADULTS
1	221							
2	221	0						
3	219	2						
4	30	186						
5	0	222						
6		224						
7		218	0					
8		83	140					
9		5	206					
10		3	222	0				
11		0	50	170				
12			4	202	0			
13			0	191	14			
14				71	134			
15				14	208	0		
16				7	216	6		
17				1	167	50		
18				0	89	126		
20					8	208		
22					2	221	0	
24					1	203	8	
26					1	122	58	
28					0	93	84	0
30						84	88	4
32						42	76	44
34						28	53	68
36						16	39	108
38						8	34	96
40						0	35	130
42							31	134
44							16	151
46							7	159
48							6	158
50							4	161
52							0	165

... continued ...

APPENDIX D3.5 (continued)

Development of Cadra cautella from initial egg density of 50 eggs per 1.7 g food.

AGE	EGGS	L_1	L_2	L_3	L_4	L_5	PUPAE	ADULTS
1	231							
2	231							
3	229	2						
4	37	194						
5	0	231						
6		229	0					
7		205	2					
8		124	92					
9		32	161					
10		16	201	0				
11		0	133	67				
12			33	171	0			
13			13	202	3			
14			4	125	53			
15			0	91	96			
16				38	163			
17				12	179	0		
18				11	178	3		
19				10	176	8		
20				6	141	41		
21				2	107	71		
24				1	50	132		
25				0	36	139		
27					26	153	0	
29					18	109	13	
31					2	83	26	
33					1	80	30	
35					0	60	35	2
37						25	41	4
39						16	43	13
41						14	44	21
43						7	35	29
45						3	20	56
57						2	11	66
59						1	8	61
51						0	7	60
53							6	60
55							5	61
57							1	62

... continued ...

APPENDIX D3.5 (continued)

Development of Cadra cautella from initial egg density of 75 eggs per 1.7 g food.

AGE	EGGS	L_1	L_2	L_3	L_4	L_5	PUPAE	ADULTS
1	345							
2	345							
3	341	4						
4	51	296						
5	0	345	0					
6		345	1					
7		332	2					
8		104	195					
9		23	295					
10		11	294	0				
11		0	185	131				
12			66	253	0			
13			18	272	4			
14			7	262	40			
15			0	152	142			
16				127	199			
17				72	215	0		
18				59	234	4		
19				47	254	8		
20				31	229	31		
21				15	204	54		
22				14	196	66		
23				13	189	75		
24				7	146	116		
27				0	53	200		
29					61	209		
31					23	198	0	
33					12	154	7	
35					7	128	20	
37					4	102	33	0
39					0	80	37	3
41						62	33	9
43						50	30	11
45						37	27	13
47						16	29	36
49						5	24	51
51						4	12	57
53						2	6	64
55						0	3	74

... continued ...

APPENDIX D3.5 (continued)

Development of Cadra cautella from initial egg density of 100 eggs per 1.7 g food.

AGE	EGGS	L_1	L_2	L_3	L_4	L_5	PUPAE	ADULTS
1	450							
2	450							
3	446	4						
4	72	378						
5	0	442						
6		450	0					
7		432	1					
8		174	232					
9		22	419	0				
10		7	385	24				
11		4	127	259				
12		0	44	361	0			
13			16	376	3			
14			6	378	8			
15			2	263	110			
16			0	80	289			
17				30	361	0		
18				17	343	12		
19				5	326	25		
21				3	300	82		
23				0	248	70		
25					158	132		
27					113	170		
29					67	219		
31					62	201		
33					51	190		
35					9	232	0	
37					5	155	2	
39					3	114	3	
41					0	128	5	
43						94	9	0
45						60	14	1
47						41	12	2
49						22	11	2
51						13	13	9
53						4	14	17
55						1	8	21
57						0	4	26
59							3	32
61							2	35
63							1	36

APPENDIX D3.6

Effect of initial egg density on mortality of Cadra cautella pupae.

DENSITY[1]	N[2]	MEAN MORTALITY[3]	S.D.
2	27	0.0257	0.1334
4	29	0.0239	0.1287
6	30	0.0000	0.0000
8	30	0.0074	0.0407
10	30	0.0187	0.0576
12	30	0.0199	0.0455
14	30	0.0200	0.0461
18	30	0.0252	0.0433
22	30	0.0334	0.0864
26	30	0.0460	0.0624
30	30	0.0442	0.0790
40	29	0.1193	0.1769
60	24	0.0416	0.0491
80	23	0.0279	0.0558
100	24	0.0600	0.0730

1 Number of eggs per g food

2 Number of vials

3 K value

APPENDIX D3.7

Effect of initial egg density on survival characteristics of Cadra cautella imagos.

Effect of initial density of Cadra cautella eggs on imago longevity.

AGE	PROPORTION OF MALE IMAGOS ALIVE							
DENSITY[1]:	1	10	25	50	75	100	150	200
0	1.00	1.00	1.00	1.00	1.00	1.00	1 00	1.00
1	1.00	0,99	1.00	1.00	0.98	0.97	0.95	0.95
2	1.00	0.99	0.99	0.99	0.93	0 95	0.95	0.90
3	1.00	0.99	0.95	0.98	0.90	0.92	0.93	0.82
4	1.00	0.98	0.93	0.92	0.85	0.91	0.88	0.73
5	1.00	0.98	0.89	0.90	0.80	0.89	0.85	0.67
6	0.99	0.95	0.87	0.85	0.75	0.85	0 76	0.57
7	0.96	0.94	0.83	0.77	0.64	0.72	0.66	0.43
8	0.94	0.91	0.78	0.68	0.56	0.64	0 54	0.27
9	0.81	0.88	0.71	0.58	0.41	0 49	0.39	0.17
10	0.65	0.83	0.61	0.47	0.34	0 39	0.29	0.13
11	0.49	0.74	0.53	0.34	0.26	0.25	0.19	0.08
12	0.38	0.57	0.37	0.22	0.16	0.18	0.15	0.02
13	0.32	0.43	0.23	0.12	0.11	0.09	0.14	0 02
14	0.24	0.22	0.15	0.05	0 06	0.05	0.05	0.00
15	0.13	0.07	0.06	0.02	0.04	0.03	0.03	0 00
16	0.05	0.03	0.03	0.01	0.01	0 02	0.00	0.00
17	0.04	0.01	0.01	0.00	0.01	0.01	0.00	0.00
18	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	PROPORTION OF FEMALE IMAGOS ALIVE							
0	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
1	1.00	0.99	0.98	1.00	0.97	1.00	0.98	0.97
2	1.00	0.99	0.98	0.97	0.95	0.99	0.95	0.95
3	1.00	0.99	0.98	0.95	0.91	0.93	0.95	0.78
4	0.98	0.99	0.95	0.89	0.88	0.88	0.78	0.55
5	0.96	0.94	0.87	0.80	0.71	0.73	0.59	0.35
6	0.86	0.87	0.79	0.72	0.55	0.57	0.46	0.20
7	0.62	0.76	0.63	0.59	0.41	0.30	0.27	0.15
8	0.51	0.62	0 42	0.40	0.21	0.21	0.22	0.12
9	0.36	0.49	0.27	0.24	0.14	0.12	0.17	0.05
10	0.16	0.37	0.18	0.09	0.05	0.05	0.10	0.00
11	0.11	0.25	0.06	0.04	0.03	0.02	0.10	0.00
12	0.06	0.12	0.05	0.03	0.02	0.02	0.07	0.00
13	0.04	0.05	0.03	0.01	0.02	0.02	0.02	0.00
14	0.02	0.02	0.00	0.00	0.02	0.01	0.00	0.00
15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

[1] Number of eggs per 1.7 g food

... continued ...

APPENDIX D3.7 (continued)

Effect of initial density of *Cadra cautella* eggs on imago life span.

SEX	DENSITY[1]	N[2]	AVERAGE LIFE SPAN (days)	
			MEAN	S D.
MALE	1	79	11.99	2 80
	10	125	12 53	2.74
	25	116	10.93	3 56
	50	118	9.89	3.30
	75	104	8.81	3.76
	100	131	9.37	3.47
	150	59	8.76	3.55
	200	60	6.75	3 12
FEMALE	1	55	8.67	2.25
	10	84	9.44	2.65
	25	62	8.21	2.44
	50	75	7.73	2.63
	75	58	6.86	2.56
	100	86	6.86	2.29
	150	41	6.66	2.91
	200	40	5.12	2.16

[1] Number of eggs per 1.7 g food

[2] Number of containers

APPENDIX D3.8

Effect of initial egg density on reproductive characteristics of Cadra cautella imagos.

Effect of initial density of Cadra cautella eggs on average daily rate of egg production.

DENSITY[1]:	1		10		25		50	
AGE	MEAN	S.D.	MEAN	S.D	MEAN	S.D.	MEAN	S.D.
1	18.5	48.5	11.7	29.9	10.0	28.6	7.9	22.4
2	95.5	76.1	54.6	63.6	54.1	59.1	44.6	51.9
3	70.1	57.7	51.4	47.2	51.7	48.6	33.7	36.6
4	53.9	46.3	46.1	40.6	50.7	47.5	17.1	20 0
5	31.1	36.2	24.7	25.6	27.6	28.7	14.1	26.8
6	15.5	21.5	22.3	25.5	15.9	19.1	5.4	11.5
7	15.6	20.9	13.9	17.2	11.0	12.7	5.8	11.3
8	8.7	13.1	10.1	16.1	6.4	10.9	1.4	2.7
9	3.3	6.0	4.6	7.3	7.5	21.9	1.3	3.3
10	1.9	4.7	4.6	7.2	2,7	5.3	2.8	5.5
11	3.3	4.9	3.5	7.6	0.4	1.2	13.7	19.5
12	3.4	7.6	1.2	2.4	11.0	12.8	0.0	0.0
13	1.3	2.3	2.1	4.5	4.7	5,7	0.0	0.0
14	0.0	0.0	0.0	0.0	0.0	-	0.0	0.0
15	0.0	-	0.0	0.0	-	-	0.0	-

DENSITY[1]:	75		100		150		200	
AGE	MEAN	S.D.	MEAN	S.D	MEAN	S.D.	MEAN	S.D.
1	2.7	13.9	17.0	36.2	5.7	18.1	5.6	18.5
2	27.3	35.3	39.0	41.3	27.6	38.0	24.5	31.9
3	30.6	35.3	30.6	34.2	23.6	23.1	13.2	18.8
4	20.5	29.3	20.5	24.1	14.6	20.3	7.7	10.0
5	17.0	25.9	12.2	20.0	8.8	16.6	7.6	12.8
6	8.5	15.6	9.1	12.2	2.9	7.7	5.4	12.4
7	10.9	14.5	5.2	10.9	2.9	7.4	0.4	1.3
8	4.5	8.1	5.1	12.6	3.9	6.6	3.1	5.3
9	2.8	8.7	9.8	27.4	0.1	0.3	0.2	0.4
10	5.9	8.8	0.7	1.1	1.9	5.3	1.0	1.7
11	13.3	23.1	5.0	10.6	2.2	4.9	0.0	-
12	0.0	0.0	0.0	0.0	3.6	8.0	0.0	-
13	0.0	-	2.0	2.8	0.8	1.5	0.0	-
14	0.0	-	6.0	8.5	0.0	0.0	0.0	-
15	0.0	-	56.0	-	-	-	0.0	-

[1] Number of eggs per 1.7 g food

... continued ...

