The nutritional ecology of a host-parasitoid interaction

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This thesis is dedicated to Jana Chržová, for her love and encouragement, Mark Williamson for his friendship and inspiration, and to my parents for always believing in me.

Abstract

A number of pyralid moths of the subfamily Phycitinae are serious pests of stored food products over much of the world. *Venturia canescens* is a solitary ichneumonid endoparasitoid that attacks the larvae of these pests. This study reports interactions between *Venturia* and three hosts, *Plodia interpunctella*, *Anagasta kuehniella*, and *Corcyra cephalonica*.

The influence of several host-related constraints on the growth and development of *Venturia* was examined. There was little difference in several fitness-related traits of wasps reared from well-fed third (L3) to fifth (L5) instars of *Plodia*, but wasps reared from second (L2) instars suffered higher mortality, took longer to complete development and were smaller than wasps reared from instars three to five. *Venturia* showed delayed larval development in L2 hosts, and did not grow rapidly until hosts entered their final (L5) instar. Parasitized L2 and L3 hosts were destroyed by the parasitoid before they attained the size of healthy larvae, and L2-L4 hosts parasitized by *Venturia* did not pupate after parasitism, although L5 hosts did.

Superparasitism adversely affected the development of *Venturia* in L3 and L5 *Plodia*, but these effects were more pronounced in L5 hosts, where parasitoid mortality and development time increased with egg number per host, but adult wasp size decreased. In L3 hosts, only development time to eclosion increased in superparasitized hosts.

Host nutrition also affected parasitoid development differently in L3 and L5 *Plodia*. Wasps reared from starved L3 hosts suffered higher mortality and took longer to complete development than wasps from well-fed L3 hosts. Conversely, wasps from starved L5 hosts were smaller, but developed more rapidly than those from well-fed hosts. When parasitized L3 hosts were starved for variable periods, parasitoid survivorship increased with the length of host access to food, with development time and adult wasp size both increasing under these conditions.

Venturia reared from four instars of a second, larger host (*Corcyra*) were themselves larger than *Plodia*-reared wasps but took longer to complete development and suffered higher mortality. *Venturia* arrested the growth of *Corcyra* at an earlier stage than *Plodia*, in response to extra nutritional resources from *Corcyra*. Wasps reared from L5 *Anagasta* took longer to complete development than those from L5 *Plodia*, but the size of emerging wasps from the two hosts was similar.

Host acceptance by *Venturia* was clearly affected by the size and species of the host it attacks. Late fifth instar *Corcyra* aggressively resisted parasitoid attack much more successfully than *Plodia*, which displayed more passive behaviour after initial parasitoid contact. Host response to simulated antennation also varied with instar and species, with earlier instars more aggressive than later instars, and *Plodia* displaying less aggression than *Corcyra*.

The lifetime reproductive success of *Venturia* was examined in response to temporal variations in host and food (honey solution) access. Constantly-fed wasps lived longer, and produced more progeny, than wasps which were alternately fed and starved, or starved from eclosion, and parasitoids supplied constantly with hosts produced more progeny early in life, than those given shorter periods of host access. However, constantly-fed wasps with limited access to hosts extended their reproductive period to a later period of adult life. Parasitoid longevity and progeny production both covaried with adult size, with larger wasps generally living longer, and enjoying higher reproductive success, than smaller wasps.

The influence of different constraints on the performance of both the larval and adult parasitoid wasp was discussed, with particular attention paid to the development of predictive models of parasitoid growth and development under nutritional stress resulting from differences in host stage, condition and superparasitism.

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During the course of my Ph.D., it dawned on me that, far from being a completely solitary endeavour, my experiments and thesis were aided considerably by the support and advice of many people. Based on this collective encouragement, I have assembled a D.E.E.B. "all-star" baseball team, complete with the most recent statistics:

Team managers were Dave Thompson and Ian Harvey. Dave was always available to support any hair-brained ideas I conjured up over three years, while Ian's expertise in behavioural ecology and especially statistics helped me to the best three seasons of my career (.321, 67 hrs, 276 rbi's). Perhaps more importantly, their encouragement during all three seasons ensured that I could retire having achieved a life-long ambition. My **first base coach**, Mike Begon, and **third base coach**, Geoff Parker, provided additional team guidance when required (e.g. during the pennant run!). The rest of this amazing team are:

First base: Douglas 'ribbee' Reed (.257, 24 hrs, 103 rbi's). **Second base:** Nina 'wizard' Weddell (.235, 7 hrs, 49 rbi's). **Shortstop:** Penny 'clutch' Cook (.315, 5 hrs, 76 rbi's). **Third base:** Steve 'slugger' Sait (.272, 10 hrs, 71 rbi's). **Left field:** Rob 'Bob' Knell (.284, 12 hrs, 80 rbi's). **Centre field:** Joe 'tater' Tomkins (.275, 45 hrs, 112 rbi's). **Right field:** Matt 'goatee' Gage (.247, 17 hrs, 58 rbi's). **Catcher:** Judith 'catfish II' Shaw (.279, 14 hrs, 57 rbi's). **Starting pitcher:** Tom 'the great' Tregenza* (W - 24, L - 5, ERA - 1.93, 217 K's; * denotes league most valuable player). **Relief pitcher:** Leigh 'Simmo' Simmons (W - 4, L - 2, ERA - 1.35, Saves - 37). **Rookie star:** Liam 'line-drive' Lynch (second base). **Team trainer and physiotherapist:** Tom 'the saint' Heyes. **Assistant trainer:** Carl 'stop clock' Wright. **Team mascots:** Curly and Rosy, the spider double act. For those individuals who know nothing about baseball, the first statistical figure (except for the pitchers) represents the batting percentage, hrs = home runs, and rbi's = runs batted in. For the pitching staff, W = victories, L = losses, ERA = earned run average (per 9 innings) and K's = strikeouts. Does this make any sense?

Many fans also supported me and the team during the three seasons, and I would especially like to thank the following people for making these years in Liverpool memorable: Gareth Richards, Eddie Wright, Ian Mitchell, Nicholas Watkins, Graham Hopkins, Yannis Yannakoudakis, Padelis Abatzis, Adrian Milton, Karen Willson, Drs. Ron Pearson, Dave Ensor and Don Young, Professor Brian Moss, the

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Chapter 9 General discussion

1. Introduction

1.1 Parasitoids, parasites and predators

The parasitic mode of life has evolved in a large number of arthropod orders (Vinson, 1976). Insects that are parasitic during the larval stages are collectively known as "parasitoids" (Reuter, 1913) or "protelean parasites" (Askew, 1971) in order to distinguish them from true or typical parasites. Parasitoids differ from typical parasites in a number of ways: only the larvae are parasitic while the adults are free-living and relatively large compared with the size of the host. A limited number of parasitoid progeny can develop on a single host, which is usually of the same taxonomic class (e.g. Insecta). Lastly, the host is always destroyed by the parasitoid. The population dynamics of parasitoids and their hosts also more closely resembles that which exists between predators and prey (Doutt, 1959). Flanders (1973), acknowledging the affinity between parasitoids and predators, described the larval habit of parasitoids as "carniveroid". However, parasitoids differ from predators in that they consume merely a single host, whereas predators must devour several in order to reach maturity. Therefore, because conditions necessary for successful parasitoid growth and development are confined to a single host individual, parasitoid fitness will largely depend upon their efficiency in utilizing these limited host resources. A major theme of my thesis will be to evaluate the effects of nutritional constraints on parasitoid development and to discuss ways that parasitoids overcome these constraints on their performance.

1.2 The pre-requisites of successful host-parasitoid associations

The relationship between hosts and parasitoids involves a number of selective events that are necessary for the successful completion of the interaction. Salt (1938) and Flanders (1953) began the process of subdividing these events, which were further distinguished by Doutt (1959, 1964) and Vinson (1975). The following steps have been recognized: (a) host habitat location; (b) host location (c) host acceptance; (d) host suitability, and (e) host regulation. The first three of these steps broadly define the host selection process, while it is often difficult to separate certain aspects of host suitability from host regulation (see below).

At emergence, an adult female parasitoid may find herself in an environment devoid of suitable hosts, or hosts which have become locally extinct. She therefore faces the problem of locating suitable hosts in which to propagate. Initially, a parasitoid must seek an appropriate environment regardless of whether it contains potential hosts or not. Plant

or associated food volatiles have been shown to play an important role in the location of patches containing hosts (Arthur, 1981) although certain plants may disorient, or even repel, searching parasitoids (Vinson, 1985). Host-produced semiochemicals (see below) such as kairomones and synonomes also orient parasitoids to host patches. Once the wasp is in the habitat of the host, she must then be able to locate individual hosts and to be able to parasitize them after they are contacted.

For most parasitoids, the species and stage of host selected is restricted by numerous factors relating to its suitability (Godfray, 1994) and other factors including the physiological state of the parasitoid (Collins & Dixon, 1986; Fletcher *et al.*, 1994). Host behavioural and morphological defences, host age or size, chemical composition, condition and whether or not it has been previously parasitized all influence the host selection process (Vinson, 1976; van Alphen & Visser, 1990). Physical factors, such as sound, vibrations, and shape are important attractants for parasitoids (Vinson, 1985). However, the most important factors leading to attack and oviposition by parasitoids are semiochemical secretions (kairomones and synonomes) released by hosts in frass, silk and mandibular secretions that alter the searching behaviour of parasitoids and may determine which communities of hosts attract parasitoids (Weseloh, 1974; Waage, 1978; Vinson, 1985, 1988). These chemical secretions frequently elicit a series of direct responses by the female wasp that functions by restricting the areas they habitually search, and result in the location of suitable hosts. Parasitoids utilize receptors on their antennae, tarsi, ovipositor and eyes to locate hosts and it has been suggested (e.g. Vinson, 1984, 1985) that their ability to do so becomes more refined as host specificity increases.

Once a host is accepted by a female parasitoid, the ability for the new generation to develop depends upon the suitability of the selected host for the development of her progeny. Several definitions have been used to describe host suitability. Salt (1938), for example, suggested that a suitable host was "one which is acceptable by the parasitoid and in which development of the parasitic stage (to eclosion) can be completed". However, in later reviews, Mackauer (1973, 1986) and Vinson & Iwantsch (1980a) omitted any aspects of host acceptance in their definitions of suitability, and stated that it should describe only interactions between the host and immature stages of the parasitoid, thus excluding any interactions between the host and adult parasitoid that prevent oviposition by physical, behavioural or chemical defences.

Host quality and suitability are often used synonymously, although recently these terms have been subdivided further. Mackauer & Sequeira (1993) define a host as

suitable only if it provides the conditions that support parasitoid development, whereas host quality is used to describe degrees of variation in host state or condition that affect dynamical processes of parasitoid growth rate, development (and survival). Various studies have shown that rates of larval parasitoid development, adult biomass, and survivorship vary in accordance with differences in host size, host age, host stage of development, host condition and diet (see Mackauer & Sequeira, 1993, and Godfray, 1994 for recent reviews). Thus, while some host types are considered unsuitable for parasitoid development, others may provide conditions that differentially affect parasitoid fitness, hence quality is assessed on this basis.

Vinson & Iwantsch (1980a) and Barbosa *et al.* (1982) believe that the terms "quality" and "suitability" can both be broadly applied to these different processes. I have used the terms "suitability" and "quality" interchangeably, and define suitability according to Barbosa *et al.*, (1982): "the extent to which the physiological environment within the host provides the conditions for successful parasitoid development, from oviposition to the production (emergence) of fertile adult wasps". The successful development of a parasitoid to adult also depends upon its capacity to evade a host's immune response, competition (heterospecific and conspecific) with other immature parasitoids, the presence of toxins detrimental to the parasitoid egg or larva, and pathogenic infection that may otherwise interfere with normal developmental processes (Vinson & Iwantsch, 1980a).

Some parasitoids may oviposit into nutritionally less suitable hosts, or hosts nearing the end of a suitable stage, and immature development may depend on the ability of the parasitoid to rearrange or alter aspects of host behaviour, development, morphology or physiology to ensure their own survival. The fitness of parasitoids within their hosts is directly dependent upon host activities, therefore natural selection is assumed to favour parasitoid-influenced changes in host suitability that improve the parasitoid's fitness. Such alterations mediated by the parasitoid are referred to as host regulation, the final step in a successful host-parasitoid interaction. It is currently one of the most fertile fields of parasitoid research (see recent papers by Beckage, Vinson, Stoltz and colleagues). Host regulation can only function within certain constraints imposed by the availability of host resources and other factors such as host immunology (Vinson & Barbosa, 1987) resulting in an interplay between host constraints and host regulation. This interplay is the major factor in determining a host's suitability. Regulation requires the adult or larval parasitoid to maintain the host in a physiologically suitable condition throughout parasitoid development, and partly depends on the

parasitoid's ability to utilize and redirect the host's metabolic energies for its own benefit (Jowyk & Smilowitz, 1978).

The effects of parasitoids on their hosts used to be attributed primarily to the effects of larval feeding, or the secretions of certain factors by parasitoid larvae inside the host, and evidence for this has been documented (e.g. Iwantsch & Smilowitz, 1975). Large cells, called teratocytes, that are liberated from the serosa of the parasitoid egg at hatching have also been found to induce physiological changes in the host (Strand & Wong, 1991; Pennachio *et al.*, 1992; Dahlman & Vinson, 1993). However, empirical evidence now suggests that factors injected by the female parasitoid at oviposition are the major regulatory mechanism used by parasitoids (Vinson & Iwantsch, 1980b; Vinson, 1984; Fedderson *et al.*, 1986; Tanaka, 1987; Berg *et al.*, 1988; Dushay & Beckage, 1993). The poison glands of many adult female ichneumonid and braconid wasps contain substances which cause varying degrees of host paralysis (Beard, 1978) or result in a delayed inhibition of host development, depending upon the host stage attacked (Shaw, 1981). DNA-containing particles, characterized as viruses, have been found in the calyx region or lateral oviducts in several species of ichneumonids and braconids (Stoltz & Vinson, 1979; Edson *et al.*, 1981; Dushay & Beckage, 1993). These particles invade host cells and tissues, and appear to affect hosts in many ways (Dahlman & Vinson, 1977; Dushay & Beckage, 1993).

1.3 Parasitoid reproductive and life-history strategies

1.3.1 Parasitoid reproductive biology

Parasitoid life-history and foraging strategies have been described using a variety of mechanistic, functional (and combined) approaches. Price (1972, 1973) showed that guilds of parasitoids attacking various stages of the pine sawfly, *Neodiprion swaneii,* exhibited adaptive differences in the form and nature of certain morphological and physiological traits, such as wing surface area, ovipositor length and ovary structure. The latter characteristic has been extensively studied (Flanders, 1942, 1950; Leius, 1963; Price, 1973; Dowell, 1978) and, more recently, other workers (e.g. Jervis & Kidd, 1986) have suggested that there is a corollary between specific aspects of host biology and ecology and the ways in which parasitoids gather and allocate nutrients for reproduction and maintenance.

Many parasitoids continue to mature eggs after the eclosion of the adult (termed synovigenic) and therefore need to acquire nutrients for continued oogenesis, or to

extend their period of reproduction by increasing their longevity (Dowell, 1978). Another group of parasitoids, termed pro-ovigenic, completes oogenesis at, or soon after, emergence (Flanders, 1950; Syme, 1975). Very few truly pro-ovigenic species have thus far been identified (M.A. Jervis, personal communication).

Several families of parasitoids include species that feed on host tissues and fluids (Flanders, 1935; reviewed in Jervis & Kidd, 1986). Host-feeding provides adult female wasps with proteins that are largely utilized for the production of eggs (Flanders, 1942). These proteins may be required prior to egg formation (Gordh, 1976; Jervis & Kidd, 1986; van Lenteren *et al.*, 1987) or for continued egg production (Quednau & Guevremont, 1975; Rosenheim & Rosen, 1992). However, many parasitoids do not host-feed (Puttler, 1961; Duodu & Davis, 1974; Dowell, 1978). In these species, egg production proceeds in the absence of adult feeding (Clausen, 1962) or with the female wasp obtaining only carbohydrates (from nectar), and water (Dowell & Horn, 1977). Parasitoids that do not host-feed gather all of the proteins necessary for oogenesis as larvae in the host (Flanders, 1942). Very little protein necessary to form a viable first instar larva is invested into each egg, which are therefore resource deficient at oviposition and termed hydropic (Jervis & Kidd, 1986). These parasitoids are generally endoparasitic, and ovulation is internally induced by the uptake of host-derived proteins through the egg membrane into the embryo, which increases greatly in size during incubation (Flanders, 1942). On the other hand, many host-feeding species produce resource-rich eggs, termed anhydropic, although there are some exceptions to this rule (Donaldson & Walter, 1988). These parasitoids may be ecto or endoparasitic, because ovulation is externally induced (Flanders, 1950). Eggs of anhydropic parasitoids do not increase greatly in size during incubation (Dowell, 1978). Many studies have shown that anhydropic parasitoids have the capacity to extend their longevity by resorbing egg proteins in the absence of hosts (e.g. Flanders, 1942; Sandlan, 1979b; Bai & Mackauer, 1990). The relationship between ovarian structure, egg production, adult feeding habits and parasitoid fecundity, longevity and foraging behaviour has been extensively studied and reviewed (Price, 1972, 1975; van Lenteren *et al.*, 1987; Jervis & Kidd, 1986, 1991; Chan & Godfray, 1993).