APPENDIX D3.8 (continued)

Effect of initial density of Cadra cautella eggs on age at which 50% of eggs have been laid.

DENSITY[1]	N[2]	AGE (days)	
		MEAN	S.D.
1	54	3.56	1.40
10	82	4.09	1.44
25	63	3.74	1.15
50	66	3.01	1.33
75	56	3.78	1.55
100	82	3.35	1.71
150	37	3.56	1.65
200	36	3.15	1.75

Effect of larval Cadra cautella density of imago lifetime fecundity.

DENSITY[1]	N[2]	TOTAL LIFETIME FECUNDITY	
		MEAN	S.D.
1	55	305.3	113.5
10	82	236.9	93.9
25	64	222.2	92.7
50	75	111.9	88.1
75	60	107.5	72.3
100	85	131.2	80.7
150	41	81.0	64.6
200	41	55.0	54.3

1 Number of eggs per 1.7 g food.

2 Number of containers (one female per container)

APPENDIX D3.9

Effect of imago density on survival characteristics of Cadra cautella imagos.

Effect of density of Cadra cautella adults on proportion of imagos alive.

DENSITY[1]:	2		4		6		8		10		12		20	
AGE	F	M	F	M	F	M	F	M	F	M	F	M	F	M
0	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
1	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1 00	1.00
2	1.00	1.00	1.00	0.97	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1 00	1.00
3	0.93	1.00	0.97	0.97	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1 00	1.00
4	0.93	1.00	0.97	0.97	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	0 99	1.00
5	0.86	1.00	0.91	0.97	1.00	1.00	1.00	1.00	1 00	1.00	1.00	0 98	0.96	1.00
6	0.72	1.00	0.81	0.91	0.94	1.00	1.00	0.98	1.00	0.98	0.97	0 98	0.89	1 00
7	0.62	0.97	0.69	0.91	0.81	1 00	0.91	0.98	0.96	0.98	0 92	0.98	0.64	0 94
8	0.34	0.97	0.47	0.91	0.55	0.93	0.54	0.95	0.80	0.98	0.62	0.98	0.39	0.80
9	0.07	0.93	0.19	0.84	0.26	0.93	0.28	0.90	0.57	0.93	0.31	0.95	0.16	0 65
10	0.07	0.83	0.06	0.69	0.13	0.83	0.15	0.81	0.28	0.89	0.20	0.86	0 08	0.49
11	0.03	0.67	0.06	0.05	0.03	0.72	0.09	0.71	0.13	0.71	0.12	0.75	0 05	0.29
12	0.00	0.53	0.03	0.38	0.03	0.55	0.07	0.50	0.00	0.51	0.09	0.50	0.02	0.10
13	0.00	0.27	0.03	0.22	0.00	0.41	0.02	0.29	0.00	0.24	0.06	0.36	0.01	0.03
14	0.00	0.07	0.00	0.00	0.00	0.28	0.00	0.10	0.00	0.09	0.06	0 25	0.01	0.02
15	0.00	0.03	0.00	0.00	0.00	0.10	0.00	0.02	0.00	0.06	0.05	0.12	0.01	0.01
16	0.00	0.03	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.02	0.05	0.01	0 00
17	0.00	0.00	0.00	0 00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00
18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Effect of density of Cadra cautella adults on imago life span.

SEX	DENSITY[1]	N[2]	AVERAGE LIFE SPAN (days)	
			MEAN	S.D.
MALE	2	30	12.30	1.99
	4	32	11.22	2.72
	6	29	12.79	2.32
	8	42	12.24	2.05
	10	55	12.36	1.86
	12	56	12.73	2.45
	20	103	10.32	1.87
FEMALE	2	28	7.75	1.86
	4	32	8.19	2.09
	6	31	8.74	1.55
	8	46	9.07	1.61
	10	54	9.74	1.36
	12	64	9.44	2.22
	20	110	8.21	1.75

[1] Number of imagos per container

[2] Number of containers

APPENDIX D3.10

Effect of imago density on reproductive characteristics of Cadra cautella.

Effect on average daily rate of egg production.

AGE	ADULT DENSITY[1]						
	2	4	6	8	10	12	20
1	13.2	28.7	16.4	11.5	14.4	24.2	17.9
2	108.3	104.1	125.4	77.0	46.0	79.7	87.5
3	89.2	101.0	88 3	127.5	88.4	11.7	89 8
4	41.7	54.4	51.5	61.0	76.8	50 4	51 3
5	27.5	33.6	29.2	40.9	46.7	46 4	24 0
6	17.6	25.8	19.9	23.7	31.9	23.8	15 4
7	5.2	5.6	18.6	18.4	16.4	14 0	10.6
8	6.7	12.9	10.3	8.7	12.4	9.4	3 7
9	6.0	5 8	10.5	2.0	4.6	3.2	3.9
10	10.0	2.0	43.0	7.4	8.5	5 8	6 1
11	48.0	0.0	3.0	1.0	2.7	0.6	1.0
12	0.0	0.0	0.0	0.0	0.0	7.5	0.0

Effect on age at which 50% of eggs have been laid.

DENSITY[1]	F[2]	N[3]	MEAN	S.D.
2	28	28	3.22	1.02
4	32	16	3.20	0 48
6	31	10	3.25	0.50
8	46	11	3.57	0.32
10	54	11	4.03	0.30
12	64	10	3.53	0.34
20	110	10	3.21	0 44

Effect on imago life-time fecundity.

DENSITY[1]	F[2]	N[3]	MEAN	S.D.
2	28	28	294.4	93.4
4	32	16	345.9	61.1
6	31	10	341.4	67.0
8	46	11	363.3	37.6
10	54	11	333.6	59.5
12	64	10	362.5	47.3
20	110	10	318.1	37.6

[1] Number of imagos (female and male) per container

[2] Total number of females in all containers

[3] Number of containers

APPENDIX D3.11

Effect of feeding on survival and reproductive characteristics of *Cadra cautella* imagos.

Effect of feeding on proportion of imagos alive.

	UNFED		FED	
AGE	MALES	FEMALES	MALES	FEMALES
0	1.00	1.00	1.00	1.00
1	1 00	1.00	1.00	1.00
2	1.00	1.00	1 00	1.00
3	1.00	1.00	1.00	1.00
4	1.00	1.00	1.00	1.00
5	1.00	0.90	1.00	0.92
6	0.96	0.70	0.83	0.76
7	0.85	0.30	0.78	0.68
8	0.70	0 07	0 61	0.56
9	0.59	0.00	0 57	0.36
10	0.37	0.00	0.22	0.20
11	0.22	0.00	0.17	0.04
12	0.04	0.00	0.09	0.04
13	0.04	0.00	0.09	0.04
14	0,00	0.00	0.09	0.00
15	0.00	0.00	0.00	0.00

Effect of feeding on average daily egg production

	UNFED		FED	
AGE	N	MEAN	N	MEAN
1	30	56.3	25	134.7
2	30	111.8	25	132.1
3	30	82.5	25	87.0
4	30	49.8	25	53.4
5	27	37.6	23	36.3
6	21	8.4	19	31.8
7	9	4.8	17	16.8
8	2	0.0	14	9.5
9	0	-	9	2.1
10	0	-	5	6.6

APPENDIX D3.13

Egg cannibalism by larvae of Cadra cautella.

Functional Form (Eq 3.1): $N_e = N_t [1 - \exp(-a_e L_s T)]$

Non-linear Least Squares Summary Statistics

L_1 on Egg	Source	df	SS	MS
	Regression	1	20601.670889	20601.670889
	Residual	58	10393.329111	179.195330
	Uncorrected Total	59	30995 000000	
	Corrected Total	58	11626 169492	
	Parameter	Estimate		S.E.
	a_e	0.0004547204		0.000055131032
L_2 on Egg	Source	df	SS	MS
	Regression	1	67458.741549	67458.741549
	Residual	59	4144.258451	70.241669
	Uncorrected Total	60	71603 000000	
	Corrected Total	59	19446 983333	
	Parameter	Estimate		S.E.
	a_e	0.001558601		0 000096975579
L_3 on Egg	Source	df	SS	MS
	Regression	1	82788.782130	82788.782130
	Residual	59	6090.217870	103 224032
	Uncorrected Total	60	88879.000000	
	Corrected Total	59	22678.183333	
	Parameter	Estimate		S.E
	a_e	0.0039671897		0.00028449488
L_4 on Egg	Source	df	SS	MS
	Regression	1	14062.463853	14062.463853
	Residual	50	2841.536147	56.830723
	Uncorrected Total	51	16904.000000	
	Corrected Total	50	5278.509804	
	Parameter	Estimate		S.E.
	a_e	0.0047969061		0.00038294613
L_5 on Egg	Source	df	SS	MS
	Regression	1	3137.6084552	3137.6084552
	Residual	49	2215.3915448	45.2120723
	Uncorrected Total	50	5353.0000000	
	Corrected Total	49	2232.5000000	
	Parameter	Estimate		S.E.
	a_e	0.0044149409		0.00057631353

APPENDIX D3.14

Cannibalism of 1st instars by larvae of Cadra cautella.

Functional Form (~~Eq.~~ 3.2): $N_{na} = N_t \exp(-a_1 L_g T)$

Non-linear Least Squares Summary Statistics

2nd on 1st	Source	df	SS	MS
	Regression	2	61837.325735	30918 662867
	Residual	28	1284.674265	45.881224
	Uncorrected Total	30	63122.000000	
	Corrected Total	29	1830.800000	
	Parameter	Estimate		S.E.
	a_1	0.00492415		0 0014010944
	N_t	51.69635537		2.2626685862
3rd on 1st	Source	df	SS	MS
	Regression	2	62093.566645	31046.783322
	Residual	27	521.433355	19.312346
	Uncorrected Total	29	62615 000000	
	Corrected Total	28	974.689655	
	Parameter	Estimate		S.E.
	a_1	0.01059723		0.0022174562
	N_t	51.92634441		1.4895206924
4th on 1st	Source	df	SS	MS
	Regression	2	68308.856079	34154.428040
	Residual	28	987.143921	35.255140
	Uncorrected Total	30	69296.000000	
	Corrected Total	29	1323.200000	
	Parameter	Estimate		S.E.
	a_1	0.01405997		0.0045803044
	N_t	53.21559318		2.1739295832
5th on 1st	Source	df	SS	MS
	Regression	2	77196.410008	38598 205004
	Residual	27	831.589992	30.799629
	Uncorrected Total	29	78028.000000	
	Corrected Total	28	855.034483	
	Parameter	Estimate		S.E.
	a_1	0.00480601		0.0055059651
	N_t	52.87140241		1.8042873635

APPENDIX D4.2

Effect of initial egg density on outcome of Cadra cautella cohort experiments.

Effect of initial egg density on larval age at pupation and imago weight at emergence

EGG DENSITY	AGE AT EMERGENCE						WEIGHT AT EMERGENCE					
	MALE			FEMALE			MALE			FEMALE		
	N	MEAN	SD	N	MEAN	SD	N	MEAN	SD	N	MEAN	SD
2	19	26 6	2.7	10	30.0	2.8	6	3 06	0 25	7	4 84	0 29
4	24	25.0	1 4	30	28 0	2.6	4	2 82	0 32	7	5.28	0 58
6	34	25.4	2 1	33	28 0	2.7	6	3 13	0 36	8	5 38	0 45
8	32	26 0	1 9	48	29 8	3.4	6	3.00	0 17	12	5.39	0 51
10	46	26 8	2.6	52	30 8	3.1	8	3.01	0 23	12	5 05	0 30
12	58	25.8	1.8	77	30 5	2.9	5	3.37	0 59	12	5 59	0 72
14	63	27.2	3.2	60	30 9	2.3	10	3.12	0 38	11	5 18	0 70
18	33	30.7	4.5	59	36 4	3.7	12	2.77	0 33	15	4.76	0.59
22	36	29.3	3 7	71	32 9	2 6	12	3.19	0 29	13	4.98	0.49
26	47	33.0	4.4	56	33 4	3.1	16	2.67	0.27	14	4 73	0.50
30	30	43.2	7.4	31	47.0	4.9	14	2.53	0.28	11	3.75	1.17
40	27	40.4	5.3	54	43.5	4.7	15	2.19	0.47	18	3 29	0.78
50	25	48.7	10 1	38	55.1	8 1	13	2.09	0.60	19	2.89	0 61
60	32	45.6	8.7	46	49.2	8.5	20	1.76	0 63	26	2.67	0 89
80	18	40.8	9.4	26	47.3	9.2	13	1.47	0.55	17	1.96	0.92
100	10	44.7	11.1	12	50.6	7.6	9	1.33	0.45	7	1.05	0 24
150	4	37.8	8.5	3	43.2	8.1	4	1.55	0.68	2	1 32	0.39

... continued ...

APPENDIX D4.2 (continued)

Effect of initial egg density on amount of food remaining, total number of larvae pupating, and pupal mortality.

EGG DENSITY	FOOD MEAN	FOOD S.D.	TOTAL MEAN	TOTAL S.D.	KPUPAE[1] MEAN	KPUPAE[1] S.D.
2	0.899	0.066	1.41	0.50	0.032	0.148
4	0.691	0.099	3.57	0.65	0.000	0.000
6	0.577	0.171	4.47	1.41	0.000	0.000
8	0.407	0.152	5.53	1.25	0.057	0.124
10	0.242	0.141	6.80	1.61	0.051	0.095
12	0.107	0.095	9.07	1.53	0.006	0.025
14	0.085	0.120	8.27	1.39	0.012	0.047
18	0.081	0.143	6.47	1.81	0.071	0.135
22	0.007	0.026	7.33	1.92	0.028	0.058
26	0.000	0.000	7.20	1.93	0.041	0.077
30	0.000	0.000	4.71	1.77	0.118	0.224
40	0.000	0.000	5.80	4.11	0.075	0.106
50	0.000	0.000	4.60	1.99	0.087	0.187
60	0.000	0.000	5.53	2.03	0.091	0.184
80	0.000	0.000	3.33	2.47	0.024	0.058
100	0.000	0.000	1.53	1.64	0.000	0.000
150	0.000	0.000	0.53	0.74	0.000	0.000

[1] K-values

APPENDIX D4.3

Effect of food density (fixed volume, varying percent food) on Cadra cautella imago age and weight at emergence.

% FOOD	AGE AT EMERGENCE						WEIGHT AT EMERGENCE					
	MALE			FEMALE			MALE			FEMALE		
	N	MEAN	S.D.	N	MEAN	S.D.	N	MEAN	S D.	N	MEAN	S.D.
1	112	32.9	1.4	72	36.4	2.1	12	3.26	0.36	9	5.66	0.63
2.5	80	32 2	0.9	72	32 6	1.8	10	3 24	0.30	9	6 11	0.56
5	136	31.8	1.0	64	33.1	1.5	17	3.71	0.34	8	6.08	0.58
7.5	88	31.6	0.8	112	33.5	1.8	11	3.65	0.24	14	6.19	0.63
10	72	31.4	0.7	120	32 0	1.1	9	3.72	0.41	15	6.07	0.49
20	104	32.2	0.9	104	35 0	2.5	13	3.80	0 21	13	6 29	0.65
30	96	31.8	0.9	112	32.9	1.5	12	3.65	0.38	14	6 31	0.74
40	88	31.6	1.1	104	33.1	2.4	11	3.26	0.39	13	6 00	0.72
50	96	32.9	2.4	112	32.6	0.7	12	3.58	0.33	14	6.36	0.57
75	144	33.0	1.2	56	34.0	1.1	18	3.67	0.49	7	5.84	0.33
100	104	34.7	1.7	80	36.0	1.4	13	3.62	0.65	10	6.01	0.66

APPENDIX D4.4 & D4.8

Effect of density of larval Cadra cautella on larval growth and survival, and amount of food remaining.

DENSITY	AGE	FOOD		WEIGHT		NUMBER	
		MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
5	12	1.00	0.04	0.22	0.10	4.0	2.0
	14	0.99	0.03	1.08	0.34	4.2	1.0
	16	0.98	0.05	0.95	0.31	2.5	1.3
	18	1.03	0.03	2.90	0.44	2.5	1.9
	20	0.94	0.05	3.70	1.82	2.0	1.6
	22	0.90	0.06	9.90	1.59	3.8	0.5
	24	0.82	0.03	16.97	4.63	3.7	1.2
	26	0.78	0.05	15.20	2.52	6.0	1.7
8	12	1.01	0.02	0.38	0.13	5.8	1.3
	14	1.06	0.05	1.33	0.42	5.5	3.1
	16	1.00	0.01	2.60	0.26	7.3	1.2
	18	0.95	0.03	4.47	0.84	5.7	1.5
	20	0.91	0.08	8.02	1.09	6.5	1.0
	22	0.75	0.06	18.50	4.20	7.0	1.4
	24	0.69	0.05	26.23	1.76	7.3	0.6
	26	0.44	0.05	33.30	5.04	11.3	3.8
12	12	1.00	0.04	0.65	0.13	9.8	1.5
	14	1.00	0.04	1.60	0.14	7.2	1.5
	16	0.97	0.02	4.20	0.42	9.8	1.0
	18	0.91	0.03	6.12	0.79	9.8	2.8
	20	0.93	0.17	10.98	2.12	9.0	1.2
	22	0.66	0.21	22.42	4.46	8.0	1.4
	24	0.60	0.08	30.13	1.55	7.3	1.2
	26	0.42	0.26	38.03	20.17	15.0	4.6
18	12	0.97	0.03	0.92	0.13	12.5	1.9
	14	0.96	0.05	3.15	1.24	14.2	2.2
	16	0.95	0.07	5.00	0.37	13.8	0.5
	18	0.88	0.07	8.32	2.81	14.0	4.2
	20	0.72	0.10	16.15	5.01	15.0	1.4
	22	0.58	0.17	29.45	10.58	12.0	4.7
	24	0.19	0.14	54.57	9.33	18.0	3.6
	26	0.08	0.04	53.87	1.73	25.0	1.7

... continued ...

APPENDIX D4.4 & D4.8 (continued)

DENSITY	AGE	FOOD		WEIGHT		NUMBER	
		MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
26	12	0.96	0.05	1.05	0.31	19.8	1.3
	14	0.96	0.03	3.78	0.57	21.0	3 9
	16	0.97	0.04	5.18	0.77	20.2	3.4
	18	0.81	0.08	11.48	2 98	21.0	2 2
	20	0.66	0.05	20.18	5.14	19.5	0.6
	22	0.46	0.11	34.70	9.06	16.5	5.3
	24	0.16	0.09	51.20	6 70	21 3	0.6
	28	0.05	0.09	66 83	7.62	20.7	5.5
40	12	0.98	0.02	1.88	0.24	28 8	2.5
	14	0.96	0.04	4.20	0.08	30.5	5.9
	16	0.86	0.02	9.12	2 42	29 8	4.6
	18	0.68	0.08	18.38	5 61	27.5	3.5
	20	0.53	0.03	24.80	2 37	31.5	3.4
	22	0.23	0.25	44.72	23.05	26.5	8.5
	24	0.00	0.00	67.33	3.57	28.0	3.6
	29	0.00	0.00	60.77	15.34	31.0	7.2
60	12	0.99	0.02	2.27	0.42	43.7	6.0
	14	0.93	0.03	5.63	0 40	44.7	4.7
	16	0.83	0.02	9.17	1.55	42.3	4.2
	18	0.71	0.06	13.27	3.35	43.3	0.6
	20	0.45	0.10	27.07	6 79	45.0	1.7
	22	0.22	0.12	41.17	3 98	42.3	3.2
	24	0.00	0.00	54.53	7.50	44.7	3.2
	26	0.00	0.00	56.80	6.16	43.7	4.6
	29	0.00	0.00	45.72	24.79	46.2	14.4
73	12	0.92	0.02	3.67	0.67	52.7	2.9
	15	0.85	0.02	10.67	1.26	58.0	5.3
	18	0.57	0.04	24.23	1.47	52.3	2.1
	21	0.26	0.09	36.37	4.68	57.3	4.6
	24	0.00	0.00	51.63	2.08	54.3	3.8
	27	0.00	0.00	67.90	1.58	48.7	3.8
	30	0.00	0.00	61.60	1.28	45.3	13.8
	33	0.00	0.00	51.80	3.46	35.0	4.4
	36	0.00	0.00	47 40	6.50	31.0	7.0
	39	0.00	0.00	37.37	5 20	24.0	3.6
	42	0.00	0.00	26.33	2.49	14.7	4.0
	45	0.00	0.00	11.40	10.02	9.3	7.2

... continued ...