1.3.2 Host exploitation strategies

Koinobiosis and Idiobiosis

Among insect parasitoids, a major life-history dichotomy has been recognized between parasitoids that develop in non-growing host stages, or paralyzed hosts, and

parasitoids developing in hosts that continue to feed, grow and metamorphose, at least during the initial stages of parasitism (Haeselbarth, 1979; Askew & Shaw, 1986). The former group, termed idiobionts, utilize ostensibly static host resources, whereas the latter, termed koinobionts, utilize potentially dynamic host resources whose suitability may be influenced by several complex factors such as host nutritional state and capacity for growth after parasitism (Mackauer, 1986).

Idiobiosis is the ancestral state in most parasitoid lineages (Gauld, 1988). Koinobiosis is considered to have evolved in response to a number of factors including the more effective defences (morphological, behavioural, physiological) of larger hosts (Salt, 1968; Gross, 1993), a greater ease in locating early host instars, compared with later stages (Slansky, 1986), a lower probability of survival in larger hosts in cases of superparasitism (both conspecific or heterospecific)(Askew, 1975) and a lower probability of the discovery of cryptic host pupae, compared with larvae (Gauld, 1988). More recently, attention has focused on an additional factor, the constraint imposed by host suitability or quality upon fitness (Mackauer & Sequeira, 1993).

Most studies examining the effect of host size at parasitism on certain fitness correlates such as adult parasitoid size, development time and survival have used idiobionts (e.g. Salt, 1940, 1941; Arthur & Wylie, 1959; van den Assem, 1971; Sandlan, 1982; Bellows, 1985; Bai, *et al.*, 1992). Large hosts contain more resources than small hosts for idiobionts, therefore parasitoid size is often a positive function of host size at oviposition (Jackson, 1937; Salt, 1940; Bai *et al.*, 1992). However, the extra host resources in larger hosts take longer to consume and assimilate, and development time may be prolonged (Arthur & Wylie, 1959).

The relationship between host size at oviposition, and fitness-related traits in koinobionts is more difficult to define, and depends, among other things, on the host's feeding rate, its diet, and corresponding capacity for growth during the course of the interaction (Mackauer, 1986). King (1989) and Cloutier *et al.* (1991) suggested that, even for koinobionts, there is a measurable correlation between initial and final host size, thus between the host selected for oviposition and the food supply for the progeny. Empirical evidence for this has been documented (King, 1989) although most studies have used parasitoids that show little flexibility in larval development, such as aphid parasitoids (e.g. Sequeira & Mackauer, 1992a, b, 1993). One of the aims of my thesis will be to examine published data for koinobiont development across a wider range of host-parasitoid associations and to further test this assumption empirically using a parasitoid that is not closely related to the aphidiids.

1.4 Defining life-history terminologies

During the course of this dissertation, certain terms are frequently used to describe specific attributes of parasitoid and host behaviour, reproduction and development. Three major terms that can be found in the literature are strategy, tactics and fitness. These terms, as they apply to the context of my thesis will therefore be defined at the outset; other terminologies which appear in different chapters are defined elsewhere in the introduction or in the chapter concerned.

1. *Strategy*

The terms "strategy" is defined in accordance with Dominey (1984) and Mackauer & Sequeira (1993) and describes a set of rules specifying which alternative pattern of responses is used in a given situation; for each species, these rules are typical and illustrate their adaptation to particular environments (for larval parasitoids, the host represents the environment).

2. *Tactics*

Tactics are option sets or mechanisms that enable evolutionary objectives to be achieved, and may vary between different individuals or phenotypes. Whereas strategies represent adaptive responses of species to their environment (for example, koinobiosis and idiobiosis represent life-history strategies), tactics are behavioural responses that may vary in a given situation, for example the various defensive behaviours of host larvae against attack from parasitoids are tactics, rather than strategies.

3. *Fitness*

The term fitness is often used by ecologists, population geneticists and others in the life sciences (see Dawkins, (1982)) for a summary of different definitions of fitness and the many shortcomings of the term). In my thesis I use the concept of fitness in the classical term as described by Darwin (= "Darwinian fitness") where it is a measure of the lifetime reproductive success of individual parasitoids; fitness is therefore the property of a genotype, which is the average survival and reproductive success of individuals of that genotype. The lifetime progeny production of an individual is a direct measure of fitness; more indirect measurements are interpreted as "fitness correlates" and include differences in individual size that may have corresponding effects upon an individual's reproductive success.

1.5 Host-parasitoid associations used in this study

This dissertation is an investigation of interactions between the solitary larval endoparasitic koinobiont wasp, *Venturia canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae) and three of its hosts, the Indian meal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), the rice moth, *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae) and the flour moth, *Anagasta kuehniella* (Zeller) (Lepidoptera: Pyralidae). The four species are particularly well suited for laboratory investigations because they are easily cultured and many generations can be reared in a comparatively short time. *Venturia* is predominantly parthenogenetic, hence there is no need to spend time mating the wasps before experiments. Details of their life-histories and biologies are found in Chapter 2.

1.6 Thesis overview

Host and parasitoid interactions have been the subject of serious investigation for over a century (Vinson, 1985). From a mechanistic point of view, there is a wealth of detailed information on the effects of parasitoid growth and development on host physiology and behaviour, in addition to the parasitoid's response to variations in the nutritional state and physiology of the host during parasitism. However, less emphasis has been placed on the role of various host-related constraints on parasitoid development from the perspective of the fitness value of different developmental characteristics and patterns of host utilization. These constraints, relating to a host's physiological and nutritional suitability, determine whether a specific host stage or species is capable of supporting parasitoid maturation to eclosion. Chapters three to six explore the influence of several constraints on the growth, development and survival of *Venturia.* I will examine different constraints imposed by superparasitism, a reduction in the quality of host diet and the species of host attacked and determine if they affect the ability of *Venturia* to develop in different instars. From these results, I will determine if suitability is a static property of the host, or if it varies in accordance with the nature of the constraint. I will discuss the possible factors responsible for the evolution of koinobiosis, and suggest why patterns of development for koinobiont parasitoids vary from one host-parasitoid association to another.

Chapter three experimentally tests the predictions of several host-size optimality models (e.g. Charnov, 1979; Charnov *et al.*, 1981; Charnov & Skinner, 1985) by monitoring the growth trajectories of *Venturia* from early-1st instar to eclosion from four different instars of *Plodia* provided with excess food throughout their larval life.

Recording the growth trajectories of parasitoids in this way provides information on the degree of physiological synchrony between host and parasitoid, for example whether the parasitoid is developing at its physiological limit in different host stages. The data will be compared with that recently obtained in a separate study from another koinobiont, *Aphidius ervi*, that develops in different nymphal instars of the pea aphid (*Acyrthosiphon pisum*).

Superparasitism (whereby a second wasp oviposits on, or in a previously parasitized host) has received considerable attention in recent years, although mostly from the functional perspective of decisions made by the ovipositing parasitoid (e.g. Visser *et al.*, 1990; Volkl & Mackauer, 1990; van Alphen *et al.*, 1992; Visser, 1993; Fletcher *et al.*, 1994). In many instances these studies have suggested that the decision to accept or reject a previously parasitized host should rest on factors such as the current energy reserves of the female wasp, its egg load and the quality of other hosts in the vicinity. This is because the progeny of a superparasitizing female are often at a competitive disadvantage in comparison with the progeny of the first female (Godfray, 1994). Fewer studies have investigated if superparasitism has any fitness-related costs on the surviving parasitoid larva in terms of increased development time or a reduction in the size of the emerging adult wasp. Thus, in order to evaluate this more clearly, Chapter four explores the effect of superparasitism on the development of *Venturia* from two instars of *Plodia*, and in hosts containing different numbers of parasitoid eggs.

Many koinobionts parasitize early host stages which must grow in order to provide the immature parasitoid with sufficient sustenance. Several studies have shown that parasitoid development is affected by the nutritional state of the host (e.g. Beckage & Riddiford, 1983; Bouletreau, 1986; Dover & Vinson, 1990) although these effects have not been tested across a range of instars. Chapter five examines the effects of host starvation on the development of *Venturia* reared from two instars of *Plodia* with considerably different growth potential after parasitism. Moreover, varying the length of starvation in hosts parasitized as third instars enables the developmental stage at which *Plodia* provides *Venturia* with the minimum amount of resources for successful development to be determined, and if the parasitoids adjust their development according to host conditions.

Venturia is capable of parasitizing and developing in at least 14 species of lepidopteran larvae (Salt, 1975). However, like many endoparasitic wasps, the host range of *Venturia* is restricted to one or two families (Krombein *et al.*, 1979), although the growth potential of different hosts varies considerably. For example, *Nemapogon*

granella rarely exceeds 10 mg prior to pupation, while *Galleria mellonella*, a less-studied host, may exceed 200 mg at the same stage (Salt, 1975). Several studies have shown that solitary endoparasitoids use different developmental strategies in hosts with different growth potential (e.g. *Hyposoter exiguae*; Beckage & Templeton, 1985). A certain minimum host size is probably required to support the development of parasitoids, therefore different host species may exhibit species-specific growth characteristics that result in their attaining the critical size for parasitoid maturation at different times during their development. In Chapter six, I examine the development, to eclosion, of *Venturia* when reared from four instars of *Plodia* and *Corcyra*, two hosts with considerably different growth potential. Healthy, late-5th instar *Plodia* larvae attain final masses comparable to early-5th instar *Corcyra*. This chapter also discusses the effects of parasitism on final host size in *Corcyra*, to determine the degree of host regulation by *Venturia*.

Whilst setting up the experiments undertaken in Chapter six, I noted that both *Plodia* and *Corcyra* exhibited a variety of escape and defence behaviours when antennally palpated by *Venturia*, with *Corcyra* adopting more aggressive responses than *Plodia*. Although host acceptance has been widely studied (reviewed in Arthur, 1981), few investigations have examined the role of host behaviour on parasitoid levels of host acceptance and preference. Most have assumed that the host plays no role in this phase (step 3) of the host-parasitoid association; however host behaviour may represent a second constraint upon parasitoid fitness by limiting the acceptability of higher (nutritional) quality hosts. Therefore, in Chapter seven, the role of host behaviour on the foraging and acceptance behaviour of *Venturia* is examined. Host behaviour is probably under the influence of several selection pressures, thus the response of 3rd (L3) to 5th (L5) hosts of both species to simulated parasitoid touch will be explored. The chapter tests the hypothesis that host size and species, as correlated with aggressive behaviour, is a limiting factor rather than a releasing stimulus for the expression of host acceptance behaviour by *Venturia*. Furthermore, the importance of host movement on acceptance is also investigated.

Chapters three to six examine the influence of several constraints on parasitoid fitness correlated with larval parasitoid development that potentially affect the size and development time of the emerging adult wasp. However, the influence of parasitoid size on lifetime reproductive success has been very little studied. In Chapter eight, I examine the lifetime reproductive success of *Venturia* from L5 *Plodia* under controlled experimental conditions. Most existing studies have used a technique for estimating parasitoid life-history parameters that have involved the continuous exposure of

parasitoids to excessive numbers of host larvae (and constant food) that have led to potentially inaccurate estimates of reproductive potential and population growth rates because parasitoids deplete their egg complements early in their adult lives and then experience prolonged periods of postreproductive survival. The reproductive success of *Venturia* is explored in response to temporal host and food (honey solution) availability, thus manipulating both parameters under a single experimental setting. The experiments determine if *Venturia* adjusts its fecundity schedule in accordance with a different set of constraints imposed by host availability and starvation.

In Chapter nine, all of the experiments undertaken are discussed and compared with existing studies. Special emphasis is placed on differences in the adaptive pattern of growth and development in koinobiont and idiobiont parasitoids, and the effect of host stage, size, species, nutritional status and other factors on host suitability and the ability of the parasitoid to regulate host development for their own benefit. The importance of further empirical investigations, examining the growth trajectories of gregarious parasitoids, or parasitoids in superparasitized or poorly-nourished hosts, are explored. Furthermore, the findings of the lifetime reproductive success experiments are discussed with regard to the theory of life-history evolution and the hypothesis of trade-offs between life-history characters.

2. Materials and methods

2.1 The biology of *Plodia interpunctella* (Hübner)

The Indian meal moth, *Plodia interpunctella* (Lepidoptera: Pyralidae; Phycitinae) is a major cosmopolitan pest of stored food products, particularly dried fruits, cereals, nuts and oilseeds (Bell, 1975; Cox & Bell, 1991). A number of studies investigating the life-cycle of *Plodia* have found development to be highly dependent on environmental conditions (Tsuji, 1958, 1959; Tzanakakis, 1959; Williams, 1964; Morere & Le Berre, 1967; Reyes, 1969; Savov, 1973). The egg-to-adult development time of *Plodia* is temperature-dependent, ranging from 60 days at 20°C to 25 days at 30°C (Bell, 1975). Humidity and food quality may also influence development (Subramanyam & Hagstrum, 1993).

Plodia passes through 5 larval instars, although up to 7 have been recorded (Miles, 1932; Morere & Le Berre, 1967; Silacek & Miller, 1972; Mossadegh, 1976) but temperature does not influence instar number (Hassan *et al.*, 1962). Low temperatures, short photoperiods, and high population densities have been found to induce diapause in later instars, although this varies between strains (Tsuji, 1963; Bell, 1977, 1982; Bell *et al.*, 1979). Constant light has also been found to induce later instars into diapause (Bell, 1979; Kikukawa & Masaki, 1984). Laboratory-reared strains have shown a reduced capacity to diapause (Sait, 1992). At maturity, late fifth instar larvae cease feeding and may leave the food medium in search of pupation sites. This behaviour is known as the "wandering phase" (Tzanakakis, 1959). Once a suitable site is located, the larvae spin cocoons, enter the pre-pupal and pupal stages and eclose as adult moths between five and ten days later. Pupal duration is temperature-dependent (Richards & Thomson, 1932) but is independent of the duration of the preceding larval stage (Fraenkel & Blewett, 1946).

Adult females are generally larger and heavier than males (Silacek & Miller, 1972) with this difference also occurring in late larval and pupal stages (Couture & Huot, 1967). Under good nutritional conditions, late fifth instar female larvae (hereafter L5) may weigh up to 30 mg (Chapter 4). Adults survive for about 7 days after emergence (Silacek & Miller, 1972) and multiple matings may occur during this time (Brower, 1975; Gage & Cook, 1994). Oviposition occurs from 24 hours after a successful mating, with eggs distributed singly or in batches (Mossadegh, 1976). Viable egg production usually ceases about four days after eclosion (Morere & Le Berre, 1967; Lum & Flaherty, 1969; Silacek & Miller, 1972). Hatching is also

temperature-dependent, occurring as early as 3 days after oviposition at 30±5°C (Silacek & Miller, 1972); 4 to 9 days at 25 to 28°C (Richards & Thomson, 1932); and 5 to 14 days at 15.5° to 18.5°C(Hill, 1928).

2.2 The biology of *Anagasta kuehniella* (Zeller)

Anagasta is also a major pest of stored food products, being especially numerous in cereals and flour mills (Cole & Cox, 1981; Cox & Bell, 1991). Although *Plodia* and *Corcyra* are probably of tropical origin, it is believed that *Anagasta* originated in temperate regions of the Northern Hemisphere because it cannot tolerate high temperatures and humidities characteristic of tropical climates (Bell, 1975; Jacob & Cox, 1976; Cox & Bell, 1991). The development of *Anagasta* varies with temperature, 10°C being the lower limit for survival and 30°C the highest (Jacob & Cox, 1976). Sterility of males is induced if they are reared at 30°C or in continuous light (Ahmad, 1936; Raichoudhury & Jacobs, 1937).

Development occurs most rapidly at 25°C with 70% relative humidity, although *Anagasta* can utilize their own metabolic water and survive when the relative humidity is very low (Fraenkel, 1941; Jacob & Cox, 1976). Wheat flour is the preferred larval food, with the life cycle being completed in 50-70 days under optimal conditions of diet and environment (Fraenkel & Blewett, 1944; Subramanyam & Hagstrum, 1993).

Larval development is similar to that of *Plodia,* although the time spent in each larval instar is longer for *Anagasta* (Brindley, 1930). Larvae are cold hardy, and can survive for several days at 10°C (Jacob & Cox, 1976). At -18°C all developmental stages are killed within 24 hours (Mathlein, 1961). Older eggs can also tolerate cold more than younger eggs (Bell, 1975). Newly emerged larvae become less resistant to cold after they commence feeding (Salt, 1936).

Oviposition does not occur at temperatures below 5°C although female moths can be induced to oviposit at slightly higher temperatures (Cox & Bell, 1991). If eggs are laid at 25°C, hatching is temperature-dependent and takes 16 days at 15°C down to 4 days at 30°C (Subramanyam & Hagstrum, 1993). The pupal stage lasts approximately twice as long as the egg stage, irrespective of temperature (Cox & Bell, 1991). Pupal size and duration is also influenced by relative humidity (Ahmad, 1936).