APPENDIX D4.4 & D4.8 (continued)

DENSITY	AGE	FOOD		WEIGHT		NUMBER	
		MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
87	12	0.94	0.03	3.60	0.00	67.0	2.6
	15	0.81	0.01	11.60	0.78	68.0	5.3
	18	0.60	0.02	21.47	0.42	71.0	2.6
	21	0.21	0.08	36.87	5.69	65.3	3.5
	24	0.00	0.00	48.03	6.65	64.3	2.9
	27	0.00	0.00	58.70	2.82	62.7	2.3
	30	0.00	0.00	64.90	5.16	59.3	4.5
	33	0.00	0.00	52.70	6.79	50.0	5.2
	36	0.00	0.00	34.20	24.68	27.3	21.5
	39	0.00	0.00	18.40	24.18	22.1	18.2
	42	0.00	0.00	22.20	16.39	18.3	12.5
	45	0.00	0.00	-	-	11.3	8.1
100	12	0.88	0.01	5.03	1 05	76.0	12.3
	15	0.74	0.07	14.00	1.66	89.0	25.1
	18	0.50	0.07	22.67	3.49	70.3	4.0
	21	0.17	0.10	41.00	9.17	76.3	5.1
	24	0.00	0.00	49.57	1.27	63.3	7.8
	27	0.00	0.00	57.47	3.99	66.7	3.1
	30	0.00	0.00	63.07	4.42	51.3	2.5
	33	0.00	0.00	54.93	5.78	48.3	1.5
	36	0.00	0.00	29.90	18.99	26.7	17.1
	39	0.00	0.00	39.07	4.52	30.0	7.9
	42	0.00	0.00	19.30	12.95	15.3	8.1
	45	0.00	0.00	19.13	1.42	13.7	4.0
150	12	0.90	0.03	6.90	0.30	119.0	11.3
	15	0.71	0.09	14.90	1.30	112.3	7.1
	18	0.39	0.08	26.13	2.55	101.3	6.4
	21	0.08	0.07	41.17	3.52	112.3	6.1
	24	0.00	0.00	47.57	7.30	90.7	5.5
	27	0.00	0.00	53.57	6.31	75.7	1.5
	30	0.00	0.00	53.03	3.10	71.0	1.0
	33	0.00	0.00	34.47	19.63	40.0	21.3
	36	0.00	0.00	39.55	1.34	47.5	4.9
	39	0.00	0.00	33.77	1.19	36.3	3.2
	42	0.00	0.00	21.87	12.36	21.3	9.6
	45	0.00	0.00	20.53	1.51	20.7	4.7

APPENDIX D4.5

Effect of egg density (constant food to egg ratio) on age and weight of male and female Cadra cautella at emergence.

FOOD - EGG DENSITY	AGE AT EMERGENCE						WEIGHT AT EMERGENCE					
	MALE			FEMALE			MALE			FEMALE		
RATIO	N	MEAN	S.D.	N	MEAN	S.D.	N	MEAN	S D	N	MEAN	S D.
10:10	18	30.1	1.6	17	30.5	1.3	14	3.60	0.64	14	6.19	0.61
15:15	27	28.9	1.5	29	29.9	1.5	14	3.27	0 48	18	6 11	0 65
20:20	40	28.9	1.0	40	30.0	1.5	17	3.44	0.45	19	6.25	0.53
25:25	47	29.6	1.7	47	30.0	1.5	18	3.64	0.38	19	6 10	0.59
30:30	56	29.1	1.1	65	29.8	0.9	17	3.59	0.33	19	6.34	0.67
35:35	73	29.2	1.2	65	29.9	1.1	20	3.85	0 47	20	6.60	0.77
40:40	81	29.7	1.3	70	30.6	1.4	26	3.83	0.49	26	6 10	0.88

APPENDIX D5.1

Development of Venturia canescens in larvae of Cadra cautella.

Course of Venturia canescens development when Cadra cautella larvae were infected at 8.5 days of age.

AGE[1]	PARASITOID STAGE					TOTAL[2]
	EGG	INSTAR 1	INSTARS 2-5	PUPAE	IMAGOS	
1	25					25
2	27	0				27
3	12	14				26
4	2	26				28
5	1	25				26
6	0	25	0			25
7		23	1			24
8		17	6			23
9		15	14			29
10		6	15			21
11		10	15	0		25
12		2	22	1		25
13		1	17	3		21
14		0	13	6		19
15			11	10		21
16			12	12		24
17			7	19		26
18			8	21		29
19			6	24		30
20			0	27		27
21				27		27
22				25		25
23				23	0	23
24				22	1	23
25				22	5	27
26				14	7	21
27				5	7	12
28				10	14	24
29				8	18	26
30				1	17	18
31				4	22	26
32				0	24	24
33					27	27
34					24	24
35					25	25
36					27	27
37					23	23
38					24	24

[1] Age of parasitoid (days)

[2] Total number of V. canescens in sample

... continued ...

APPENDIX D5.1 (continued)

Course of *Venturia canescens* development when *Cadra cautella* larvae were infected at 18.5 days of age.

AGE[1]	PARASITOID STAGE					TOTAL[2]
	EGG	INSTAR 1	INSTARS 2-5	PUPAE	IMAGO	
1	33					33
2	32	0				32
3	10	27				37
4	1	29	0			30
5	0	20	9			29
6		2	33			35
7		0	40			40
8			28	0		28
9			26	5		31
10			24	10		34
11			15	22		37
12			8	22		30
13			1	31		32
14			0	33		33
15			1	36		37
16			0	39		39
17				31		31
18				27		27
19				29	0	29
20				24	8	32
21				16	15	31
22				6	28	34
23				2	31	33
24				0	35	35
25					34	34
26					31	31
27					32	32

[1] Age of parasitoid (days)
[2] Total number of *V. canescens* in sample

APPENDIX D5.2

Effect of Cadra cautella larval age (A) and density (B) at infection on the age of Venturia canescens at imago emergence.

A. AGE[1]	N	EMERGENCE[2] MEAN	S.D.
1 5	19	34.3	2.93
4 5	55	31.1	2.82
6 5	153	31.0	3.53
8.5	92	26.7	3.12
10.5	223	25.7	5.85
12.5	227	24.4	3.08
14.5	237	23.1	3.00
17.5	134	22.7	2.67
20.5	229	21.7	1.46
23.5	120	22.6	1.94
26.5	13	21.4	0.65
29.5	12	22.7	1.42

[1] Host larval age at infection (days)

[2] Wasp age at imago emergence (days)

B. DENSITY[1]	N	EMERGENCE[2] MEAN	S.D.
5.9	81	23.9	1.93
14.7	86	31.4	5.35
29.4	87	31.6	6.03
44.1	51	32.3	4.36
58.8	228	33.7	4.47
88.2	42	41.2	7.14
117.6	60	43.7	6.83

[1] Initial host egg density (eggs/g food)

[2] Wasp age at imago emergence (days)

APPENDIX D5.3

Age-specific survival of imagos of Venturia canescens under varying conditions of food availability.

UNFED		FED	
AGE	NUMBER ALIVE	AGE	NUMBER ALIVE
0.00	585	0 0	110
0.21	585	0 5	110
0.38	584	1.5	110
0.54	577	2.5	110
0 71	574	3 5	106
0.88	573	4 5	102
1.04	558	5.5	91
1.21	538	6 5	88
1.38	517	7.5	88
1.54	487	8.5	80
1.71	403	9.5	77
1.88	339	10.5	75
2.04	241	11.5	72
2.21	141	12.5	67
2.38	99	13.5	54
2.54	67	14.5	42
2.71	39	15.5	24
2.88	18	16.5	5
3.04	7	17.5	1
3.21	1	18.5	0
3.30	0		

APPENDIX D5.4

Number of progeny produced per day through the lifetime of Venturia canescens. Imagos were either deprived of food and water (A) or provided with a 20% honey solution (B).

	AGE[1]	N	PROGENY[2]	
			MEAN	S.D
A.	1	19	12.9	6.62
	2	19	19.3	7.21
	3	12	11 6	6.19
B.	1	15	18.1	7 43
	2	15	20 3	6 01
	3	15	17 3	6.63
	4	15	20.7	6 87
	5	15	20.7	6.15
	6	14	18.3	6.38
	7	14	18.7	6.82
	8	13	16.7	5 53
	9	12	15.8	6.28
	10	12	15.4	5.00
	11	12	15.5	6.19
	12	11	14.2	8.54
	13	11	9.1	7.02
	14	10	7.4	5.66
	15	9	7.7	6.16
	16	8	5.4	4.60
	17	8	3.6	4.24
	18	8	2.7	2 55
	19	7	2.3	2.21
	20	7	0.4	0.79
	21	6	0.5	1.22
	22	6	0.2	0.41
	23	5	0.0	-

[1] Imago age (days)
[2] Number of V. canescens produced per day

APPENDIX D5.5

Effect of Cadra cautella larval age (A) and density (B) at infection on the weight at eclosion of Venturia canescens imagos.

A. AGE[1]	N	WEIGHT[2] MEAN	S.D.
1.5	10	1 33	0.236
4.5	10	1.50	0 266
6 5	10	1 38	0 162
8.5	10	1 39	0.152
10.5	10	1 30	0 163
12.5	10	1 58	0.169
14 5	10	1 37	0.216
17 5	10	2 03	0 306
20.5	10	1 80	0.424
23.5	10	1.64	0 353
26.5	10	1.63	0 221
29.5	10	1.52	0 365

[1] Larval age at infection (days)

[2] Imago dry weight (mg)

B. DENSITY[1]	N	WEIGHT[2] MEAN	S.D.
5.9	10	1.17	0.134
14.7	15	1.27	0.167
29.4	15	0.92	0.248
44.1	15	1.10	0.217
58.8	15	1.08	0.142
88.2	15	1.00	0.314
117.6	15	0.82	0.243

[1] Initial egg density (eggs/g food)

[2] Imago dry weight (mg)

APPENDIX D5.6

Observed data and statistical analyses of Venturia canescens instar-specific functional responses.

INSTAR	AGE AT INFECTION (days)
1	2.5
2	6.5
3	8.5
4	12.5
5-mid	17.5
5-late	20.5

Type II Response (Eq. 5.1):

$$N_a = N_t [1 - \exp(-aTP_t/(1+aT_hN_t))]$$

Type III Response (Eq. 5.2):

$$N_a = N_t [1 - \exp(-a'TN_tP_t/(1+a'T_hN_t^2))]$$

P_t = 1 parasitoid
T = 1 day

The non-linear curve fitting procedure was used to estimate the parameters of both equations. These expressions were then re-estimated using a common handling time (T_h) for all instars. The common handling time (T_h) was estimated by averaging the individual estimates calculated for instars 3, 4, and mid-5. These common handling time estimates were:

Type II	T_h = 0.0470043
Type III	T_h = 0.0494072

... continued ...

APPENDIX D5.6 (continued)

Data and parameter estimates for 1st instar host larvae.

DENSITY[1]	N	PROGENY[2]	
		MEAN	S.D.
3.7	6	0.0	-
7.4	6	0.3	0.82
14.8	6	0.7	0 82
22.3	6	1.2	1.17
29.7	6	1.0	0 89
44.5	6	1.7	1 21
59.4	6	2.2	1.47

[1] Host larval density (larvae/g food)
[2] Number of V canescens progeny produced in 1 day

Non-linear Least Squares Summary Statistics

FUNCTION	SOURCE	DF	SS	MS
Type II	Regression	2	61.590422	30 7952112
	Residual	40	36.409578	0.9102394
Type II[1]	Regression	1	61.528169	61.5281693
	Residual	41	36.474183	0.0889614
Type III	Regression	2	60.640590	30.3202952
	Residual	40	37.359409	0.9339852
Type III[2]	Regression	1	55.385587	55.3855866
	Residual	41	42.614413	1.0393759
	Uncorrected Total	42	98.000000	
	Corrected Total	41	56.000000	

	PARAMETER	ESTIMATE	SE
Type II	a	0.04581338	0.02014546
	T_h	0.10419574	0.20529352
Type II[1]	a	0.04091863	0.00536455
Type III	a'	0.00051923	0.00057893
	T_h	0.00	1.23132505
Type III[2]	a'	0.00080769	0.00012282

[1] Handling time (T_h) fixed at 0.0470043
[2] Handling time (T_h) fixed at 0.0494072

... continued ...

APPENDIX D5.6 (continued)

Data and parameter estimates for 2nd instar host larvae.

DENSITY[1]	N	PROGENY[2]	
		MEAN	S.D.
6.5	6	2.3	1.03
19.4	6	2.7	2.50
48.8	6	6.5	4.23
65.0	6	10.0	6.36
81.2	6	10.2	7.83
97.5	6	12.8	10.13
129.3	6	14.3	5.65

[1] Host larval density (larvae/g food)
[2] Number of V. canescens progeny produced in 1 day

Non-linear Least Squares Summary Statistics

FUNCTION	SOURCE	DF	SS	MS
Type II	Regression	2	3752.0759	1876.03795
	Residual	40	1324.9241	33.12310
Type II[1]	Regression	1	3721.9760	3721.97600
	Residual	41	1355.0240	33.04937
Type III	Regression	2	3734.6986	1867.34930
	Residual	40	1342.3014	33.55754
Type III[2]	Regression	1	3729.3133	3729.31328
	Residual	41	1347.3014	32.87041
	Uncorrected Total	42	5077.0000	
	Corrected Total	41	2110.0000	

	PARAMETER	ESTIMATE	SE
Type II	a	0.19302722	0.08894726
	T_h	0.02455981	0.02475056
Type II[1]	a	0.30090927	0.06723299
Type III	a'	0.00518401	0.00283656
	T_h	0.05518427	0.01389216
Type III[2]	a'	0.00429279	0.00113111

[1] Handling time (T_h) fixed at 0.0470043
[2] Handling time (T_h) fixed at 0.0494072

... continued ...

APPENDIX D5.6 (continued)

Data and parameter estimates for 3rd instar host larvae.

DENSITY[1]	N	PROGENY[2]	
		MEAN	S.D.
0.2	6	3.5	1.64
0.4	6	7.2	5.81
0.7	6	16.3	9.67
1.0	6	18.8	11.44
1.5	6	16.0	7.62
2.0	6	16.0	10.64
3.0	6	20.0	3 69
4.0	6	17.2	3.66

[1] Host larval density (larvae/g food)
[2] Number of V. canescens progeny produced in 1 day

Non-linear Least Squares Summary Statistics

FUNCTION	SOURCE	DF	SS	MS
Type II	Regression	2	11036.313	5518.1567
	Residual	46	2609.687	56.7323
Type II[1]	Regression	1	11036.045	11036.0450
	Residual	47	2609.955	55.5310
Type III	Regression	2	11133.179	5566.5895
	Residual	46	2512.821	54.6265
Type III[2]	Regression	1	11133.079	11133.0794
	Residual	47	2512.921	53.4664
	Uncorrected Total	48	13646.000	
	Corrected Total	47	3727.250	

	PARAMETER	ESTIMATE	SE
Type II	a	98.499575	87.759806
	T_h	0.046582	0.006651
Type II[1]	a	102.591295	60.503197
Type III	a'	208.122559	169.733431
	T_h	0.049594	0.004547
Type III[2]	a'	205.915277	150.043243

[1] Handling time (T_h) fixed at 0.0470043
[2] Handling time (T_h) fixed at 0.0494072

... continued ...

APPENDIX D5.6 (continued)

Data and parameter estimates for 4th instar host larvae.

DENSITY[1]	N	PROGENY[2]	
		MEAN	S.D.
0.1	6	1.8	2.23
0.2	6	5.2	3.71
0.4	6	11.8	3.97
0.7	6	14.2	6.59
1.0	6	17.7	7.00
1.5	6	19.3	6.80
2.0	6	16.2	3.31
3.0	6	18.5	4.64

[1] Host larval density (larvae/g food)
[2] Number of V. canescens progeny produced in 1 day

Non-linear Least Squares Summary Statistics

FUNCTION	SOURCE	DF	SS	MS
Type II	Regression	2	9825.6243	4912.81216
	Residual	46	1164.3757	25.31252
Type II[1]	Regression	1	9823.3427	9823.34266
	Residual	47	1166.6573	24.82250
Type III	Regression	2	9887.3296	4943.66481
	Residual	46	1102.6704	23.97109
Type III[2]	Regression	1	9886.1507	9886.15066
	Residual	47	1103.8493	23.48616
	Uncorrected Total	48	10990.000	
	Corrected Total	47	2773.667	
	PARAMETER		ESTIMATE	SE
Type II	a		136.293437	102.155569
	T_h		0.045607	0.004897
Type II[1]	a		162.050765	88.107640
Type III	a'		403.982551	265.069713
	T_h		0.048709	0.003182
Type III[2]	a'		422.861314	261.849386

[1] Handling time (T_h) fixed at 0.0470043
[2] Handling time (T_h) fixed at 0.0494072

... continued ...

APPENDIX D5.6 (continued)

Data and parameter estimates for mid-5th instar host larvae.

DENSITY[1]	N	PROGENY[2]	
		MEAN	S.D.
0.1	6	2.0	2 10
0.2	6	5.2	3 66
0.4	6	14.7	3.56
0.7	6	13.0	3 63
1.0	6	18.3	5.89
1.5	6	17.3	7.03
2.0	6	17.8	9.00
3.0	6	17.2	8.13

[1] Host larval density (larvae/g food)
[2] Number of V. canescens progeny produced in 1 day

Non-linear Least Squares Summary Statistics

FUNCTION	SOURCE	DF	SS	MS
Type II	Regression	2	9785.6689	4892.83445
	Residual	46	1573.3311	34 20285
Type II[1]	Regression	1	9782.0347	9782.03474
	Residual	47	1576.9653	33.55245
Type III	Regression	2	9837.2398	4918.61992
	Residual	46	1521.7601	33.08174
Type III[2]	Regression	1	9836.5881	9836.58814
	Residual	47	1522.4119	32.39174
	Uncorrected Total	48	11359.000	
	Corrected Total	47	3011.312	
	PARAMETER		ESTIMATE	SE
Type II	a		286.010459	486.898722
	T_h		0.048824	0.005749
Type II[1]	a		197.990745	147.044825
Type III	a'		608.803501	578.734232
	T_h		0.049918	0.003775
Type III[2]	a'		588.176738	504.737735

[1] Handling time (T_h) fixed at 0.0470043
[2] Handling time (T_h) fixed at 0.0494072

... continued ...

APPENDIX D5.6 (continued)

Data and parameter estimates for late-5th instar host larvae.