The size of adult moths is correlated with the weight of the final-instar larva at pupation (Daumal & Boinel, 1994). Reproductive potential is independent of oviposition (Chauvin, 1969) and ovulated eggs are not resorbed (Daumel & Boinel, 1994). Adult female moths are able to mature over 500 eggs, although many are probably infertile because they never produce this many progeny, even when conditions are favourable (Ahmad, 1936). The number of fertile eggs laid per female is affected by temperature, with 170-200 oviposited in the optimal temperature range (20°C - 25°C) (Ahmad, 1936). Fewer eggs are laid at 30°C or below 15°C (Brindley, 1930). Unsuccessful pairing is the most important cause of infertility at suitable temperatures (Daumal & Boinel, 1994). Mated females live for 9-11 days at 18°C and 5-7 days at 30°C.

2.3 The biology of *Corcyra cephalonica* (Stainton)

Corcyra cephalonica (Lepidoptera: Pyralidae; Gallerinae) is also a serious pest of stored products, particularly in more humid tropical regions of south east Asia and Africa. It infests a wide range of foodstuffs, particularly groundnuts, maize, rice and cocoa beans (Cox *et al.*, 1991). Amongst stored product pest Lepidoptera, it is second only to *Anagasta cautella* (Walker) in terms of frequency of importation in stored products to Britain and numbers found (Freeman, 1976). The development of *Corcyra*, like that of *Plodia*, is highly dependent on environmental conditions (Carmona, 1958; Kamel & Hassanein, 1967; Rahman & Jahan, 1979; Cox *et al.*, 1981; Osman *et al.*, 1984; Etman *et al.*, 1988; Cox & Bell, 1991; Subramanyam & Hagstrum, 1993). Temperature and relative humidity significantly influence duration of the life-cycle of *Corcyra*. The egg-to-adult development time varies from 182 days at 17.5°C to 26 days at 30°C (Cox *et al.*, 1981). *Corcyra* requires a higher relative humidity than most other pest moths of stored products, being unable to develop at levels below 15% (optimum 80%; Cox & Bell, 1991), although at over 90% mold accounts for high larval and pupal mortality. In Brazil, *Corcyra* outcompetes *Anagasta kuehniella* in humid equatorial climates, but is competitively excluded by *Anagasta* in drier subtropical areas.

Corcyra completes 5 larval instars, although Russell *et al.* (1980) found that larger female larvae may pass through 6 instars if they exceed a size threshold prior to pupation. Diapause has rarely been observed in *Corcyra*, although, like *Plodia*, it is probably influenced by temperature and photoperiod (Etman *et al.*, 1988). Below 18°C it is unlikely that *Corcyra* could multiply rapidly enough to reach pest status in temperate regions (Cox & Bell, 1991) although it survives mild winters in Britain

probably through diapause as a late larval instar. In Britain it has bred during midwinter in warehouses where heavy infestations caused peanuts to heat (Freeman, 1976). Unlike *Plodia*, final instar *Corcyra* are more reluctant to leave the food medium during the "wandering phase" and do so only when densities exceed a very high threshold (personal observations). Consequently, the larvae appear to tolerate the presence of conspecifics in much closer proximity than other related species (eg. *Plodia* and *Anagasta* spp.). Larvae spin a tough, closely-woven double-layered cocoon near the surface of the medium (Etman *et al.*, 1988; Cox & Bell, 1991). Pupal duration is temperature dependent: at 28°C, it averages approximately 10 days, with males emerging 1-2 days earlier than females (Etman *et al.*, 1988). Under good nutritional conditions, final instar larvae may weigh in excess of 60 mg (or twice the mass of late 5th instar *Plodia*) with males being slightly smaller than females (Salt, 1975; Etman *et al.*, 1988).

Adult lifespan varies with sex and mating status; at 28°C mated males lived 9.1 days (virgin males 7.0) while mated females lived 8.3 days (virgin females 8.0; Etman *et al.*, 1988). Females generally mate only once during their lifetimes (Shazali & Smith, 1986) usually at night (Etman *et al.*, 1988). Fecundity is extremely variable, averaging about 200 eggs for both mated and virgin females (Russell *et al.*, 1980). Eggs are laid singly, egg production ceasing about 5 days after emergence (Pajni *et al.*, 1978). Egg duration is influenced by temperature, but not by relative humidity (Etman *et al.*, 1988; Cox *et al.*, 1981). *Corcyra* eggs are not as cold tolerant as are those from *Plodia* and *Anagasta* (Cox *et al.*, 1981). No eggs hatch at 10°C or less, and only 10% of larvae emerge at 20% relative humidity (Cox & Bell, 1991). Hatching occurs about 4 days after oviposition at 28°C (Etman *et al.*, 1988).

2.4 The biology of *Venturia canescens* (Gravenhorst)

Venturia canescens (Hymenoptera: Ichneumonidae) has formerly been known under the generic names *Devorgilla*, *Exidechthis*, *Idechthis* and *Nemeritis*. It is a cosmopolitan solitary koinobiont endoparasitoid that attacks a number of closely related lepidopteran pests of stored products (Diamond, 1929; Beling, 1932; Ahmad, 1936; Simmonds, 1943; Corbet & Rotheram, 1965; Salt, 1975).

Venturia reproduces parthenogenetically through a modified form of automictic thelytoky (Speicher, 1937; Narbel-Hofstater, 1964; Speicher *et al.*, 1965). Males are rarely, if ever encountered; in the course of my study, none has been observed, but males have been recorded by Beling (1932). *Venturia* produces copious numbers of

hydropic eggs (Flanders, 1950; Jervis & Kidd, 1986) the proteins for egg production being secured during larval feeding on the host (Dowell, 1978). Adult wasps do not host-feed but nevertheless are synovigenic (Flanders, 1950; Dowell, 1978; Jervis & Kidd, 1986; Rosenheim & Rosen, 1992; see 2.4). Under conditions of host-deprivation, eggs continue to be ovulated for up to 6 days after eclosion at 25°C, when the oviducts become greatly distended with mature eggs.

Venturia covers its eggs with virus-like particles that effectively protect it from the cellular encapsulation of its habitual hosts (Salt, 1968; Fedderson *et al.*, 1986; Berg *et al.*, 1988). The particles consist primarily of glycoproteins with no detectable nucleic acid component but DNA is not packaged into the particles (Fedderson *et al.*, 1986). Several other braconid and ichneumonid wasps have been found to carry virus-like particles in their calyx glands containing measurable amounts of DNA (Edson *et al.*, 1981) and these particles appear to be produced in a similar fashion to the particles found in the reproductive tract of *Venturia* (Fedderson *et al.*, 1986).

The development of *Venturia* is influenced by environmental factors such as temperature (Ahmad, 1936).which also affects egg production and rate of ovulation in adult wasps (Trudeau & Gordon, 1989). At 15°C, *Venturia* (L5 *A. kuehniella* as host) spent 103 days as a pre-adult; this decreased to 55.5 days at 18°C, 30 days at 23°C, and 21 days at 30°C (Ahmad, 1936). Below 15°C, *Venturia* cannot develop, even though the host continues to do so (Ahmad, 1936).

Venturia has been studied extensively for over 70 years (eg. Diamond, 1929; Beling, 1932; Ahmad, 1936; Simmonds, 1943; Williams, 1952; Takahashi, 1962; Corbet & Rotheram, 1965; Corbet, 1968, 1971; Cook & Hubbard, 1977; Waage, 1978, 1979; Fedderson *et al.*, 1986; Hubbard *et al.*, 1987; Berg *et al.*, 1988; Trudeau & Gordon, 1989; Gordon *et al.*, 1991; Hughes *et al.*, 1994a,b). In most studies, *A. kuehniella* has served as host, but more recently other closely related hosts have been used, for example *Plodia* (Rogers, 1972; Podoler, 1974; Hughes *et al.*, 1994a,b) and *A. cautella* (Hubbard *et al.*, 1987; Trudeau & Gordon, 1989; Gordon *et al.*, 1991). Salt (1975) found that *Venturia* can develop, with varying degrees of success, from 14 host species.

2.5 The influence of host deprivation and oviposition experience on egg load and maturation in *Venturia*

2.5.1 Age and egg load in *Venturia*

In order to test the relationship between adult size and egg load, 10 newly-emerged wasps varying considerably in size were killed in 70% alcohol, placed on a moistened slide, and dissected by holding the first metasomal tergite with forceps and carefully pulling the ovipositor distally with another pair of forceps. Ovulated eggs were counted by cutting the oviducts below the ovaries, and carefully teasing them into the suspension. Wasp size was determined by comparing hind tibia lengths. The procedure was repeated in 50 five-day old wasps.

At emergence, adult wasps are ready to oviposit, but the number of mature eggs available for oviposition is largely dependent on the size of the wasp. The number of ovulated eggs in the lateral oviducts of adult parasitoids less than 12 hours after eclosion varied significantly with adult wasp size ($r = 0.91$, n = 10, $P < 0.001$; Fig. 2.1). Soon after emergence, large parasitoids (hind tibia length > 1.80 mm) store over 5 times as many eggs in their oviducts as small parasitoids (hind tibia length < 1.40 mm).

There is also a significant correlation between parasitoid size and egg load in 5-day old adult wasps ($r = 0.73$, n = 50, $P < 0.01$, Fig 2.2). The largest wasps, with hind tibia lengths of almost 2.0 mm, stored approximately twice as many eggs in their oviducts (180-220) as individuals with hind tibia lengths of 1.4 mm (90-110).

2.5.2 Egg maturation and ovulation in *Venturia*

The aim of this study was to determine if *Venturia* are able to mature (ovulate) additional eggs after reaching egg storage capacity in the lateral oviducts and following a number of oviposition experiences.

Parasitoids were isolated from culture as pupae and placed in glass vials (refer to 2.7). For each treatment, the following procedure was applied. The contents of a culture jar containing 20-22 day old late L5 *Plodia* larvae was emptied onto a coarse sieve which was placed over 2 finer sieves and a container base. The contaminated medium was shaken vigorously to enable finer food medium to be filtered from the host-containing material, which remained in the top (coarse) sieve. This sieve was then placed over a second base, with a heat lamp being situated 5-10 cm over the

medium. This drove the larvae down through the coarse sieve and into the base, where they could be easily removed. Using a pair of soft forceps, hosts were placed into small plastic tubs in groups of 50.

Larvae were chilled in a freezer for approximately 5 minutes at -10°C and were then placed in groups of 125 onto a patch (this consisted of a standard-sized Petri dish filled to within 5mm of the surface with plaster of Paris). Approximately 2 grams of finely milled wheat bran was evenly spread over the patch containing hosts, and this was covered by nylon bolting cloth which was firmly secured by two elastic bands. The patches were than left in a plastic box for 24 hours before being presented to parasitoids. This enabled the hosts to release copious quantities of mandibular secretions, silk and frass which are known to contain kairomones that elicit probing behaviour by *Venturia* (Corbet, 1971; Waage, 1978). During the experiments, each wasp had access to two patches (250 larvae) that were placed into a large plastic boxes and contained sufficient bran to reach the top rim of each patch.

Ovarian maturation is at its maximum 5-7 days after the emergence of *Venturia* (Fig. 2.3). Thus, 40 wasps were deprived of hosts for 5 days, then placed, in groups of 5, into boxes containing two patches for 24 hours. At the conclusion of this period 30 wasps were transferred singly to plastic vials with a drop of honey smeared on the inside lid of each vial. The other ten wasps were immediately frozen, then dissected under a stereomicroscope. The number of mature eggs (those recognized in the calyx gland and oviducts as being transparent and ellipsoidal) were counted. This procedure was repeated over the following three days, with ten wasps removed daily, dissected, and egg loads determined. A separate group of 80 wasps was used as controls. Groups of ten wasps were dissected on days one, three and 5-10 after eclosion, and their egg loads counted (as above). None of these wasps had access to hosts at any time during their life.

Egg load is a positive function of adult wasp size in *Venturia* (Figs. 2.1, 2.2, and Chapter 6). Therefore, it was necessary to standardize, as much as possible, wasp size (hind tibia length) for this experiment. One-way ANOVA revealed that the size of wasps did not vary significantly between treatment ($F = 0.57$, d.f. = 9, 90, $P > 0.05$). Tukey's pairwise comparisons also showed that the mean hind tibia length of wasps from did not differ significantly between any of the treatments ($P > 0.05$). The mean hind tibia length of wasps in each age/treatment group was between 1.59 and 1.66mm.

Fig. 2.1 The relationship between adult *Venturia* size, measured as hind tibia length, and the number of mature eggs carried in the lateral oviducts when less than twelve hours old.

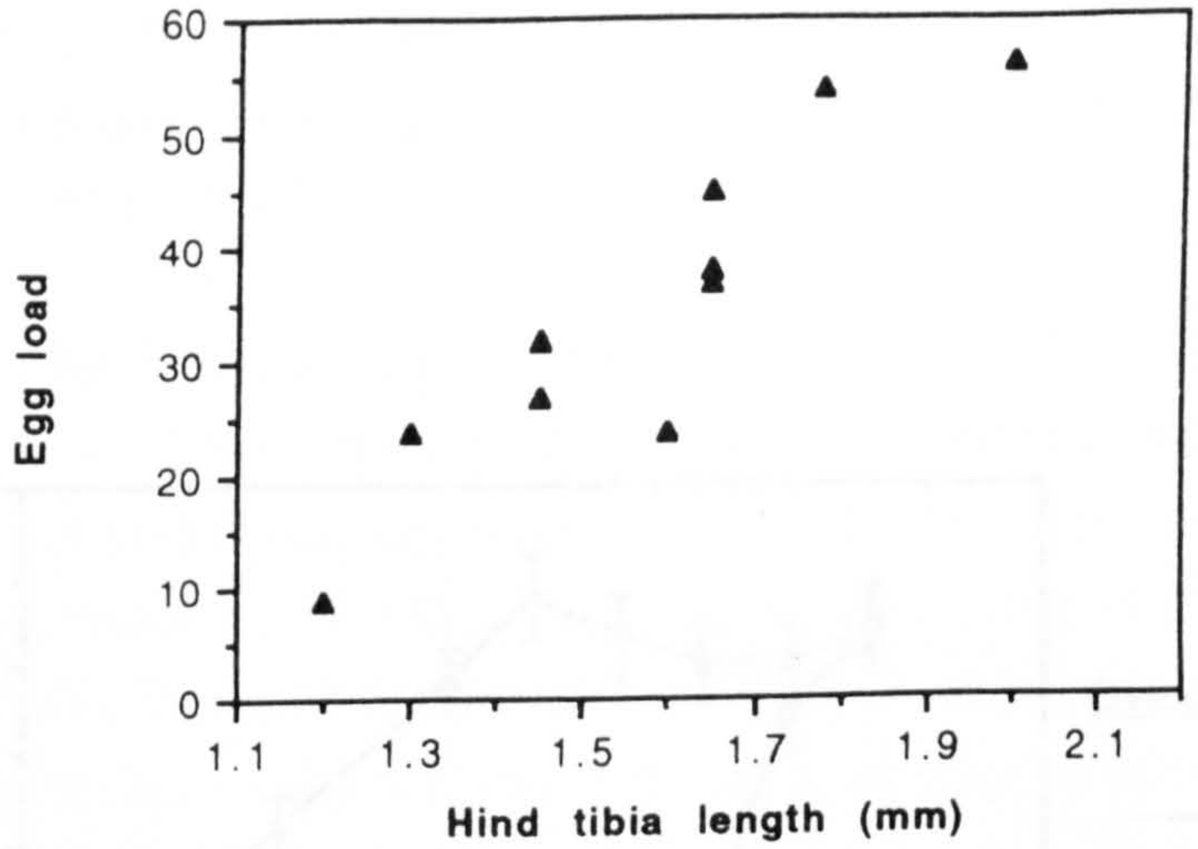


Fig. 2.2 The relationship between adult *Venturia* size, measured as hind tibia length, and the number of mature eggs carried in the lateral oviducts when five days old.