DENSITY[1]	N	PROGENY[2]	
		MEAN	S.D.
0.1	6	1.2	2.04
0.2	6	3.5	2.35
0.4	6	4.8	3.13
0.7	6	7.8	3.25
1.0	6	13.0	5.83
1.5	6	11.0	6.32
2.0	6	14.7	4.68
3.0	6	16.3	3.50

[1] Host larval density (larvae/g food)
[2] Number of V. canescens progeny produced in 1 day

Non-linear Least Squares Summary Statistics

FUNCTION	SOURCE	DF	SS	MS
Type II	Regression	2	5153.2316	2576.61584
	Residual	46	758.7684	16.49496
Type II[1]	Regression	1	5150.0595	5150.05947
	Residual	47	761.9405	16.21151
Type III	Regression	2	5135.8181	2567.90903
	Residual	46	776.1819	16.87352
Type III[2]	Regression	1	5064.2934	5064.29337
	Residual	47	847.7066	18.03631
	Uncorrected Total	48	5912.0000	
	Corrected Total	47	1987.9167	

	PARAMETER	ESTIMATE	SE
Type II	a	23.6154818	7.14694927
	T_h	0.0435625	0.00801708
Type II[1]	a	26.3739650	4.54241500
Type III	a'	55.9293436	21.8911936
	T_h	0.0599573	0.0052158
Type III[2]	a'	31.9128166	7.7992613

[1] Handling time (T_h) fixed at 0.0470043
[2] Handling time (T_h) fixed at 0.0494072

APPENDIX D5.8

Data and parameter estimates for the determination of the degree of mortality of 2nd instar Cadra cautella due to oviposition wounds inflicted by Venturia canescens.

The number of C. cautella imagos emerging and the proportion of hosts surviving in the control containers (no wasps present).

DENSITY[1]	N	EMERGENCE[2]		HATCH[3]	
		MEAN	S.D.	MEAN	S.D.
10	6	6.5	1.87	0.650	0.1871
30	6	18.2	2.14	0.606	0.0712
60	6	40.8	12 43	0.681	0 2072
100	6	59.8	12 30	0.598	0 1230
150	6	101.3	6.11	0.676	0.0367
200	6	128.3	2.86	0.644	0.0143

[1] Initial host density (eggs/g food)
[2] Total number of hosts emerging per container
[3] Fraction of host eggs surviving to adult emergence

The number of V. canescens and E. cautella imagos emerging from the containers where one wasp was present.

DENSITY[1]	N	WASP[2]		MOTH[3]		TOTAL[4]	
		MEAN	S.D.	MEAN	S.D.	MEAN	S.D.
10	6	0.8	0.75	3.3	1.37	4.2	1.60
30	6	4.0	2.10	7.0	4.90	11.0	4.98
60	6	7.2	4.40	15.2	6.18	22.3	7.20
100	6	11.2	5.85	22.5	18.40	33.7	14.26
150	6	13.4	5.73	60.6	19.82	74.0	19.07
200	6	14.5	8.85	93.5	21 08	108.0	13 43

[1] Initial egg density (eggs/g food).
[2] Number of V. canescens emerging per container.
[3] Number of C. cautella emerging per container.
[4] Number of insects emerging per container (wasps + moths).

... continued ...

APPENDIX D5.8 (continued)

The estimated number of C. cautella larave killed due to oviposition wounds and total number of hosts attacked.

N_t [1]	N_k [2]		N_a [3]		PROPORTION[4]	
	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.
6.4	2.3	1.60	3.1	1.37	0.717	0.2378
19.3	8.3	4.98	12.3	4.90	0.638	0.1892
38.6	16.3	7.20	23.4	6.18	0.687	0.1894
64.3	30.7	14.26	41.8	18.40	0.733	0.0802
96.5	22.5	19.07	35.9	19.82	0.517	0.4101
128.7	20.7	13.43	35.2	21.08	0.449	0.4071

[1] Number of host larvae available per container.
[2] Number of host larave killed (N_t - Total) per container (N_p)
[3] Number of host larave attacked ($N_p + N_k$) per container
[4] Fraction of host attacked that died (N_k/N_a)

Non-linear Least Squares Summary Statistics

Source	df	SS	MS
Regression	2	26148.817	13074.408
Residual	33	8266.653	250.505
Uncorrected Total	35	34415.470	
Corrected Total	39	12577.005	

Parameter	Estimate	S.E.
a	1.5136602	0.51400254
T_h	0.0175012	0.00682554

APPENDIX D6.1 & D6.2

Weekly counts of dead imagos in single-species long-term population cages of Cadra cautella (Series L1).

	REP 1			REP 2			REP 3	REP 4	REP 5
TIME	MALE	FEMALE	TOTAL[1]	MALE	FEMALE	TOTAL	TOTAL	TOTAL	TOTAL
5	0	0	0	0	0	0	0	0	0
6			138			272	119	214	356
7			116			133	175	247	202
8	37	40	117	84	64	172	167	271	153
9	44	53	152	55	70	148	88	115	79
10	107	111	235	76	60	157	188	119	99
11	145	135	360	68	112	191	685	150	268
12	217	188	415	215	227	464	311	261	370
13	148	108	269	181	90	271	134	83	159
14	31	36	70	137	151	309	119	106	293
15	98	124	250	148	140	328	127	112	305
16	59	61	122	122	98	214	46	55	181
17	54	60	119	56	64	120	75	98	109
18	74	83	163	53	37	93	59	95	80
19	67	49	120	26	12	44	49	69	48
20	33	40	81	21	57	86	70	121	133
21	112	119	267	106	106	225	178	130	146
22	86	56	187	87	68	180	69		72
23	39	35	109	62	85	180			
24	47	72	160	73	92	189			
25	79	61	210	75	88	187			
26	102	94	253	115	106	255			
27	162	132	357	155	196	405			
28	119	121	313	194	171	399			
29	105	85	224	110	122	298			
30	39	64	132	57	94	187			
31	43	49	128	52	59	148			
32	49	42	132	82	60	179			
33	43	37	116	46	62	132			
34	126	125	287	105	130	264			
35	179	120	364	199	191	446			
36	120	154	318	152	128	357			
37	79	67	186	132	126	272			
38	92	63	175	106	83	209			

[1] Some imagos could not be sexed. Thus the TOTAL column may not be the sum of males plus females.

APPENDIX D6.3

Changes through time in the estimated population sizes of larvae and pupae, and in the actual numbers of adults in a single-species population cage of *Cadra cautella* (Series L1, replicate 1).

WEEK	L1	L2	L3	L4	L5	PUPAE	ADULTS
9	2569	772	2232	2087	1617	471	201
10	1928	572	704	1499	1124	528	235
11	13773	968	446	504	718	337	0
12	11255	3245	1547	276	896	55	245
13	2243	2087	2065	833	787	254	42
14	1334	694	2317	1045	605	255	142
15	1686	218	771	1159	820	265	78
16	1837	180	378	655	642	196	110
17	2496	734	187	485	739	180	96
18	2582	1563	1049	464	1019	171	89
19	1104	658	1128	333	526	315	55
20	3433	705	1073	425	502	249	219
21	4372	1689	1109	722	771	92	141
22	1791	2835	1577	658	812	100	52
23	1044	1380	1886	565	574	183	39
24	1156	879	1523	1070	761	347	59
25	1402	767	825	1304	1328	357	89
26	867	439	503	1395	767	438	109
27	1354	532	674	389	801	413	168
28	3616	907	521	380	757	326	111
29	3582	2769	1334	760	834	237	86
30	1042	1351	1981	960	790	244	55
31	928	646	1837	997	714	172	92
32	673	493	1263	1122	1164	198	49
33	328	493	662	676	1254	371	51
34	604	367	899	435	1129	421	149
35	1459	529	850	637	1219	603	148
36	1377	1256	744	388	844	508	118
37	1680	1132	1162	715	752	145	79
38	516	1453	1545	687	773	228	58

APPENDIX D6 5

Distribution of Cadra cautella stages among the different ages of food units in a single-species population cage (series L1, replicate 1)

Host Population Larvae

WEEK	FOOD UNIT AGE								
	1	2	3	4	5	6	7	8	9
9	5263	660	718	656	305	421	449	450	354
10	4653	264	116	206	263	153	85	63	25
11	13126	2442	145	231	158	77	91	72	68
12	10055	6031	790	88	116	34	36	47	23
13	5707	1914	87	144	37	51	46	18	11
14	4977	710	102	75	53	43	20	14	4
15	3487	561	196	69	131	102	42	50	15
16	2831	536	87	69	100	34	3	20	13
17	3543	743	174	106	32	13	26	2	3
18	4246	1964	181	119	68	13	46	32	[illegible]
19	3099	413	152	25	26	17	13	2	1
20	3654	2203	203	25	16	30	0	2	5
21	5291	2269	696	200	105	55	13	27	8
22	5384	1493	558	138	53	34	10	2	1
23	3617	1262	312	94	121	21	0	14	8
24	4505	256	283	156	68	60	49	9	3
25	4440	545	232	119	79	77	98	34	4
26	3302	347	83	88	42	34	23	38	14
27	3108	297	94	31	21	128	33	18	20
28	5448	545	65	25	42	26	13	11	5
29	7086	2030	102	25	11	4	16	7	0
30	4745	1056	247	25	37	0	7	7	1
31	3571	965	464	88	21	4	7	2	1
32	3691	594	363	44	11	4	3	5	1
33	2627	495	145	63	21	30	16	11	5
34	2673	446	145	75	58	26	7	5	0
35	4126	404	73	0	47	9	29	2	3
36	3626	866	51	44	11	4	3	0	4
37	4153	1096	58	88	21	17	3	5	0
38	3117	1229	522	81	16	4	0	2	1

... continued ...