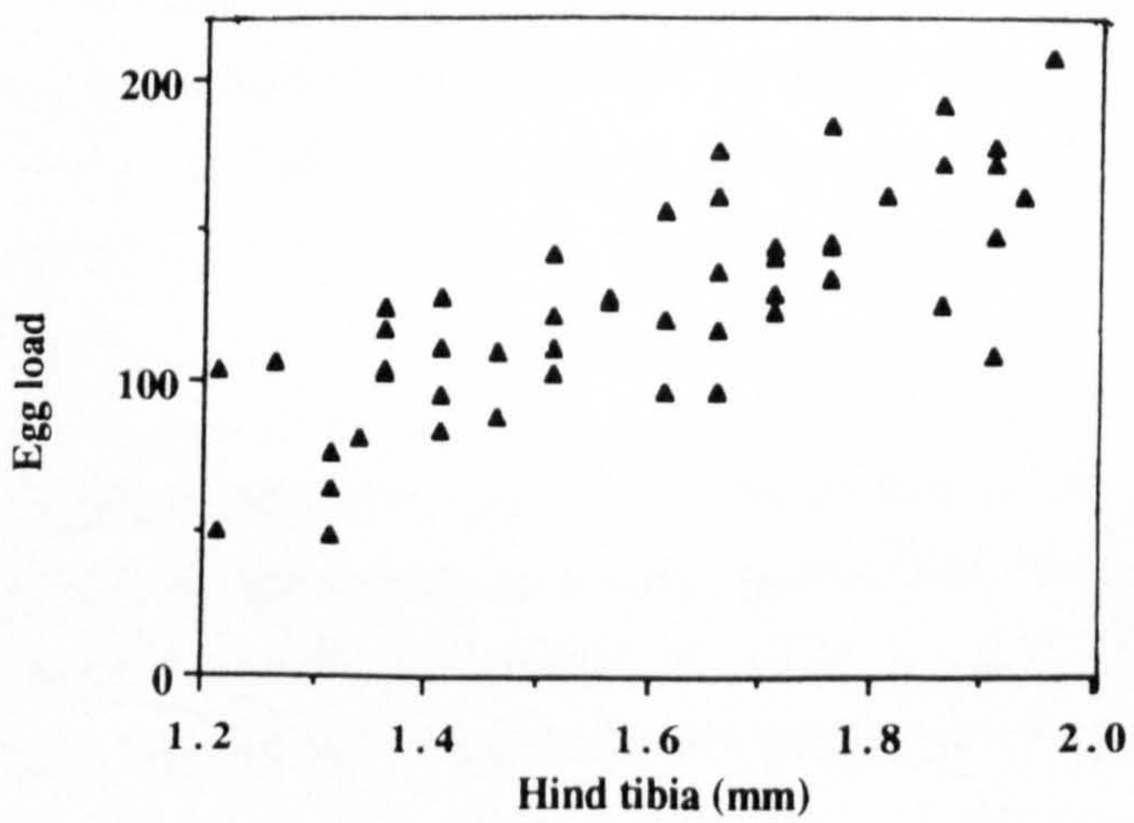
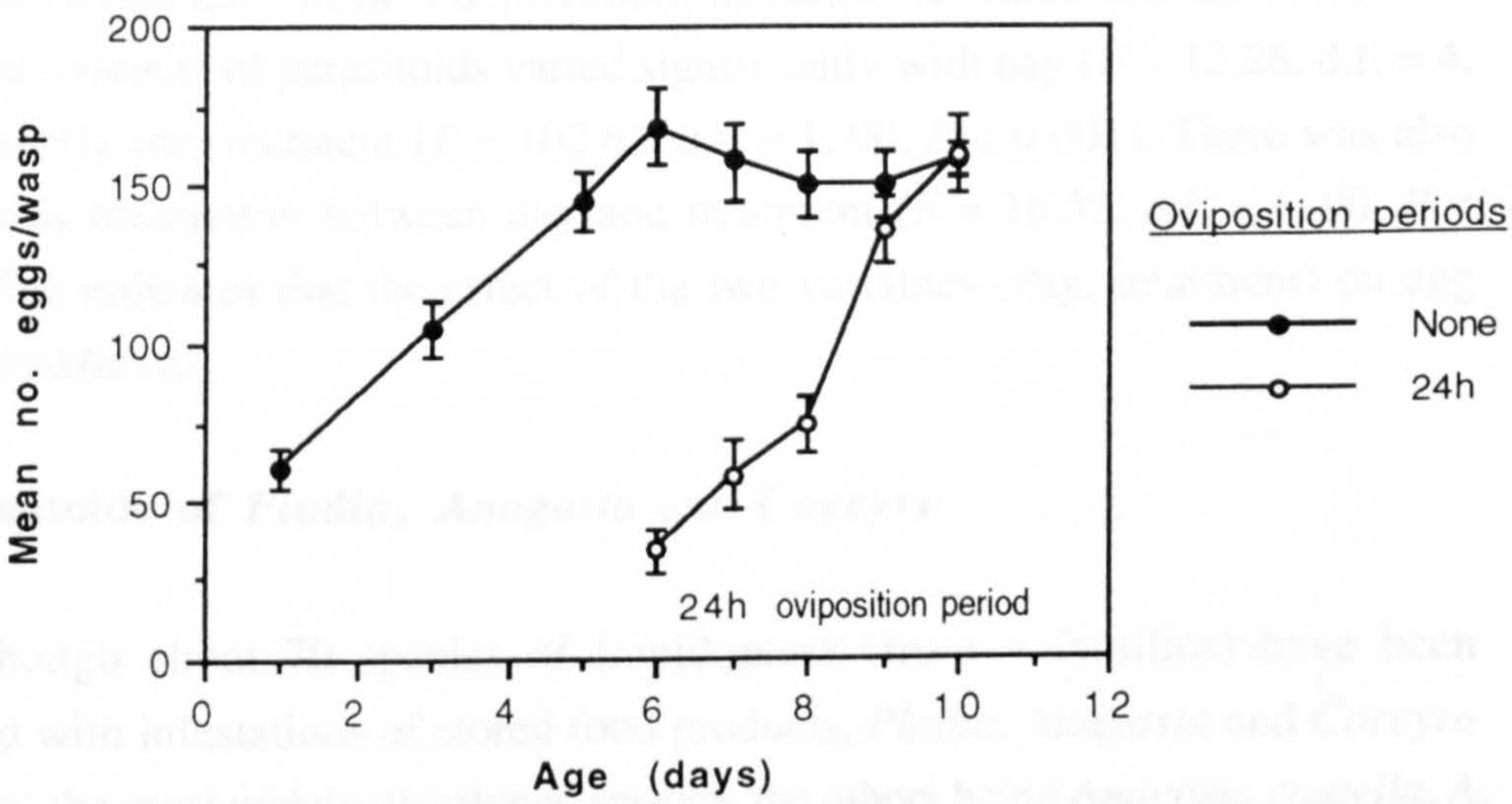


Fig. 2.3. Average number of mature eggs carried in the lateral oviducts of adult *Venturia* of different ages after zero and 24 hours oviposition in L5 *Plodia* larvae.



When *Venturia* is deprived of hosts after eclosion, the number of mature eggs in the oviducts increases over several days reaching a maximum of approximately 160 at 6 days of age, declining slightly to about 150 after 8 days, then remaining fairly constant up to the 10th day after emergence (Fig. 2.3). Females provided excess hosts for 24 hours between the 5th and 6th day after eclosion laid up to 80% of their available eggs but replenished their egg supply over the next 4 days, acquiring the same complement of eggs as females of corresponding ages that were not provided with hosts (Fig. 2.3).

A two-way ANOVA for egg number, with day (6-10) and treatment (oviposition experience or host deprivation) as factors revealed that the number of eggs in the oviducts of parasitoids varied significantly with day ($F = 12.26$, d.f. = 4, 90, $P < 0.001$) and treatment ($F = 102.63$, d.f. = 1, 90, $P < 0.001$). There was also a significant interaction between day and treatment ($F = 16.35$, d.f. = 4, 90, $P < 0.001$). This indicates that the effect of the two variables (day, treatment) on egg number is additive.

2.6 Parasitoids of *Plodia*, *Anagasta* and *Corcyra*

Although about 70 species of Lepidoptera (from 4 families) have been associated with infestations of stored food products, *Plodia, Anagasta* and *Corcyra* are three of the most widely distributed species, the others being *Anagasta cautella, A. elutella, A. figulilella* and *Sitrotega cerealella* (Richards & Thompson, 1932; Cox & Bell, 1991). Apart from their feeding, the polyphagous larval stages cause considerable damage to a variety of stored food products through the production of large quantities of frass and silk, of which the latter seriously clogs machinery used in this industry. *Corcyra*, and to a lesser extent *Anagasta* and *Plodia* produce particularly dense webbing (Cox & Bell, 1991). The adult stages have no direct effect upon the stored product.

Control of these pests has been effectively undertaken in the past using a number of synthetic chemical insecticides such as malathion, but *Plodia* in particular has developed some resistance to them (Zettler *et al.*, 1973; Attia, 1977). Although a comprehensive analysis has not yet been made of hymenopteran parasitoids that attack stored product pest Lepidoptera, a considerable body of information has been accrued which shows that a large parasitoid fauna is at least potentially associated with these pests. However, until recently, analysis of this fauna has been hampered

by a poor taxonomic knowledge of the species involved (Cox & Bell, 1991). It is clear that *Plodia*, *Corcyra* and *Anagasta* spp. are attacked by a number of egg, larval and pupal parasitoids primarily from the superfamilies Chalcidoidea, Chrysidoidea and Ichneumonoidea (Cox & Bell, 1991). The ichneumonoids constitute the most important group of parasitoids that attack lepidopterous pests of stored products (Cox & Bell, 1991). Larval populations are often heavily parasitized by braconid and ichneumonid wasps, which may also transmit pathogenic micro-organisms (Podoler, 1974; Beegle & Oatman, 1975). The two most widely known larval parasitoids of these pests are *Venturia,* and the gregarious ectoparasitic idiobiont *Bracon hebetor* Say (Hymenoptera: Braconidae). Several pimpline ichneumonids are known pupal parasitoids of *A. kuehniella* and *A. elutella.*

Early studies showed that *Plodia, Corcyra* and *Anagasta* (most information being available on the last species) are probably hosts to over 20 parasitoid species (Waterston, 1921; Richards & Thomson, 1932) although an updated review is urgently required. It is quite probable that the actual number of parasitoids that attack these hosts is considerably greater. For example, although widely reported as a parasitoid of *Plodia* and *Anagasta,* it was not known that *Venturia* can successfully develop from *Corcyra* until experiments by Salt (1975) revealed this to be so.

2.7 Culturing methods for *Plodia, Anagasta, Corcyra* and *Venturia*

All experiments were conducted and cultures maintained at 25°C (±2°C) with a 16:8 hour light:dark photoperiod.

1. *Plodia interpunctella* and *Anagasta kuehniella*

The original stock of *Plodia* was supplied from a colony reared at Dundee University, Scotland. They had been maintained as an outbred colony for 10 years and were sent to Liverpool in October 1991 prior to the commencement of my experimental work. Additional moths were supplied from an outbred colony originating at Imperial College, Silwood Park, UK. These had been at Liverpool for about 5 years, being used for other research in the department.

Anagasta was supplied from a culture maintained at the Ministry of Agriculture, Fisheries and Food laboratories in Slough, Berkshire.

The diet on which they were reared followed that of Rogers (1972) and was prepared in large plastic tubs (5kg capacity) as follows:

1 kg of wheat middlings;

100 g of dried brewer's yeast;

100 ml of glycerol.

The medium was thoroughly mixed by hand, and stored in a freezer (-10°C) before use. Each day, the culture was set up with between 5 and 10 jars each containing 250-350 *Plodia* eggs and 75 grams of food medium. The open end of each jar was covered by a piece fine net curtain and secured with elastic bands. Eggs were measured and counted using a sealed and calibrated plastic pipette. They were obtained by placing over 300 adult moths from culture into a pail (diameter 20 cm) with coarse netting (diameter 2 mm) placed over the open end, secured by two large elastic bands. A small hole was cut in the base of the pail, and filled with dampened wool to provide a source of moisture for the adult moths. The pail was then inverted (open end facing downward) and placed over a large funnel which itself projected through a bunsen burner stand. Finally, a small jar was placed under the small aperture of the funnel to catch *Plodia* eggs which passed from the pail, and down the funnel. As cultures were set up daily, each jar contained larvae of similar age, and it was therefore possible to ascertain age and instar with some accuracy for experiments.

Anagasta was cultured in smaller numbers by placing 30-50 adult moths into a jar containing approximately 50 g of prepared food medium (see above). The moths were allowed to mate and oviposit into the medium, and this procedure was followed for successive generations. When required, L5 larvae were extracted about 40 days after oviposition for experiments (see Chapter 6). The culture was only maintained for one year because most of the experimentation was done using *Plodia* and *Corcyra* as hosts.

2. *Corcyra cephalonica*

The original culture of *Corcyra* was supplied from an outbred colony maintained for several years at Imperial College, Silwood Park, U.K. They were sent to Liverpool in November, 1992.

Corcyra were reared on a diet used at Silwood Park (M. Lane, personal communication) which was prepared in large (5 kg) plastic tubs. The preparation was as follows:

600 mg wheat middlings;
400 mg dried brewer's yeast;
400 mg fine milled cornmeal;
100 ml glycerol.

The medium was thoroughly mixed by hand and stored in a freezer (-10°C) between applications. *Corcyra* was used much less frequently for experiments than *Plodia,* hence cultures were only set up every 2-4 weeks as required. Between 50 and 70 adult moths were placed into 1 kg jars containing approximately 500 g of food medium so that eggs could be laid directly onto the food surface. As eggs were deposited over a period of several days, each culture maintained larvae of different ages and instars. The open end of the jar was covered by 2 layers of fine curtain netting and secured by several elastic bands.

3. *Venturia canescens*

Venturia was obtained from a culture maintained for many years at the University of Dundee, Scotland from which parasitoids have recently been sent to Ministry of Agriculture Laboratories in Slough, Berkshire. These were also supplied for my research.

Venturia was cultured in clear plastic boxes (17.5 x 11.0 x 5.0 cm) containing over 200 L4 and L5 *Plodia* larvae from the main stock. 10-15 adult wasps (aged over 5 days) were placed into the container with the hosts. Under culture conditions, *Venturia* attains its maximum eggload about 5-7 days after eclosion, and at this time they are very keen to forage, usually beginning immediate and intensive probing of the contaminated medium.

Some parasitized pupae were individually removed 16-18 days after parasitism and placed individually into glass vials for experiments; the rest were left in the boxes and were subsequently used to "re-stock" the culture. Upon eclosion, several pure drops of honey were smeared inside the box, providing a source of adult nutrition for the wasps (Jervis & Kidd, 1986). Honey is defined as the concentrated solution of sugars prepared by bees from the nectar of flowering plants (Pryce-Jones, 1950).

Figures on following pages:

Fig. 2.4 Adult *Venturia canescens* (x 10) probing host-contaminated food medium. The larva in the foreground is a fifth instar of the flour moth, *Anagasta kuehniella*.

Fig. 2.5 A size comparison of adult *Venturia canescens*, and the final four instars (L2-L5) of its host, the Indian meal moth *Plodia interpunctella* (x 10). The third instar larva is undergoing head-slippage in preparation for moult to the fourth instar.

Fig. 2.6 A size comparison of adult *Venturia canescens*, and the final four instars (L2-L5) of its host, the rice moth *Corcyra cephalonica* (x 8). The parasitoid on the slide is the same specimen as shown in Fig. 2.5. Note that *Corcyra* is much larger than *Plodia* during all corresponding stages of larval development.

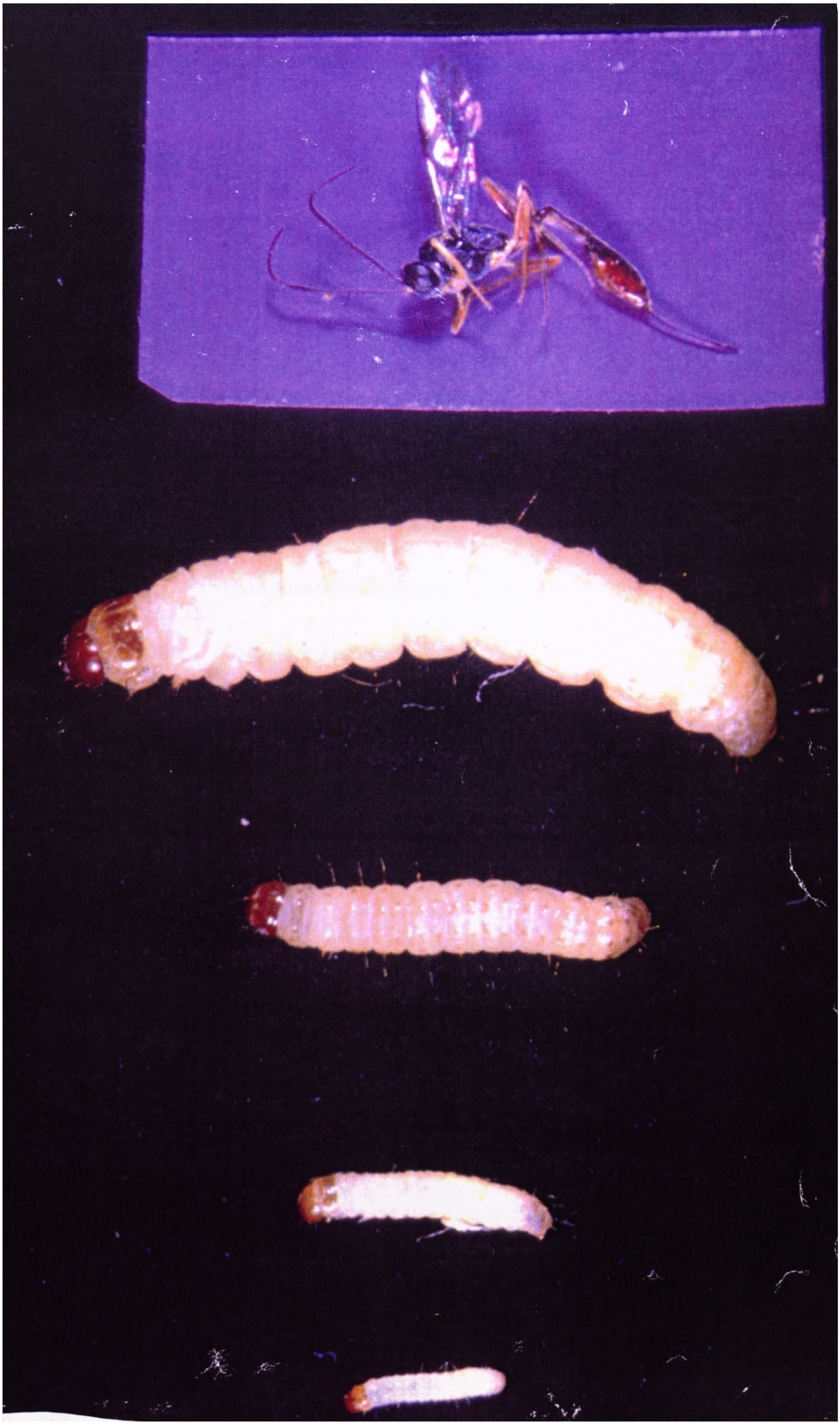


Table 2.1 Head capsule width and corresponding age for L2-L5 instars of *Plodia*.