APPENDIX D6.5 (continued)

Host Population Pupae

WEEK	FOOD UNIT AGE								
	1	2	3	4	5	6	7	8	9
9	9	182	87	94	37	38	3	11	10
10	0	132	116	125	47	30	26	32	11
11	19	74	51	38	84	21	26	5	20
12	0	33	7	0	0	4	0	9	1
13	19	17	145	19	26	9	16	0	4
14	9	91	94	6	16	9	3	25	3
15	19	107	44	25	11	13	29	14	5
16	19	58	65	6	26	4	10	5	4
17	9	99	22	13	11	13	3	5	6
18	0	83	29	6	26	21	0	2	4
19	0	107	109	63	21	9	7	0	0
20	0	58	73	44	21	13	23	11	8
21	0	25	44	6	5	4	3	5	0
22	0	33	36	25	5	0	0	0	0
23	28	66	51	6	0	21	7	2	3
24	9	74	152	50	16	17	13	11	4
25	9	99	94	69	52	13	29	7	5
26	46	107	102	50	26	26	10	34	11
27	9	173	87	38	26	13	20	32	16
28	28	83	65	25	53	26	23	16	9
29	9	99	36	19	21	9	36	5	4
30	19	99	65	19	11	13	10	7	3
31	0	74	65	19	11	0	3	0	0
32	0	66	22	75	5	4	10	11	5
33	19	58	167	50	26	26	16	9	1
34	9	91	138	50	74	38	3	14	5
35	9	190	181	38	58	60	52	7	9
36	37	206	181	31	32	9	0	11	1
37	0	43	7	56	5	17	10	7	0
38	37	41	87	19	16	21	7	0	0

APPENDIX D6.6

Weekly counts of dead imagos in long-term population cages of Cadra cautella and Venturia canescens when no host refuges were provided (Series L1)

	REP 1		REP 2		REP 3		REP 4		REP 5	
TIME	H	P	H	P	H	P	H	P	H	P
5	0	0	0	0	0	0	0	0	0	0
6	166	0	173	0	264	0	215	0	247	0
7	271	0	190	0	139	0	174	0	134	0
8	189	51	131	85	96	29	91	59	119	53
9	76	56	68	57	39	22	59	24	25	22
10	43	33	29	17	32	5	24	14	40	10
11	38	185	28	130	89	188	61	295	53	193
12	23	274	45	309	327	289	91	326	109	239
13	38	176	29	164	64	47	18	138	55	100
14	4	76	7	203	5	89	4	68	5	190
15	2	50	3	179	0	71	1	60	1	196
16	1	122	2	84	1	46	1	39	0	59
17	1	90	1	26	0	37	0	20	0	25
18	0	48	1	18	3	16	1	25	8	16
19	0	24	8	8	6	39	3	36	0	17
20	0	62	4	18	1	149	1	89	0	43
21	0	37	1	15	1	106	1	34	0	33
22	0	14	0	5	1	16	0	9	0	5
23	0	0	0	9	0	15	0	2	0	5
24			0	18	0	13			0	11

APPENDIX D6.7

Distribution of host and parasitoid stages among different ages of food in a population cage of Cadra cautella and Venturia canescens.

Numbers of host larvae and host and parasitoid pupae through time.

LARVAE	FOOD UNIT AGE								
WEEK	1	2	3	4	5	6	7	8	9
9	4366	1394	485	694	493	1232	1469	1219	449
10	2765	396	298	106	226	149	169	70	63
11	5735	569	276	88	121	148	62	45	28
12	8140	5264	58	81	63	60	55	24	10
13	3598	718	58	19	5	17	7	7	1
14	2729	569	152	56	11	13	0	5	6
15	1018	355	87	25	0	9	7	2	1
16	749	58	15	0	0	4	3	0	1
17	435	198	51	19	5	21	3	0	4
18	213	149	80	13	0	0	0	2	1
19	231	124	51	13	0	0	0	2	0
20	83	41	15	0	0	0	3	5	0
21	111	25	44	13	0	0	0	0	0
22	37	25	15	6	0	0	0	0	0
23	19	33	0	6	0	4	0	0	0
24	0	8	7	6	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0

PUPAE	FOOD UNIT AGE								
	1	2	3	4	5	6	7	8	9
9	0	75	146	25	48	26	7	10	3
10	19	190	225	194	115	42	88	88	27
11	0	67	130	50	63	52	46	18	25
12	0	91	29	25	16	17	7	10	4
13	0	25	65	0	5	13	3	0	0
14	9	17	7	13	0	0	3	7	0
15	9	25	51	31	21	4	3	0	1
16	9	0	22	6	5	0	0	0	0
17	0	8	7	0	0	0	0	0	0
18	19	124	22	0	5	0	0	2	1
19	0	50	152	13	5	0	3	0	0
20	0	8	22	0	5	0	3	0	0
21	0	17	15	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0
23	9	0	15	0	0	0	0	0	0
24	0	0	58	6	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0

... continued ...

APPENDIX D6.7 (continued)

Changes through time in numbers of host population in each stage.

WEEK	L1	L2	L3	L4	L5	PUPAE	ADULTS
9	1638	1439	3266	3162	2299	158	28
10	132	127	620	1397	1966	367	0
11	5485	493	250	186	660	144	0
12	10306	2566	358	189	337	7	73
13	646	1911	1481	210	182	3	2
14	74	514	1409	1059	488	0	1
15	49	152	754	435	104	0	1
16	9	36	227	412	147	0	0
17	49	22	130	298	236	1	3
18	17	7	28	108	297	0	7
19	170	43	32	75	100	0	0
20	0	38	63	17	29	0	1
21	0	7	39	21	14	0	0
22	0	0	16	7	23	0	0
23	0	0	0	8	54	0	0
24	0	0	0	0	22	0	0
25	0	0	0	0	0	0	0

APPENDIX D6.8

Weekly counts of dead imagos in long-term population cages of Cadra cautella and Venturia canescens where host refuges provided 0%, 11%, 26% or 44% cover (Series L2).

	CONTROL		0% COVER				11% COVER			
	REP 1	REP 2	REP 1		REP 2		REP 1		REP 2	
TIME	H	H	H	P	H	P	H	P	H	P
5	0	0	0	0	0	0	0	0	0	0
6	38	11	38	0	42	0	56	0	24	0
7	171	107	140	0	143	0	139	0	162	0
8	137	86	83	9	93	10	97	10	102	9
9	46	60	46	9	56	8	27	9	42	10
10	30	22	21	0	22	2	7	0	16	0
11	37	52	43	10	52	10	9	0	34	6
12	244	669	340	25	367	12	53	2	278	9
13	309	135	258	8	226	1	649	6	188	3
14	298	67	138	180	107	78	581	2	174	87
15	250	119	46	141	65	74	185	17	103	83
16	126	105	5	18	28	18	53	33	23	23
17	113	109	0	30	18	155	30	15	8	59
18	137	208	0	8	20	166	23	45	1	20
19	205	261	0	22	9	56	17	71	0	14
20	430	155	1	47	0	25	22	72	0	20
21	354	188	0	39	0	23	20	160	1	33
22	286	129	0	32	0	11	11	185	0	43
23	263	67	0	15	0	14	1	84	0	19
24	168	35	1	6	0	6	1	22	0	12
25	78	44	0	6	0	5	0	13	0	4
26	95		0	1	0	6	0	4		

... continued ...

APPENDIX D6.8 (continued)

	25% COVER				44% COVER			
	REP 1		REP 2		REP 1		REP 2	
TIME	H	P	H	P	H	P	H	P
5	0	0	0	0	0	0	0	0
6	75	0	6	0	27	0	20	0
7	184	0	153	0	156	0	138	0
8	90	8	112	8	74	9	117	8
9	48	9	40	12	86	10	65	11
10	17	1	18	0	22	1	18	0
11	45	10	37	6	116	13	88	11
12	271	26	360	13	283	6	379	24
13	219	6	211	0	252	4	217	8
14	118	99	89	64	162	96	112	101
15	98	133	76	73	149	51	76	104
16	18	46	17	20	41	54	19	67
17	2	58	15	50	19	115	10	98
18	2	13	4	83	14	164	4	100
19	0	9	0	56	5	105	2	42
20	0	18	0	48	1	40	0	30
21	1	30	0	42	4	53	0	47
22	0	43	0	52	0	39	0	23
23	1	20	0	11	1	19	0	18
24	0	15	0	6	0	16	0	4
25	0	5	0	9	0	24	1	4
26	0	3			0	10		

APPENDIX D6.9
Weekly counts of dead imagos in long-term population cages of Cadra cautella and Venturia canescens where host refuges provide 0%, 25%, 50% or 75% cover (Series L3).

	CONTROL		0% COVER				25% COVER			
	REP 1	REP 2	REP 1		REP 2		REP 1		REP 2	
TIME	H	H	H	P	H	P	H	P	H	P
5	0	0	0	0	0	0	0	0	0	0
6	42	35	37	0	38	0	17	0	41	0
7	85	60	103	18	74	30	100	23	65	62
8	104	112	106	5	68	2	52	3	28	5
9	92	91	10	2	2	2	11	10	2	36
10	121	97	2	84	10	76	5	36	2	67
11	31	17	6	3	4	6	10	5	3	9
12	76	57	5	16	7	17	23	105	4	38
13	509	337	31	286	28	322	155	467	54	458
14	333	361	102	442	99	197	110	421	132	105
15	127	285	11	105	17	141	6	62	18	169
16	72	289	1	143	2	244	2	45	3	49
17	83	313	0	117	1	127	1	38	0	18
18	167	386	0	24	1	46	3	89	4	29
19	418	245	0	1	1	92	20	294	5	57
20	354	560	0	2	0	153	1	97	0	10
21	50	216	0	0	0	52	0	10	0	0
22	3	20	0	0	0	5	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0

	50% COVER				75% COVER			
	REP 1		REP 2		REP 1		REP 2	
TIME	H	P	H	P	H	P	H	P
5	0	0	0	0	0	0	0	0
6	24	0	46	0	19	0	83	0
7	59	68	66	49	58	66	201	13
8	83	12	95	6	24	2	48	0
9	4	46	7	19	6	55	19	0
10	4	39	5	31	7	29	11	5
11	4	1	6	15	8	2	3	0
12	4	34	18	36	34	72	106	11
13	140	305	156	283	131	304	385	22
14	118	287	141	267	79	239	149	12
15	23	225	17	129	6	118	21	100
16	16	180	7	154	2	58	9	47
17	16	89	7	62	0	25	30	36
18	9	62	1	12	0	20	43	123
19	10	253	0	7	0	6	13	63
20	28	273	0	3	0	1	2	8
21	8	138	0	0	0	1	1	1
22	3	29	0	0	0	0	1	1
23	0	0	0	0	0	0	0	0

APPENDIX D6.10

Weekly counts of dead imagos in long-term population experiments of *Cadra cautella* and *Venturia canescens* using the small cages (Series S).

Single-species cages of host population alone.

TIME	REP 1	REP 2	REP 3	REP 4	REP 5
7	0	0	0	0	0
8	12	13	22	20	4
9	16	22	16	22	15
10	10	7	28	11	17
11	6	0	8	3	21
12	8	3	0	1	7
13	10	3	9	0	4
14	76	35	77	16	8
15	177	160	284	91	21
16	69	76	106	51	61
17	45	25	55	24	149
18	88	23	45	3	85
19	98	8	56	10	37
20	128	83	84	135	17
21	159	144	274	222	40
22	123	80	103	89	86
23	120	82	115	7	189
24	88	101	31	5	225
25	197	94	3	0	60
26	121	35	1	0	7
27	4	2	0	0	0

... continued ...

APPENDIX D6.10 (continued)

Host-parasitoid populations not provided with food.

	REP 1		REP 2		REP 3		REP 4		REP 5	
TIME	H	P	H	P	H	P	H	P	H	P
7	0	0	0	0	0	0	0	0	0	0
8	7	3	13	20	16	9	9	9	10	6
9	13	0	7	4	9	2	20	4	16	3
10	12	5	11	2	10	1	6	2	10	2
11	3	3	6	3	4	7	6	6	5	3
12	20	5	6	4	4	6	5	7	1	2
13	6	2	1	6	3	10	4	10	1	2
14	46	12	41	40	51	49	27	47	59	22
15	72	35	84	22	99	59	53	76	180	38
16	58	28	38	19	21	43	49	53	55	26
17	34	23	47	45	3	22	17	31	2	14
18	17	26	27	39	5	6	14	24	3	3
19	38	35	10	59	27	55	20	69	30	58
20	41	53	11	183	96	79	33	116	74	54
21	26	40	27	50	57	49	21	102	37	38
22	25	21	11	30	26	72	3	26	34	58
23	8	19	40	41	7	25	6	13	36	37
24	27	20	31	41	4	3	0	6	5	13
25	11	21	16	15	3	3	0	0	2	6
26	2	6	6	5	1	2			0	1
27	1	0	1	0	1	0				

... continued ...

APPENDIX D6.10 (continued)

Host-parasitoid populations provided with food.

	REP 1		REP 2		REP 3		REP 4		REP 5	
TIME	H	P	H	P	H	P	H	P	H	P
7	0	0	0	0	0	0	0	0	0	0
8	7	0	0	0	2	1	4	0	1	2
9	6	0	2	0	5	1	2	0	2	0
10	3	0	7	1	9	0	5	1	10	3
11	2	2	10	8	7	20	10	21	13	7
12	11	20	13	18	7	14	3	7	7	7
13	6	9	6	11	8	9	1	10	7	7
14	9	39	33	66	30	35	30	57	11	23
15	27	96	51	89	44	21	29	50	56	150
16	18	29	16	25	31	26	4	21	32	128
17	4	6	14	21	26	9	11	12	4	51
18	15	3	33	31	33	8	17	20	0	11
19	35	74	42	30	32	30	111	54	2	15
20	62	60	43	84	37	53	73	172	31	37
21	18	38	32	61	51	65	4	34	22	68
22	5	21	10	20	7	7	2	17	3	11
23	20	31	18	28	0	9	1	4	4	21
24	20	5	22	22	2	6	2	4	0	9
25	4	9	10	44	0	1	0	0	0	1
26	3	8	1	1	0	0				
27	1	0	0	0	0	3				

APPENDIX M5.1

Different attack equations are needed to describe the functional responses of parasitoids and predators. This is because parasitized hosts remain available for further encounters by searching parasitoids and as a result the number of hosts available remains constant over the course of an experiment. In contrast a searching predator completely consumes encountered prey which results in prey density decreasing over the course of an experiment. The Type II functional response equations used to describe these are:

Parasitoids: $N_p = N_t [1-\exp\{-aTP_t/(1+aT_h N_t)\}]$ Eq. 5.1

Predators: $N_a = N_t [1-\exp\{-aP_t(T-T_h N_a/P_.)\}]$ Eq. 5.3

The situation regarding 2nd instar C. cautella mortality due to ovipositor wounds by V. canescens may be an intermediate case. We assume that a proportion of oviposition events results in the death of the host as opposed to successful infection and we further assume that these wounded larvae die quickly and are as such unavailable for further encounters with searching parasitoids. These assumptions lead to the situation of a series of encounters some of which lead to a decrease in host density while others do not. This requires a different form for the attack equation. The appropriate attack equation has been developed following the techniques presented by Hassell (1978, Appendix 1).

For a Type II predator response the instaneous prey encounter rate is:

$$u(t) = a \cdot P_t/(1+a \cdot T_h \cdot N(t)) \qquad \text{Eq. AM5.1}$$

where N(t) is the number of prey not attacked up to time t. If p(t) is the probability of a prey not being attacked up to time t, then

$$N(t) = N_t p(t) \qquad \text{Eq. AM5.2}$$

Incorporating those encounters that do not result in host (prey) death but in parasitism leads to

$$N(t)=N_t p(t)+N_t (1-p(t))(1-q) \qquad \text{Eq. AM5.3}$$

where q is the probability that an encounter results in host death rather than infection.

Substituting equation AM5.3 into equation AM5.1 gives

$$u(t)=aP_t/(1+aT_h N_t (1-q-qp(t))) \qquad \text{Eq. AM5.4}$$

The basic equation relating p(t) and u(t) is given by Hassell (1978) as

$$dp(t)/p(t)=-u(t)dt \qquad \text{Eq. AM5.5}$$

Substituting (Eq. A9.4) into (Eq. A9.5) and rearranging gives

$$1+aT_h N_t (1-q-qp)dp(t)/p(t)=-aP_t dt \qquad \text{Eq. AM5.6}$$

On integrating

$$[1+aT_h N_t (1-q-q)/p(t)]dp(t)= aP_t dt \qquad \text{Eq. AM5.7}$$

gives

$$p(t)=\exp[-aP_t T-aT_h N_t q(1-p(t))/1+aT_h N_t (1-q)] \qquad \text{Eq. AM5.8}$$

By definition

$$N_a=N_t (1-p(t)) \qquad \text{Eq. AM5 9}$$

Combining this with (Eq. AM5.8) gives the desired equation

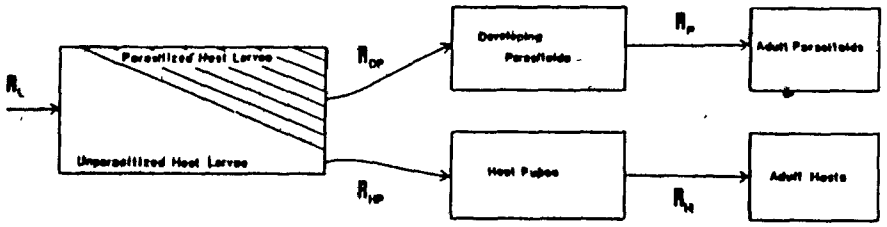
$$N_a=N_t [1-\exp(-aP_t (T-T_h N_a q/P_t)/(1+aT_h N_t (1-q)))] \qquad \text{Eq.AM5.10}$$

Note that when q = 0 equation 5.3 is recovered, while equation 5.1 is obtained if q = 1.

APPENDIX M7.1

A continuous-time host-parasitoid model.

1. Model Life Histories:



Variables:
- $L(t)$ - density of host larvae
- $P(t)$ - density of adult parasitoids
- $H(t)$ - density of adult hosts
- $R_L(t)$ - rate of recruitment of host larvae
- $R_{DP}(t)$ - rate of recruitment of developing parasitoids
- $R_{HP}(t)$ - rate of recruitment of host pupae
- $R_P(t)$ - rate of recruitment of adult parasitoids
- $R_H(t)$ - rate of recruitment of unparasitized hosts

Parameters:

δ_L - per capita death rate for host larvae (parasitized and unparasitized); 0.0/day[1]

δ_P - per capita death rate for adult parasitoids; 0.5/day

δ_H - per capita death rate for adult hosts; 0.1/day

S_D - survival probability for developing parasitoids; 1.0/day

S_P - survival probability for host pupae; 1.0/day

a - attach coefficient - adult parasitoids on host larvae; 0.3/day

β - 'net' fecundity of adult hosts (larval recruits per adult per unit time); 84/day

τ_L - larval development time (hosts); 26 days

τ_D - development time (parasitoids) [$\tau_L + \tau_D$ - time from host egg to adult parasitoid]; 14 days

τ_P - stage duration for host pupae; 8 days

τ_E - egg duration; 4 days

[1] Parameter values used in the numerical solution illustrated in Fig. 7.2

The two adult stages are described by the equations:

$$H(t)=R_H(t)-\delta_H H(t)$$
$$P(t)=R_P(t)-\delta_P P(t) \qquad \text{Eq. AM7.1}$$

where

$$R_H(t)=R_L(t-\tau_L-\tau_P)\exp\left(-a\int_{t-\tau_L-\tau_P}^{t-\tau_P} P(t')dt'\right)\exp(-\delta_L\tau_L)S_P \qquad \text{Eq. AM7 2}$$

and

$$R_P(t)=R_L(t-\tau_L-\tau_P)\left(1-\exp\left(-a\int_{t-\tau_L-\tau_P}^{t-\tau_P} P(t')dt'\right)\right)\exp(-\delta_L\tau_L)S_D \qquad \text{Eq. AM7.3}$$

and

$$R_L(t)=\beta H(t-\tau_E)+I_L \qquad \text{Eq. AM7 4}$$

Equations AM7.1, 2, 3 and 4 fully specify the model

A simplified model:

Set $\delta_L=0$, $S_P=S_D=1$, $\tau_E=\tau_P=\tau_D=0$ and define $\tau=\tau_P+\tau_L$, so that equations AM7.3-4 simplify to:

$$R_H(t)=R_L(t-\tau)\exp\left(-a\int_{t-\tau}^{t-\tau_P} P(t')dt'\right) \qquad \text{Eq AM7.2a}$$

and

$$R_P(t)=R_L(t-\tau)\left(1-\exp\left(-a\int_{t-\tau}^{t-\tau_P} P(t')dt'\right)\right) \qquad \text{Eq.AM7.3a}$$

and

$$R_L(t)=\beta H(t)+I_L \qquad \text{Eq. AM7.4a}$$

Equations AM7.1 and AM7.2a, 3a and 4a now specify the simplified model

Steady States for the Simplified Model:

$$\delta_H H^* - R_H = (\beta H^* + I_L)\exp(-aP^*\tau_L) \qquad \text{Eq. AM7.5}$$

$$\delta_P P^* - R_P = (\beta H^* + I_L)(1 - \exp(-aP^*\tau_L)) \qquad \text{Eq. AM7.6}$$

$$P^* = (a\tau_L)^{-1}\ln(\rho) \qquad \text{Eq. AM7.7}$$

$$H^* = (a\tau_L)^{-1}(\delta_P/\delta_H)\ln(\rho)/(\rho - 1) \qquad \text{Eq. AM7.7}$$

where

$$\rho = \beta/\delta_H .$$

Note similarity to Nicholson-Bailey Model. The factor (δ_P/δ_H) is the only difference.