Head capsule width

Instar	Width (mm)
2	0.28 - 0.33
3	0.40 - 0.45
4	0.60 - 0.70
5	0.85 - 1.15

Age of larvae*

10 days (late 2nd instar)

13 days (late 3rd instar)

16 days (late 3rd instar)

21 days (late 5th instar)

* Days after oviposition

Table 2.2 Head capsule width and corresponding age for L2-L5 instars of *Corcyra*.

Head capsule width

Instar	Width (mm)
2	0.50 - 0.60
3	0.70 - 0.85
4	1.00 - 1.20
5	1.40 - 1.50

Age of larvae*

12 days (late 2nd instar)

18 days (late 3rd instar)

24 days (late 4th instar)

32 days (late 5th instar)

* Days after oviposition

3. The effect of host instar on development of *Venturia canescens*

3.1 Introduction

Many recent models of parasitoid life-history strategies have assumed that host size is a measure of suitability for parasitoid development. Larger hosts are usually expected to be better than small hosts because they contain more resources for the developing parasitoid larva (Charnov, 1979; Charnov *et al.*, 1981; Charnov & Skinner, 1984; Waage, 1986). Ecological models of host-parasitoid interactions often assume that the host can be represented as a single stage and much of the development of predator-prey models has been devoted to host-parasitoid interactions for this reason (Hassell & Godfray, 1992).

Most of these models have been supported from studies of idiobiont parasitoids, where, adult wasp size is often positively correlated with host size (Salt, 1941; Arthur & Wylie, 1959; Vinson, 1972; Sandlan, 1979a; Strand *et al.*, 1988; King, 1989). For koinobionts, the relationship between host size at oviposition and adult wasp size is harder to predict and depends upon a number of complex and potentially interacting factors (Chapter 1). Variations in adult size can influence parasitoid reproductive success by increasing their longevity, fecundity and searching efficiency (Sandlan, 1979a; Vinson & Iwantsch, 1980a; Bellows, 1985).

The potential for host growth after parasitism by koinobionts is dependent upon several parameters that may vary both within and between host-parasitoid associations. First, the host's feeding rate and the nutritional content of the food medium determine its potential for growth, which has corresponding effects upon the development of the parasitoid larva (Guillot & Vinson, 1973; Zohdy & Zohdy, 1976; Beckage & Riddiford, 1983; Liu, 1985; Mackauer 1986; Slansky 1986). Second, some parasitoids that attack a range of host instars display varying degrees of developmental plasticity, spending variable and often extended periods as first instar larvae when developing in small or unsuitable hosts (Clausen, 1962; Doutt, 1964; Corbet, 1968; Smilowitz & Iwantsch, 1973; Sato 1980, Sato *et al.*, 1986). Finally, many parasitoids may regulate host behaviour, development, morphology and physiology due to injection of factors by the ovipositing wasp such as polydnaviruses, venoms and teratocytes, which are carried in the reproductive tracts of some ichneumonids and braconids (Vinson & Barras, 1970; Vinson, 1972; Cloutier & Mackauer, 1980; Vinson & Iwantsch, 1980b; Stoltz, 1986; Strand *et al.*, 1988). However, it is evident that some of the alterations

are also the result of selective tissue feeding by the parasitoid larvae (Vinson & Iwantsch, 1980b; Thompson, 1983). Many solitary parasitoids inhibit host growth, particularly during the latter stages of parasitism, or when the host exceeds its most suitable size or instar (Vinson & Barras, 1970; Jones & Lewis, 1971; Iwantsch & Smilowitz, 1975; Vinson & Iwantsch 1980b; Tanaka *et al.*, 1984), although in some associations growth is not affected, or may even be augmented (Cloutier & Mackauer, 1979, 1980; Slansky, 1986; Cloutier *et al.*, 1991).

Sequeira and Mackauer (1992a) investigated the effect of host instar on the development of the koinobiont parasitoid *Aphidius ervi* (Hymenoptera: Aphidiidae). They found that, regardless of instar of pea aphid *(Acyrthosiphon pisum)* attacked, the egg-to-adult development time of the wasp remained approximately constant, but the size of the emerging wasps increased as later instars were parasitized. This represents one extreme of a continuum, the other extreme of which is to delay parasitoid growth until the host has reached its maximum size. If this happens we would expect wasp size to be unaffected by instar at parasitism, but development time to be extended. The relative costs and benefits of delayed development and reduced adult size are likely to depend on the ecology of both the host and the parasitoid. *Venturia* is afforded some protection from predation and cannibalism, since its host constructs a cryptic, pre-pupal cocoon. In contrast hosts of *A. ervi* exhibit similar behaviour patterns, irrespective of development stage. Thus we might expect the response of *Venturia* to variation in host instar to differ from that of *A. ervi.*

In this chapter I will examine the growth trajectories (from egg to eclosion) of *Venturia* reared from four instars of *Plodia.* Variations in the growth trajectories of the parasitoid are discussed in relation to the host instar and its future growth potential. Furthermore, by analyzing variations in fitness-related traits of eclosed adult parasitoids (development time, mortality, dry mass) from different host instars I will argue that host quality under conditions of excess food is not simply a positive function of host size at oviposition, as has been demonstrated in many previous studies with idiobiont parasitoids.

3.2 Materials and Methods

Hosts and parasitoids were reared according to the method in section 2.2.

Instar identification and parasitism.

In order to obtain a larva of a given instar, L2 larvae were placed in vials with approximately 1 g of food medium and parasitized the same day in L2, and after 4 days (L3), 8 days (L4), or 12 days (L5). Individual larvae were presented to wasps, which were permitted to encounter a host only once (to avoid superparasitism). After parasitism, they were returned to the vials under the conditions described.

3.2.1 Parasitoid mortality, development time and adult size

Approximately 50 L2-L5 hosts were singly parasitized and placed in vials with 1 g of food medium. Adult wasp eclosion was checked several times during the day, enabling development time to be recorded. Eclosing wasps were killed by freezing, their hind tibia measured using an eyepiece graticule, oven dried for five days at 60°C and weighed on a Cahn 29 automatic microbalance. Hosts that produced adult moths, or in which both host and parasitoid failed to eclose, were recorded as parasitoid mortality.

3.2.2 Relationship between post-feeding ('wandering') host size and parasitoid size

In order to test the relationship between non-growing host size and adult *Venturia* size, 25 post-feeding L5 Plodia of a range of sizes were singly parasitized and weighed (FW) on a Cahn 29 microbalance (accuracy 0.1 mg). Once parasitized, the hosts were placed in vials with 1 g of food medium until wasp eclosion. Eclosing wasps were killed by freezing and hind tibia measurements were made.

3.2.3 Growth of unparasitized hosts

To compare the growth of parasitized *Plodia* larvae with healthy larvae, 150 L3 hosts were reared under the same conditions as those parasitized by *Venturia.* Ten randomly chosen larvae were removed daily, killed by freezing, dried in the oven as described above and weighed on a Cahn 29 microbalance (accuracy 0.01mg).

3.2.4 Growth of *Venturia* and parasitized hosts

The method of Mackauer (1986) and Sequeira & Mackauer (1992a) was followed. From the day of parasitism until the third day (fourth day for L2 hosts owing to their small size) five parasitized hosts were randomly selected from vials; these were dried in an oven at 60°C for five days and were then removed and weighed (as above). Each day from the fourth day after parasitism (fifth day for L2 hosts) until parasitoid

eclosion, five hosts were randomly selected, and dissected on a pre-weighed aluminium tray in order to separate the parasitoid larva from the host. Both were dried in the oven as described above and weighed.

3.2.5 Relationship between adult size and longevity

In order to test the effect of wasp size on longevity, a number of newly-eclosed parasitoids were immediately transferred to plastic containers and fed 50% honey solution (changed daily to prevent fermentation). Each day, dead wasps were removed, longevity recorded and hind tibia lengths measured.

3.3 Results

3.3.1 Parasitoid mortality, development time and adult size

Parasitoid mortality varied with host instar ($X^2 = 35.4$, d.f. = 3, $P < 0.001$: Fig. 3.1a). Close to 50 % of the parasitoids developing from L2 perished, most during the first two days after oviposition when *Venturia* would still be in the egg stage (Salt, 1968). Survivorship was highest in L3 and L4 hosts, with over 90% successful emergence from these instars. In L5 hosts, parasitoid mortality increased to 16 %. Encapsulation was rare: two larvae in each of L2 and L4, one in L3 and three in L5 hosts were encapsulated as defined by the emergence of an adult moth.

Development times of *Venturia* from oviposition to adult eclosion varied significantly with host instar ($F = 113.3$, d.f. = 3, 165, $P < 0.001$; Fig. 3.1b). Parasitoids from L2 hosts took approximately 4 days longer to eclose than those from L3 to L5 hosts.

The size of adult wasps, as defined by dry mass, varied significantly with host instar at parasitism (one-way ANOVA, $F = 12.8$, d.f. = 3, 165; $P < 0.001$; Fig. 3.1c). *Venturia* developing from L2 hosts were significantly smaller than their counterparts from L3-L5 hosts (Tukey-Kramer tests, Sokal and Rohlf 1981).

3.3.2 Relationship between post-feeding L5 host size and adult wasp size

There is a significant positive correlation between adult wasp size and L5 (post-feeding) host size (n = 26, $r = 0.89$, $P < 0.001$; Fig 3.2). The largest wasp emerged

Fig. 3.1. Development of *Venturia* reared on four instars of *Plodia*. (A) Mortality. Bars show 95 % confidence limits for percentages (Rohlf & Sokal 1981, Table W). Sample sizes are: L2- 67; L3 - 47; L4 - 47; L5 - 53. (B) Development time in days,from oviposition to adult eclosion. Points with the same letter do not differ significantly (Tukey-Kramer tests, $P > 0.05$, Sokal & Rohlf 1981). Bars show 95% confidence limits for percentages. Sample sizes are: L2- 37; L3 - 44; L4 - 44; L5 - 44. (C) Size of adult *Venturia* (dry mass in mg). Points with the same letter do not differ significantly (Tukey-Kramer tests, $P > 0.05$, Sokal & Rohlf 1981). Bars show 95% confidence limits for percentages. Sample sizes are: L2- 37; L3 - 44; L4 - 44; L5 - 44.

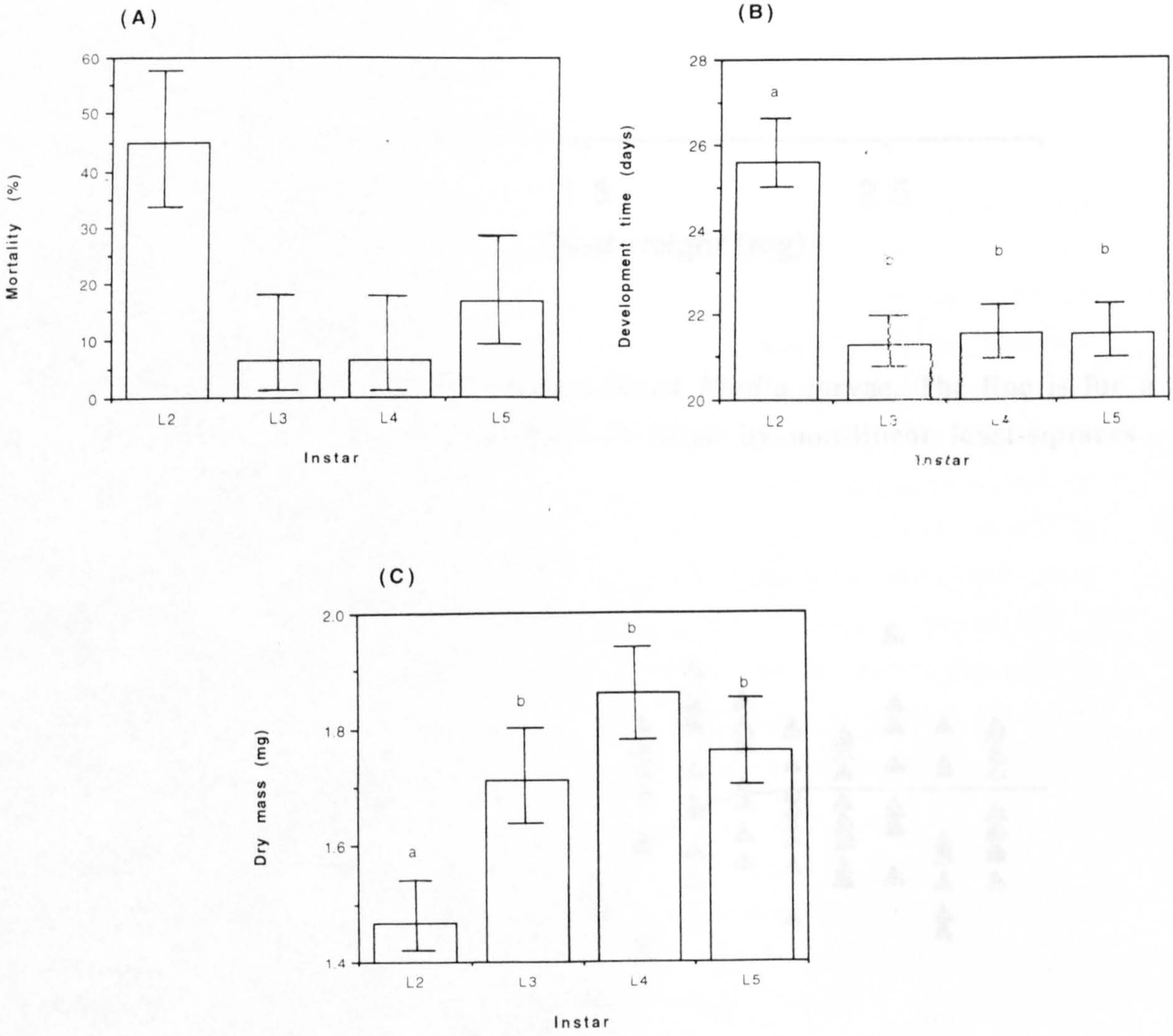


Fig. 3.2. Relationship between the size of adult *Venturia* (hind tibia length) emerging from different sizes (measured as fresh mass in mg) post-feeding L5 *Plodia* hosts.

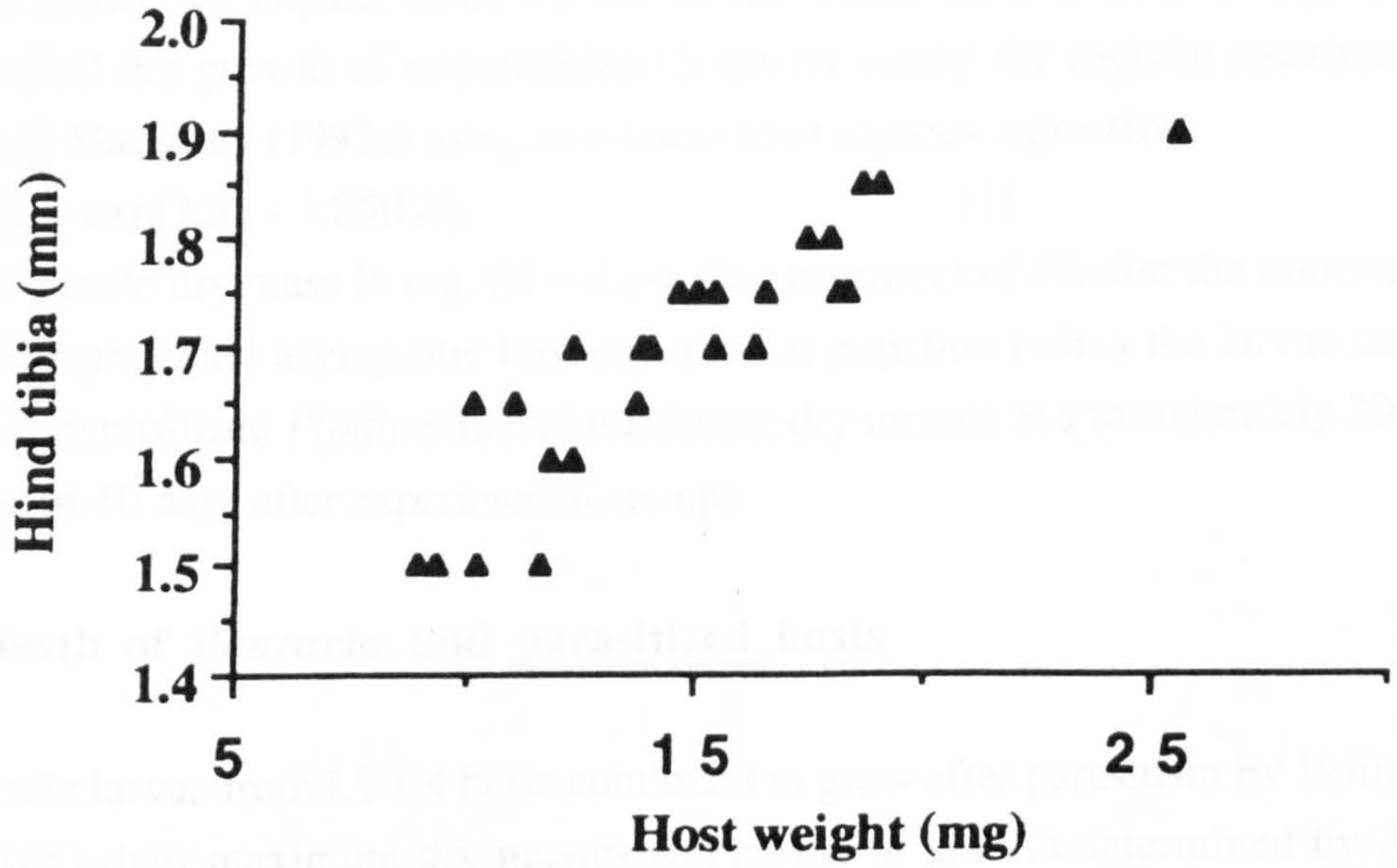
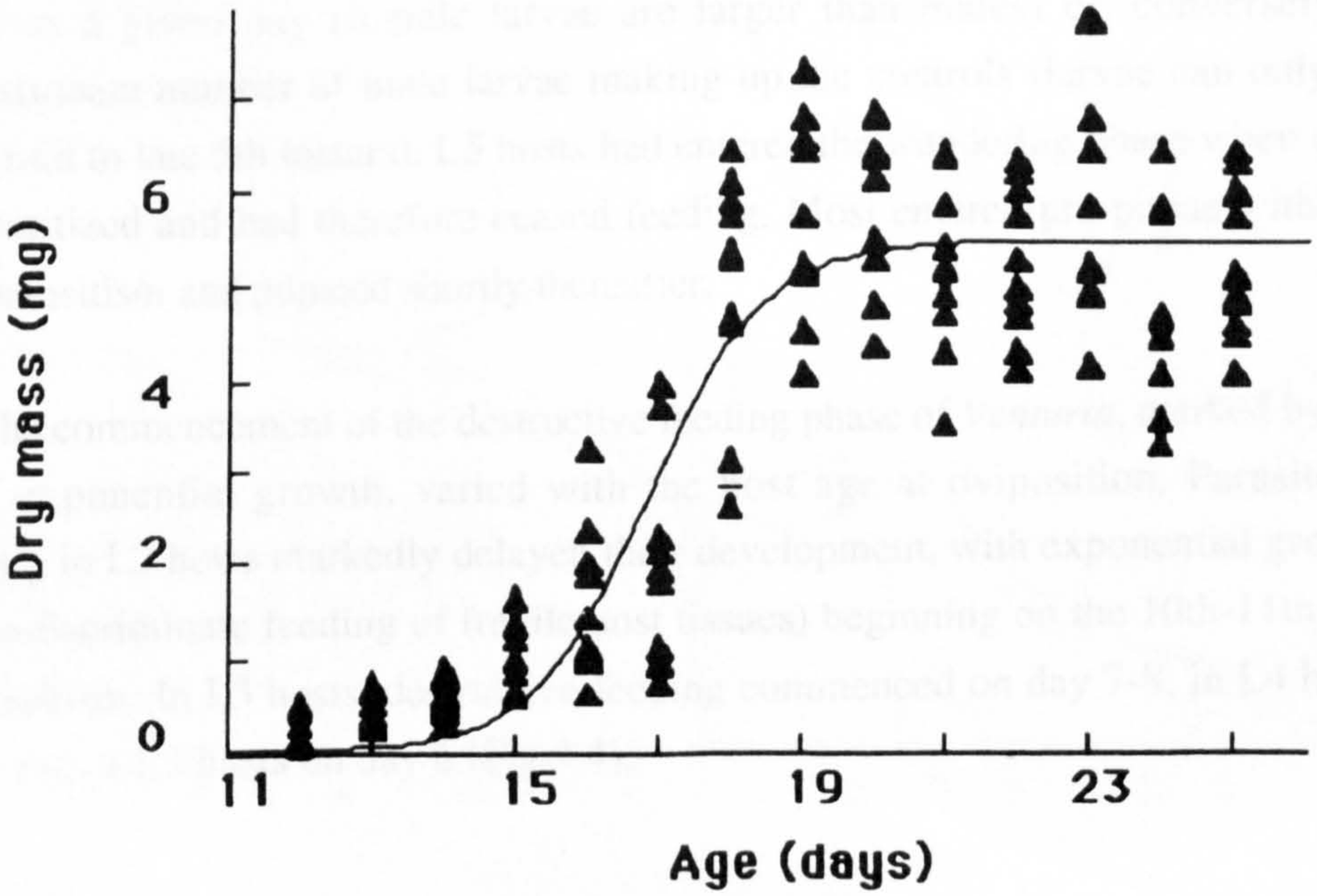


Fig. 3.3. The growth of unparasitized *Plodia* larvae. The line is for a logistic equation (equation 1) fitted by non-linear least-squares regression.



from a host that weighed 26mg at parasitism while the smallest wasps emerged from hosts that weighed < 10mg at parasitism.

3.3.3 Growth of unparasitized hosts

The growth of unparasitized *Plodia* larvae (controls) is shown in Fig. 3.3. I have described the growth of unparasitized hosts by fitting the logistic equation of Scqueira and Mackauer (1992a) using non-linear least-squares regression:

$$H = 5.46/[1 + \exp(7.31 - 1.25tH)], \quad (1)$$

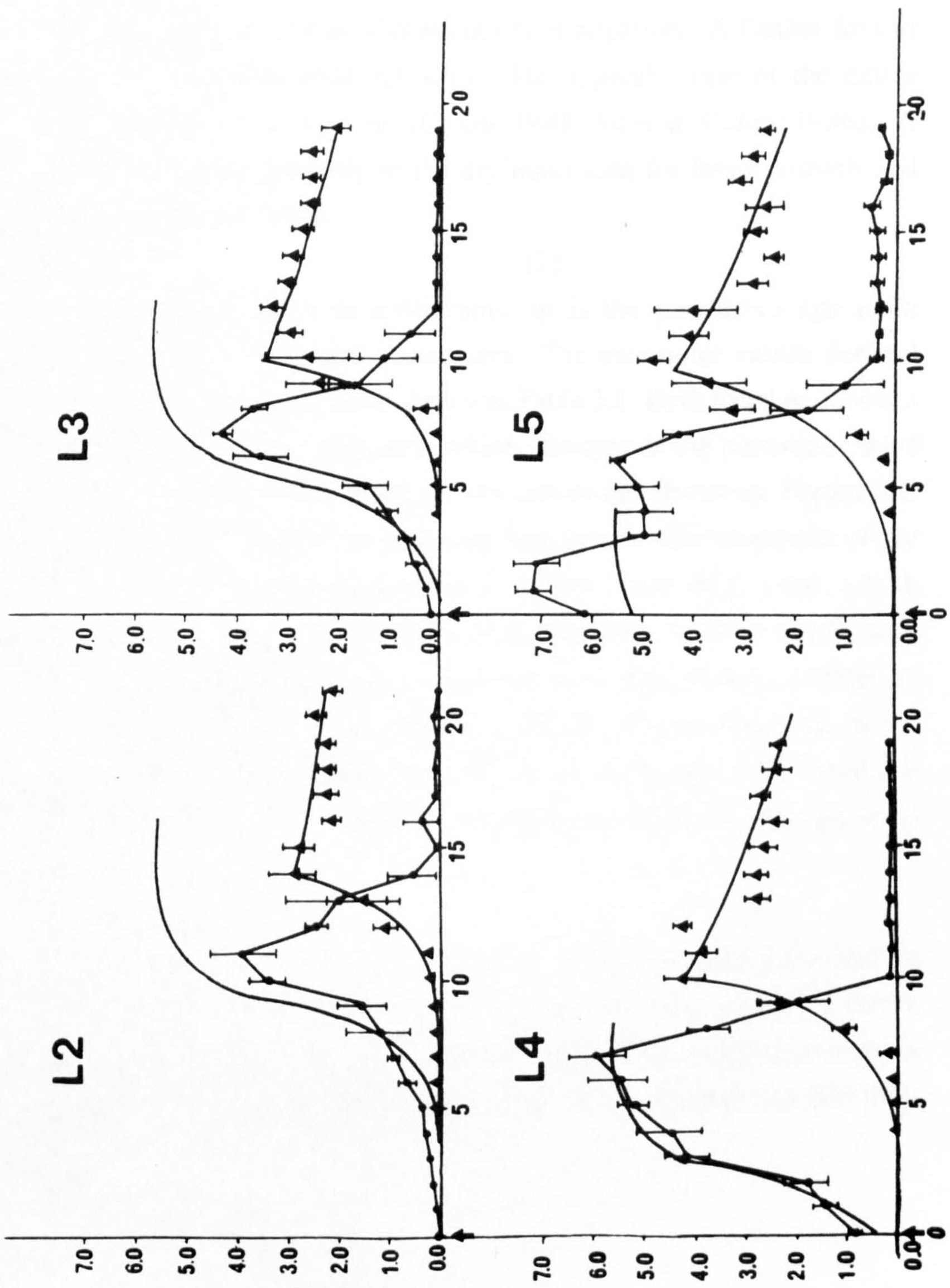
where H = *Plodia* dry mass in mg, tH = days after treatment of *Plodia*; the numerator describes the projected asymptotic host dry mass at pupation (when the larvae cease feeding). Unparasitized *Plodia* attained maximum dry masses at approximately 20-22 days of age (8-10 days after experimental set-up).

3.3.4 Growth of *Venturia* and parasitized hosts

Plodia larvae from L2-L4 hosts continued to grow after parasitism by *Venturia* (Fig.3.4) with their maximum dry masses and period of growth determined by their age when parasitized. In general, the parasitized hosts grew at the same rate as unparasitized hosts (Fig. 3.4) but their dry masses fell abruptly when the parasitoid began to grow exponentially and convert host biomass into its own. The maximum dry masses attained by parasitized *Plodia* depended upon instar at parasitism. L2 hosts reached 70% of control size, L3 hosts 78%, while L4 hosts grew to a size comparable with the controls. L5 hosts were actually slightly larger than controls at parasitism (Fig. 3.4). This could be because of an excess of female hosts with parasitoids being weighed on a given day (female larvae are larger than males) or, conversely, a disproportionate number of male larvae making up the controls (larvae can only be sexed as mid to late 5th instars). L5 hosts had entered the wandering phase when they were parasitized and had therefore ceased feeding. Most entered pre-pupae within 2 days of parasitism and pupated shortly thereafter.

The commencement of the destructive feeding phase of *Venturia*, marked by the onset of exponential growth, varied with the host age at oviposition. Parasitoids developing in L2 hosts markedly delayed their development, with exponential growth (hence, indiscriminate feeding of fragile host tissues) beginning on the 10th-11th day after parasitism. In L3 hosts, destructive feeding commenced on day 7-8; in L4 hosts day 6-7; and in L5 hosts on day 6 (Fig.3.4).

Fig. 3.4. The development of *Venturia* larvae (triangles) in each of four larval instars of Plodia (circles) parasitized at different ages: (A) - L2; (B) - L3; (C) - L4; (D) L5. Also shown on each graph is the growth of unparasitized *Plodia* larvae (Fig. 3). Bars represent standard errors of the mean (n=5 in each case). Arrows indicate day on which parasitized.



The period of time between oviposition and the maximum dry masses of *Venturia* larvae (just prior to pupation) varied with host instar. Parasitoids from L2 hosts attained maximum mass on day 14, those from L3 and L4 hosts on day 12, and from L5 hosts on day 10. In L2, L3 and most L4 hosts, the parasitoid larvae consumed all host tissues before spinning, and prevented pupation, leaving only the larval head capsule. Conversely, L5 hosts usually pupated, but the tanned pupal cuticle was not consumed by *Venturia*, which spun a cocoon inside of it. The unconsumed host pupal cuticle constituted as much as 10% of the overall host dry mass (Fig. 3.4d).

The development of *Venturia* showed an exponential increase in dry mass during the growth phase followed by an abrupt cut-off at pupation. A further loss in dry mass occurred after pupation until eclosion. The typical shape of the entire trajectory has been described as a 'J-curve' (Calow 1981, Sibly & Calow 1986). A curvilinear function was fitted separately to the dry mass data for larval growth and pupation (Sequeira & Mackauer, 1992a):

$$P = \exp(a + btp), \qquad (2)$$

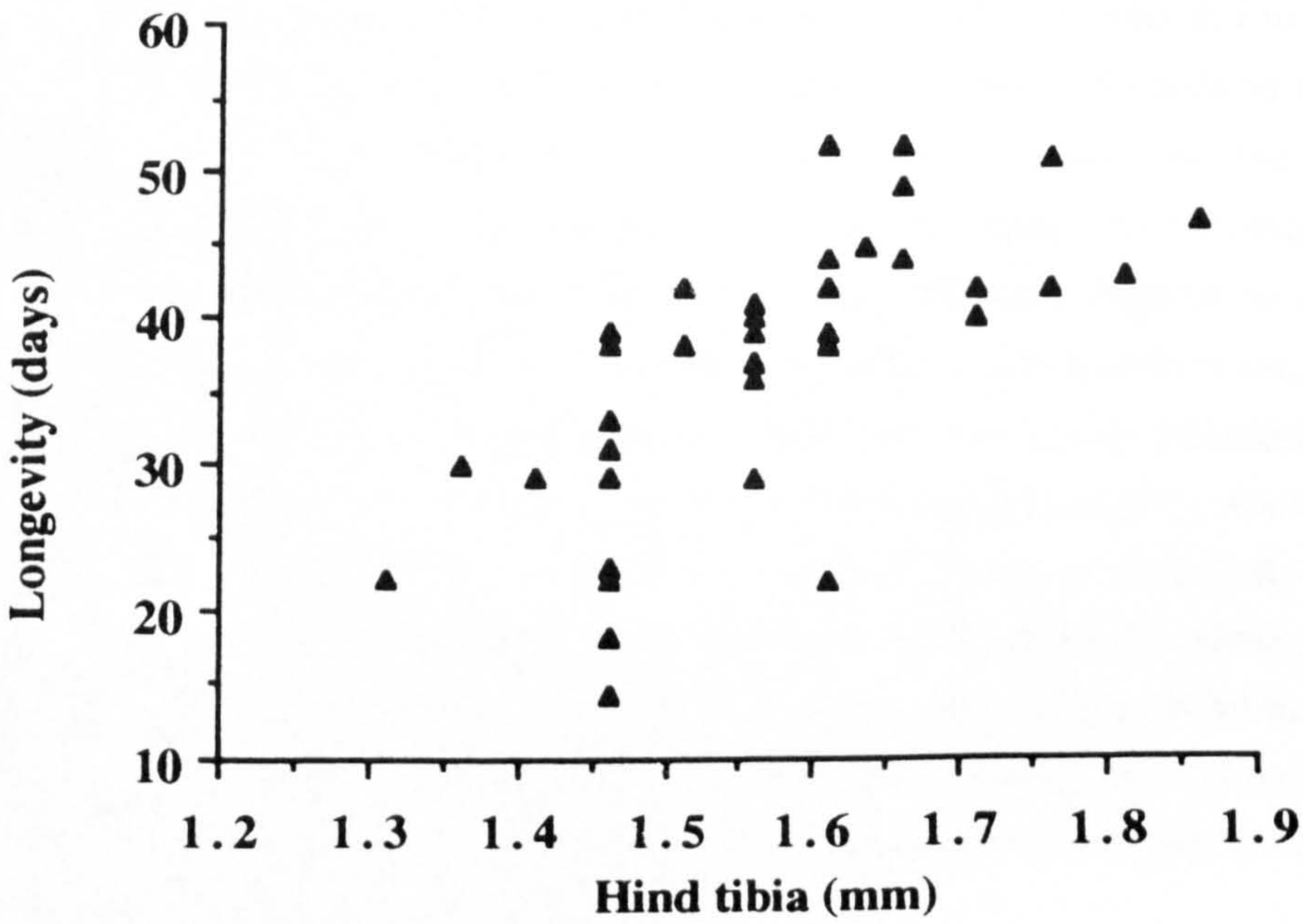
where P is the parasitoid dry mass in milligrams, tp is the parasitoid age from parasitism in days, and a and b are fitted parameters. The parameter values derived from the data being fitted to the equation are shown in Table 3.1. Both fitted parameters a and b describe the type of growth trajectory, which changes as the parasitoid larva passes from one instar to the next. The fitted growth curves are shown on Figure 3.4. *Venturia* larvae grow at different rates in different host instars. Development of the parasitoid in L2 hosts shows a prolonged phase as a first instar (Fig. 3.4a), which progressively decreases in duration from L3 to L5 instars (Fig. 3.4b-d). In L5 hosts the duration of parasitoid first instar is exceedingly short or non-existent, indicating that, upon hatching, *Venturia* larvae begin immediate exponential growth. The plotted growth trajectories also predict that maximum parasitoid size is reached on the tenth day after oviposition from L3 to L5 hosts, but that this is delayed until the 14th day in L2 hosts.

The maximum sizes of parasitized L2 and L3 hosts were significantly smaller than controls (L2: $t = 3.60$, d.f. =14, $P < 0.05$; L3: $t = 3.88$, d.f. = 14, $P < 0.05$). However there was no difference in the maximum size of L4 hosts relative to controls ($t = 0.56$, d.f. = 14, $P > 0.05$). L5 hosts were parasitized after they had reached their maximum size (Fig. 3.4).

Table 3.1. Estimates of parameters a and b from equation 2, describing the development of *Venturia* from 4 instars of its host, *Plodia*. Figures in brackets show standard error (SE). Max DM = day on which maximum parasitoid dry mass was reached.

Growth parameters			
Host Instar	**a (SE)**	**b (SE)**	**Max DM**
	Logarithmic growth phase		
2	-8.17 (1.29)	0.60 (0.09)	14
3	-6.46 (0.78)	0.78 (0.11)	10
4	-5.76 (0.64)	0.72 (0.07)	10
5	-2.88 (0.56)	0.46 (0.06)	10
	Pupation phase		
2	1.66 (0.26)	-0.04 (0.02)	
3	1.73 (0.09)	-0.05 (0.01)	
4	2.15 (0.14)	-0.07 (0.01)	
5	2.15 (0.17)	-0.07 (0.01)	

Fig. 3.5. The relationship between adult *Venturia* size, measured as hind tibia length, and longevity. Wasps were housed in groups of 13 from emergence and provided with 50% honey solution ad libitum.



3.3.5 Relationship between adult size and longevity

The average life expectancy of *Venturia* was 37.9 days. There is a significant positive correlation between parasitoid size and longevity (n = 39, $r = 0.68$, $P < 0.001$, Fig. 3.5). Most of the parasitoids showed signs of senescence several days before death, characterized by a progressive loss of flight and locomotory capability

3.4 Discussion

Under good nutritional conditions, host instar-related variations in size have corresponding effects upon several fitness-related traits in adult *Venturia.* Furthermore *Venturia* attacks hosts varying considerably in mass (Fig.3.4a-d). Parasitoid mortality was lowest in L3 and L4 hosts (Fig 3.1a) presumably because of the reduced immunological response which is characteristic of earlier instars in holometabolous insects (Slansky, 1986). Parasitoid mortality was significantly highest in L2 hosts (Fig. 3.1a) probably because of the physical damage inflicted by insertion and removal of the female ovipositor. The parasitoid-host size ratio obviously increases with a decrease in host size, and with L2 hosts the ratio in terms of dry mass approaches 20 to 1. Most of the L2 hosts that died succumbed within 48 hours of oviposition. In L5 hosts, *Venturia* mortality (Fig 3.1a) was mostly due to encapsulation, although some parasitoids failed to pupate, and perished as early or late instars. Whether this is because of physiological changes which may occur during host development (Greenblatt & Barbosa, 1982; Slansky, 1986), or the parasitoids inability to dispose of excessive biomass (Salt, 1964), is unclear.

Host instar at oviposition exerted significant effects over the development time of *Venturia* from oviposition to adult eclosion (Fig. 3.1b). Parasitoids from L2 hosts took approximately 4 more days to eclose than those from L3-L5 hosts. Thus, there would appear to be a host developmental threshold between late L2 and late L3 instars below which parasitoid development time increases, and above which it is reduced. Similarly, adult wasp size varied with host instar (Fig. 3.1c). However, this was due to the smaller wasps that emerged from hosts parasitized as L2 instars, because the difference in sizes of eclosing wasps from L3 to L5 instars was not significant. Therefore, L2 instars are of lower quality than later host stages because of the higher mortality, longer development time, and smaller size of wasps that develop in them.

A significant correlation was found between the size of post-feeding L5 hosts and adult parasitoids (Fig 4.2) This is presumably due to differences in host size and

therefore, resource availability. Interestingly, this corresponds to the results of studies with idiobiont parasitoids (for example, Arthur & Wylie, 1959). Therefore, once the host has ceased feeding, and has attained its maximum size, a positive correlation between host and adult wasp size, even in solitary koinobionts, is expected. However, exceptions may occur in associations where many of the host tissues are not consumed by the parasitoid prior to egression (Jones & Lewis, 1971).

A closer examination of the growth trajectories of *Plodia* and *Venturia* allows the host-influenced differences in wasp size and development rate to be understood. Maximum host growth is reduced in L2 and L3, (but not L4) instars, relative to controls.(Fig. 3.4a-c). This parasitoid-mediated effect presumably accounts for the smaller wasps eclosing from L2 hosts (Fig. 3.1c). In many idiobiont-host associations, early parasitoid instars feed rapaciously upon host tissues, overcoming host defences by overwhelming them (Smith, 1932). However, koinobionts may have to persist within their hosts through several instars (Slansky, 1986). During this time, the parasitoid remains as a slowly-growing first instar and must avoid the hosts immunological response. Parasitoid survival may be achieved by migrating to an area of the host which is less vulnerable for the young larva (for example, the midgut region; Vinson & Iwantsch, 1980a) or through active regulation of host growth by the parasitoid (Vinson & Iwantsch, 1980b). In this form of regulation, the host is physiologically stressed and does not grow as large as unparasitized controls (Salt, 1968; Jones & Lewis, 1971; Vinson, 1972; Tanaka et al., 1984; Strand *et al.*, 1988).

A reduction in host growth potential when earlier instars are parasitized has other fitness-related benefits for the developing parasitoid. L5 *Venturia* larvae possess weak mandibles, and therefore the parasitoid is unable to egress from the host and pupate unless most tissues are consumed (Salt, 1964). Therefore, parasitoid development time is potentially reduced in smaller final-instar hosts because they contain less biomass to consume and assimilate. Evidence is presented in Chapter 5 showing that parasitoid development time increases with final host size in starved hosts.

Venturia exploits nutritionally less suitable early host instars by delaying development until the host is large enough to provide sufficient food, a characteristic feature of many ichneumonids, braconids and all platygasterids (Gauld & Bolton, 1988). This strategy enables early instar parasitoid larvae to feed and grow in their hosts without seriously debilitating them. Results from the host dissections suggested that developmental retardation was not due to parasitoid diapause because parasitoids

continually increased in size, albeit slowly, in small, early instar hosts (Fig. 3.4a,b). The reason that there is very little difference in dry mass and development time between wasps from L3 to L5 hosts may be due to a combination of parasitoid self-regulation and rapid host growth rate. *Venturia* cannot develop in hosts that do not reach at least early 5th instar (Chapter 5). However, after parasitism, L3 hosts provided with excess food grew so rapidly that by the time of egg hatch (typically 60-70 hours after parasitism; Salt, 1968) they were mid to late 4th instars (Fig. 3.4b). Rapid parasitoid growth thereafter (through commencement of destructive feeding) did not seriously debilitate the host until it had moulted and reached its mid-5th instar; therefore, developmental arrest was not necessary for *Venturia* to obtain sufficient food. However, when L2 instars were attacked rapid host growth did not compensate for lack of nutrients accounting for the slowed rate of parasitoid development (Fig.3.4a). Evidence of developmental delay can be seen in a number of gregarious and solitary parasitoids that attack slow growing holometabolous hosts. The gregarious braconid *Apanteles* (= *Cotesia*) *glomeratus* took 2 days longer as larvae to egress from their hosts *Pieris rapae* when oviposited into 1st as opposed to 2nd or 3rd instars (Sato, 1980). *A. kariyai* also develops more slowly in middle, as opposed to later instars of its host *Psuedaletia separata* (Tagawa *et al.*, 1982) Development of the solitary parasitoid *Chelonus annulipes* does not proceed beyond the first instar until host larvae are about to pupate (Bradley & Arbuthnot, 1938). *Hyposoter exiguae* retards its development when oviposited into 1st instars of its host, *Trichoplusia ni* (Smilowitz & Iwantsch, 1973). Similarly, *Cardiochiles nigriceps* took one day longer from emerge from their host, *Heliothis zea* , parasitized as 2nd as opposed to 4th instars (Vinson & Barras, 1970). Similar findings have been found within both hymenopterous and dipterous koinobiont taxa (eg. Miles & King, 1975; Nechols & Kikuchi, 1985).

Host metamorphosis was suppressed in L2-L4 hosts, with *Plodia* larvae constructing pre-pupal cells, but they were consumed by the parasitoid larvae before pupation, leaving only the larval head capsule. *Venturia* larvae were presumably responsible for this regulation, because pupation occurred when L5 instars were parasitized. The precise processes responsible for this phenomenon are unclear, but probably involve selective tissue feeding, with corresponding disruption of the hosts endocrine metabolism (Jones, 1985). *Venturia* eggs laid into L5 hosts are able to survive the physiological changes associated with host metamorphosis, which makes the prevention of pupation via parental regulation unnecessary. In other associations, host development must be arrested prior to pupation to ensure a suitable physiological environment for the developing parasitoid (Jones, 1970; Jones & Lewis, 1971; Smilowitz & Iwantsch, 1973; Smilowitz & Iwantsch, 1975; Sato, 1980; Vinson &

Iwantsch, 1980b; Tanaka *et al.*, 1986; Strand et al., 1988). Like *Venturia, Apanteles* (= *Cotesia*) *glomeratus* prevents pupation of its host, *Pieris rapae*, through selective tissue feeding by the parasitoid larvae (Sato, 1980). Eggs laid into terminal (=5th) instar hosts cannot prevent pupation, and the parasitoids perish. Depending on the age or instar of the host at parasitism, regulation of host growth by the solitary parasitoids *Microplitis croceipes* and *Cardiochiles nigriceps* may involve both input by the ovipositing female and the parasitoid larvae (Vinson & Barras, 1970; Jones & Lewis, 1971) Early instar hosts grow, albeit at a reduced rate, after parasitism until they reach a size suitable for parasitoid development; the growth of later instars, presumably because they have passed the most suitable stage, is arrested at oviposition through the injection of poison gland secretions and calyx fluid by the ovipositing female (Shaw, 1981). Calyx fluid contains polydnavirus particles that are now known to contribute to developmental arrest of the host (Strand & Dover, 1991; Dushay & Beckage, 1993) in addition to blocking encapsulation (Stoltz & Vinson, 1979; Edson *et al.*, 1981; Tanaka, 1987; reviewed in Stoltz, 1993). Regulation is a common feature in hymenopteran parasitoids (Vinson & Iwantsch, 1980b) and serves to maintain the host in a suitable physiological condition throughout parasitoid development (Smilowitz & Iwantsch, 1973). Thus, the pupation of L2-L4 hosts containing sufficiently developed parasitoids could create an unsuitable, and potentially lethal environment for *Venturia*, and therefore it is prevented through selective feeding by the wasp larvae. However, pupation of L5 hosts provided less resources for the wasp larvae because the tanned pupal cuticle is presumably undigestable because it was not consumed. A further consequence of development in a non-feeding host stage is their reduction in weight due to respiration and water loss through evaporation, so that less biomass is potentially available to the parasitoid larvae when it enters the destructive feeding phase. Destructive feeding is characterized by a change in nutrient acquisition from haemolymph ingestion to the consumption of vital organs such as fat bodies, fragile tissues, and undigested embryos (Barbosa *et al.*, 1982; Liu, 1985; Sequeira & Mackauer, 1992a). Analysis of the data has shown that the adult parasitoid, irrespective of host instar at reception of the parasitoid egg, was largely determined by the size of the host when the parasitoid entered its destructive feeding phase (Fig. 3.4). Parasitoids developing from L4 hosts began destructive feeding when the host reached the peak of its growth trajectory; the size of these hosts was comparable to healthy larvae. Those developing from L2 and L3 hosts also began destructive feeding at this stage, but the maximum size of these hosts was less than from L4 hosts.

Recent studies have shown that, even for koinobionts, age-related variations in host size may affect parasitoid size, with smaller wasps developing from earlier host

stages (Cloutier *et al.*, 1991; Sequeira & Mackauer, 1992a). Waage (1982) predicted that, for koinobionts, host size at oviposition is not a good indicator of the amount of resources available to wasp progeny, and King (1989), reviewing host size-dependent sex-ratios in parasitoids, found that, for most of the idiobionts and all of the koinobionts thus far examined, larger wasps developed from larger hosts. The koinobiont data, however, was based on a limited number of species, none of which exhibit such a high level of developmental plasticity as *Venturia*. In particular, my results with *Venturia* markedly contrast with studies of aphidiid koinobiont development. I suggest these differences are adaptively mediated by one or more factors. First, they may be responses to differences in the ecology of the host. Aphids remain exposed on their host plant throughout their life-history, and thus are always vulnerable to predation. This could favour rapid development of their parasitoids, but with a cost in terms of reduced adult size. *Plodia*, on the other hand, constructs a cryptic cocoon in which it pupates. This makes it less vulnerable to predation than developing larvae, thus it could pay *Venturia* to delay rapid development until its host has formed a cocoon, and gain an additional benefit of increased adult size (Gauld, 1988; Gauld & Bolton, 1988).

Another possibility is that *Venturia* may be adopting this strategy to maximise biomass exploited per unit of host resources (Chapter 9). The fitness gain from increased adult size must be balanced against fitness losses incurred by increasing development time. For *Venturia*, increased size may therefore be of greater importance. This strategy favours the evolution of delayed parasitoid development until the host has attained a critical stage or size (Mackauer & Sequeira, 1993). Besides *Venturia*, the development of *Hyposoter exiguae* and *Microplitis* species conformsto this pattern of development (Puttler, 1961; Jones & Lewis, 1971; Smilowitz & Iwantsch, 1973; Campbell & Duffey, 1979; Tanaka *et al.*, 1984; Strand *et al.*, 1988).

Patterns of host quality affect aphidiid koinobiont parasitoids differently. Their developmental strategy optimizes several characters that determine fitness. Therefore, the developmental strategy of aphidiids incorporates trade-offs that optimize both adult size and development time. The effect of host size on parasitoid growth and development is variable because aphidiids appear to be able to adjust their growth rate in accordance with host resource availability. This allows the parasitoid to balance any fitness gains (from increased biomass) against fitness losses (from increased development time). As a result, the growth trajectories of aphidiid wasps differ from the type of pattern shown by *Venturia* (Mackauer & Sequeira, 1993).

Other host-related factors, however, may be important determinants of parasitoid development patterns for koinobionts. The development of several closely related ichneumonids is very markedly different from that shown by *Venturia.* Adult *Campoletis sonorensis* and *Hyposoter exiguae* were larger from older instars of their hosts, *Heliothis virescens* and *Trichoplusia ni,* than younger instars (Jowyk & Smilowitz, 1978; Gunasena *et al.*, 1989). Although there was evidence of some developmental delay by these parasitoids when parasitizing younger hosts, the size of the adult parasitoid depended upon host instar at parasitism in both cases. The major difference between these associations and the *Venturia-Plodia* association is the growth potential of the hosts. Healthy *H. virescens* and *T. ni* attain sizes of approximately 500 mg (compared to *Plodia*'s 30 mg). *C. sonorensis* and *H. exiguae* must regulate host growth in order to successfully develop from them and rarely parasitize final instars (in view of the hosts behavioural and physiological defences) (Campbell & Duffey, 1979; Beckage & Templeton, 1985; Gunasena *et al.*, 1989). Later instars do not grow after parasitism, due to the polydnavirus injected into the host with the parasitoid's egg (Stoltz & Vinson, 1979; Vinson et al., 1979). Although *Venturia* similarly injects a virus like particle into the host at parasitism (Fedderson *et al.*, 1986), host weight gain is much less affected than in these other associations, probably because *Venturia* depends upon the host growing close to the size of healthy larvae in order to provide enough food for their own development. Furthermore, *Venturia* regularly parasitizes final instar hosts. Both *C. sonorensis* and *H. exiguae* consume all host contents when developing from L1-L3 hosts, but not from L4 hosts. Conversely, *Venturia* consume all host tissues irrespective of instar parasitized. Perhaps most interestingly, all three parasitoid species grow to about the same size (8 mg fresh weight) in spite of the enormous variability in the growth potential of their hosts.

The ability of koinobionts like *Venturia* to retard their development until the host reaches a certain stage is an adaptive mechanism which broadens the range of instars suitable for attack, reducing selection pressures for a fixed maternal response to oviposit in a limited range of hosts (Mackauer, 1973; Cloutier *et al.*, 1991). Many endoparasitic koinobionts are also fairly limited in the potential range of host species they attack due to the taxonomic specificity of the host immunological response (Slansky, 1986). By lowering the standards of host acceptance, a parasitoid can adapt to new instars while previously suitable ones become less so, because of adaptive changes in the hosts response to parasitism (Mackauer, 1973). This could be the case with *Hyposoter exiguae* and its host *Trichoplusia ni*: parasitoids are larger and develop more rapidly from larger hosts, but survivorship in these is lowest, hence earlier instars are preferred (Smilowitz and Iwantsch, 1975). Thus, optimal host selection may be

based on an evolutionary compromise between different fitness correlates (Campbell & Duffey, 1979). The preference of smaller, less suitable early instar hosts may also be due to reduced behavioural defences that they exhibit, or because they are easier to locate than later, scarcer instars (Slansky, 1986; Kouame & Mackauer, 1991). *Venturia* produces large numbers of hydropic eggs (Chapters 1 & 2), and may be time limited under natural conditions. In this case, optimal host selection should be based upon a compromise between maximising the fitness gain per egg and the efficient allocation of foraging time (Bai & Mackauer, 1990; Kouame & Mackauer, 1991; Driessen & Hemerik, 1992). Therefore, the selection of lower quality hosts can still improve a female parasitoid's fitness.

In these experiments, I have established that differences in host size at oviposition can affect the survivorship, adult size and rate of development of *Venturia.* Such host-instar related variations in these parameters may have corresponding effects upon the lifetime reproductive success, hence the fitness, of an individual parasitoid. Larger wasps carry significantly higher egg loads than their smaller counterparts (Chapters 2 & 6) and also live longer (Fig. 3.5). Thus, even if the host-encounter rate is the same across a range of parasitoid sizes, larger wasps may potentially encounter more hosts and lay more eggs during their lifetime. Bellows (1985) found that the daily and lifetime oviposition rates of *Lariophagus distinguendis* were greater in larger wasps, as well as the number of ovarian eggs at eclosion, and that larger wasps developed from later instars of its hosts *Callosobruchus maculatus* and *C. chinensis.* Therefore, host-mediated variations in parasitoid size may significantly influence a parasitoids' overall fitness. Development times of *Venturia* also varied across the range of host instars, which can influence the fitness of an individual through its intrinsic rate of increase (Lewontin, 1965). Similarly, parasitoid survival also varied in hosts of different sizes, with a higher proportion of wasps successfully completing development in middle, rather than in earlier or later instars.

Koinobionts, through self and host regulation, are able to develop in a wide range of instars. This enables them to exploit hosts which may vary considerably in size, mass and growth potential (Mackauer, 1986). For *Venturia,* reproductive success is probably maximised by also attacking less suitable early instar hosts, although fitness under a given set of conditions is optimized only through development in the most suitable host instar. When provided with excess food, L3-L5 hosts provide the most favourable conditions in terms of adult size, rapid development, and survival. However, the extent to which these experimental conditions can be expected to occur naturally is debatable. *Plodia* were reared under conditions of low density and high

nutrition. Therefore, development times for parasitoids across the entire range of acceptable instars would not surprisingly be minimised, because their development rate is positively correlated with that of the host. Moreover, stress induced by increasing the host density relative to food availability, or through controlled starvation, was found to significantly increase the egg to eclosion times of *Venturia* developing from L3, but not L5 hosts (Chapter 5). However, it is likely that, as environmental quality decreases, the development rates of *Venturia* from L2-L4 instars (but not L5 instars) will increase, as has been demonstrated in other associations (Mackauer & Kambhampati, 1984; Liu, 1985). The most suitable instar for parasitoid development depends critically upon the nature of the host's environment and it will ultimately be determined by quantitative and qualitative aspects of the host's nutrition, and not simply by its total biomass. Integrating a variety of conditions which may occur, the fitness of *Venturia*'s progeny is therefore probably maximised by selecting L5 hosts. Most importantly, mid to late L5 hosts contain the minimum amount of resources necessary for *Venturia* to successfully complete its development, and my interpretation of suitability is based on this criterion. However, as suggested earlier, a relaxation of the conditions for host selection to less than absolute (through the acceptance of less suitable instars according to certain physiological and environmental criteria) is probably an adaptive mechanism which facilitates an overall increase in parasitoid fitness in the long run.

4. The effect of superparasitism on the development of *Venturia canescens*

4.1 Introduction

Many hymenopteran parasitoids are able to distinguish between parasitized and unparasitized hosts through the perception of external or internal markers at oviposition (Salt, 1937; Guillot & Vinson, 1972; van Lenteren, 1981; Hubbard *et al.*, 1987; Volkl & Mackauer, 1990; van Alphen & Visser, 1990; Visser, 1993). Solitary wasps usually reject hosts that have been previously marked by themselves, or by conspecifics. Superparasitism occurs when a host is parasitized more than once by the same or another female parasitoid of the same species (Wylie, 1965; van Lenteren, 1976; van Alphen & Nell, 1982; Waage, 1986; van Alphen, 1988; Bai & Mackauer, 1990; Volkl & Mackauer, 1990; van Alphen & Visser, 1990).

Until recently, superparasitism was believed to be maladaptive, because it resulted in egg wastage and so a decrease in fitness of the ovipositing female (van Lenteren, 1981; Gardner *et al.*, 1984). However, recent evidence has demonstrated that, under certain sets of conditions, superparasitism may be adaptive (van Alphen & Nell, 1982; Bakker *et al.*, 1985; Waage, 1986; Hubbard *et al.*, 1987; Mangel, 1989a,b; van Alphen & Visser, 1990; Visser *et al.*, 1990; Speirs *et al.*, 1991; Visser, 1993). By ovipositing into an already parasitized host when unparasitized hosts are unavailable, a female parasitoid may increase her fitness if there is a chance that her progeny will outcompete other wasp larvae.

Although superparasitism may have fitness consequences for the parasitoid mother, all models of superparasitism thus far discussed (for example, van der Hoeven & Hemerik, 1990; Volkl & Mackauer, 1990; van Alphen & Visser, 1990; Visser, 1993) assume that superparasitism confers no fitness costs to the surviving larva. To date, very few studies have investigated this assumption. Simmonds (1943) and Wylie (1983) found that development times of the parasitoids *Venturia* and *Microctonus vittatae* were longer in superparasitized, as opposed to singly parasitized hosts, but neither experiment quantified the number of eggs per host, and other fitness traits were ignored. Vinson & Sroka (1978) found that superparasitism also increased larval development times of the braconid parasitoid *Cardiochiles nigriceps,* but that survivorship decreased with a corresponding increase in number of eggs per host. However, as in the other studies, the effect of superparasitism on the size of the surviving adult parasitoids was not investigated. Bai & Mackauer (1992)

investigated the effect of superparasitism on development rate and adult size in the solitary wasp, *Aphidius ervi* (Hymenoptera: Aphidiidae). They found that adult wasps emerging from superparasitized aphid hosts were larger than those from singly parasitized hosts, but that development times were unchanged. Therefore, the effects of superparasitism on the fitness of the surviving larva varies from taxon to taxon.

Most studies examining the effect of superparasitism on host suitability have been undertaken with koinobiont parasitoids. For koinobionts, parasitoid larvae may compete for resources in superparasitized hosts during early development, with the cost of superparasitism resting on the ability of the survivor to compensate during its later development (Bai & Mackauer, 1992). None of the previous studies, however, have determined if the effects of superparasitism on parasitoid development vary with host instar. This may be important because the growth potential of the host may vary in accordance with instar parasitized (Jones & Lewis, 1971; Smilowitz & Iwantsch, 1973; Iwantsch & Smilowitz, 1975; Tanaka *et al.*, 1984; Strand *et al.*, 1988).

In this chapter I examine the effect of superparasitism upon mortality, development time, adult size of *Venturia* reared from two instars of *Plodia.* In the following chapter I will show that host quality varies from instar to instar in terms of these fitness traits. Specifically, the aim of this experiment is to determine if the consequences of superparasitism upon these parameters varies between third instar hosts that have considerable growth potential, and late-fifth instar (wandering) hosts, that have very limited growth potential.

4.2 Materials and methods

Plodia used in the experiments were either late L3 instars or post-feeding L5 instars. Larvae had been removed from culture on either day 13 (L3), or day 21 (L5) and were reared under conditions of excess food throughout the experiments.

To obtain singly parasitized hosts, *Plodia* larvae were presented individually to adult wasps, which were allowed to parasitize a host once. After parasitism hosts were placed singly in vials with excess food until parasitoid eclosion.

To obtain superparasitized hosts, a singly parasitized host was presented to a different *Venturia* female, which was allowed to superparasitize once (two eggs per host) or to three conspecific wasps, which each superparasitized (four eggs per host). If, at any time, L3 or L5 hosts were rejected more than twice for superparasitism, this

host was discarded and that trial abandoned. The duration of time between initial and final parasitization never exceeded 15 minutes. Data were obtained from between 50 and 70 hosts for each egg/instar combination.

Adult wasp eclosion was checked several times during the day which enabled development times to be accurately recorded. They were then placed individually in glass vials, oven dried for 3 days at 100°C, and weighed on a Cahn automatic electrobalance to provide adult wasp dry mass data. In addition to the eclosion data, encapsulation and host/ parasitoid mortality were recorded separately (for initial analysis), and later combined under "parasitoid mortality". An encapsulation was recorded if a parasitized host produced an adult moth instead of a wasp; if neither wasp nor moth emerged, mortality was recorded and the host was dissected in order to determine at what stage (if possible) the parasitoid had died within the host.

4.3 Results

Of the 343 larvae parasitized only four produced adult moths (three from singly-parasitized L3 hosts and one from a singly parasitized L5 host. A further 48 larvae died during the experiment, producing neither wasp nor moth. These data were analyzed as a three-way contingency table using a log-linear model (Sokal & Rohlf, 1981), with instar, number of eggs,and whether or not a wasp emerged (parasitoid mortality) as factors. The overall hypothesis of independence could be rejected (G = 25.62, d.f. = 7, $P < 0.005$). The only significant interaction was that between instar and parasitoid mortality (G = 16.44, d.f. = 3, $P < 0.005$). Thus parasitoid mortality was not significantly affected by the number of eggs per host. L5 hosts were more adversely affected by superparasitism than L3 hosts. *Venturia* failed to eclose from 16% of singly parasitized L5 hosts, which increased to 20% in hosts with 2 eggs, and 36% in hosts with 4 eggs (Fig. 4.1). A dissection of these hosts, which had all pupated, revealed that *Venturia* usually died during mid to late larval development. A higher percentage of parasitoids completed development from all L3 treatments (Fig. 4.1), with between 88% and 94% of wasps emerging successfully. L3 hosts all entered pre-pupae, but did not pupate and the parasitoids consumed the entire host except for the larval head capsules.

A two-way ANOVA on development time, with number of eggs and host instar as factors, revealed a significant interaction between number of eggs and host instar (F = 14.07, d.f. = 2, 285, $P < 0.001$) indicating that the effect superparasitism on development time varied according to host instar. Tukey-Kramer tests (Sokal &

Rohlf, 1981) were used to conduct *a posteriori* multiple comparisons of treatment means; however, not all possible comparisons were conducted. Comparisons were made of the effects of number of eggs within each instar and of the effect of instar with the same number of eggs, giving nine comparisons in all. The test procedure was modified to allow for this (Toothaker, 1992). There was no significant difference between the development times of wasps from parasitized and singly-superparasitized L3 hosts ($P > 0.05$; Fig 4.2) but development time was significantly increased when the host contained 4, as opposed to one or two parasitoid eggs ($P < 0.001$; Fig 4.2).

In L5 hosts, significant differences in development time existed between all treatments ($P < 0.001$; Fig. 4.2) with the number of eggs per host thereby influencing parasitoid development rate more than in L3 hosts. Furthermore, parasitoid development time also varied significantly between instars in superparasitized hosts with the same number of eggs per host. Although the rate of development of *Venturia* in singly parasitized L3 and L5 hosts was not significantly different ($P > 0.05$), superparasitism affected L5 hosts more than L3 hosts (Fig. 4.2), with development times of wasps from hosts with two and four eggs being significantly different between the two instars ($P < 0.01$).

A similar analysis was used to investigate the effect of instar and number of eggs on the mass the adult wasps. A two-way ANOVA again revealed a significant interaction between number of eggs and instar ($F = 12.79$, d.f. = 2, $P < 0.001$). Adult wasp dry mass was relatively unaffected in L3 *Plodia*, regardless of the number of eggs per host ($P > 0.05$; Fig 4.3). However, adult parasitoid size was affected by superparasitism in L5 hosts, with significantly smaller wasps eclosing from hosts containing two and four, as opposed to one parasitoid egg ($P < 0.01$; Fig 4.3). There was no significant difference in the size of adult *Venturia* eclosing from superparasitized L5 hosts ($P > 0.05$). However, although the sizes of wasps from singly parasitized L3 and L5 hosts were similar ($P > 0.05$), the effects of superparasitism were different between the two instars, with the sizes of emerging wasps from both superparasitized treatments in L5 hosts significantly smaller than their counterparts from L3 hosts (Fig. 4.3).

Fig. 4.1. Mortality of *Venturia* reared from (a) L3 and (b) L5 *Plodia* containing 1, 2 or 4 parasitoid eggs. Bars show 95% confidence limits for percentages (Table 23 in Rohlf & Sokal, 1981). Sample sizes are: L3 (1) 47, (2) 68, (4) 70; L5 (1) 53, (2) 55, (4) 50

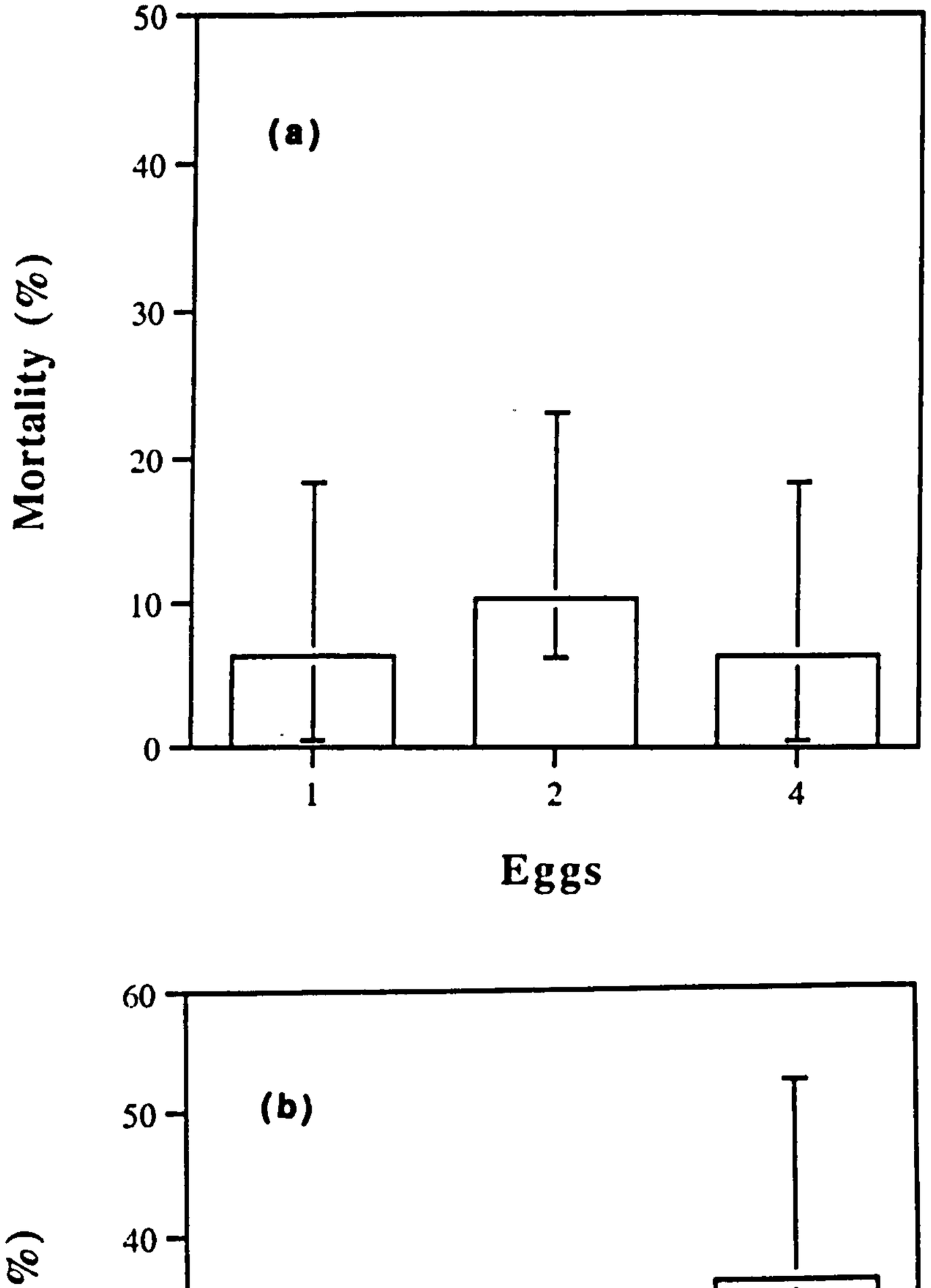


Fig. 4.2. Development time, in days, of *Venturia* from oviposition to adult eclosion, reared from (a) L3 and (b) L5 instars of *Plodia* containing 1, 2 or 4 parasitoid eggs. Points with the same letter do not differ significantly ($P > 0.05$). Bars represent 95% confidence limits. Sample sizes are: L3 (1) 44, (2) 61, (4) 66, L5 (1) 44, (2) 44, (4) 32.

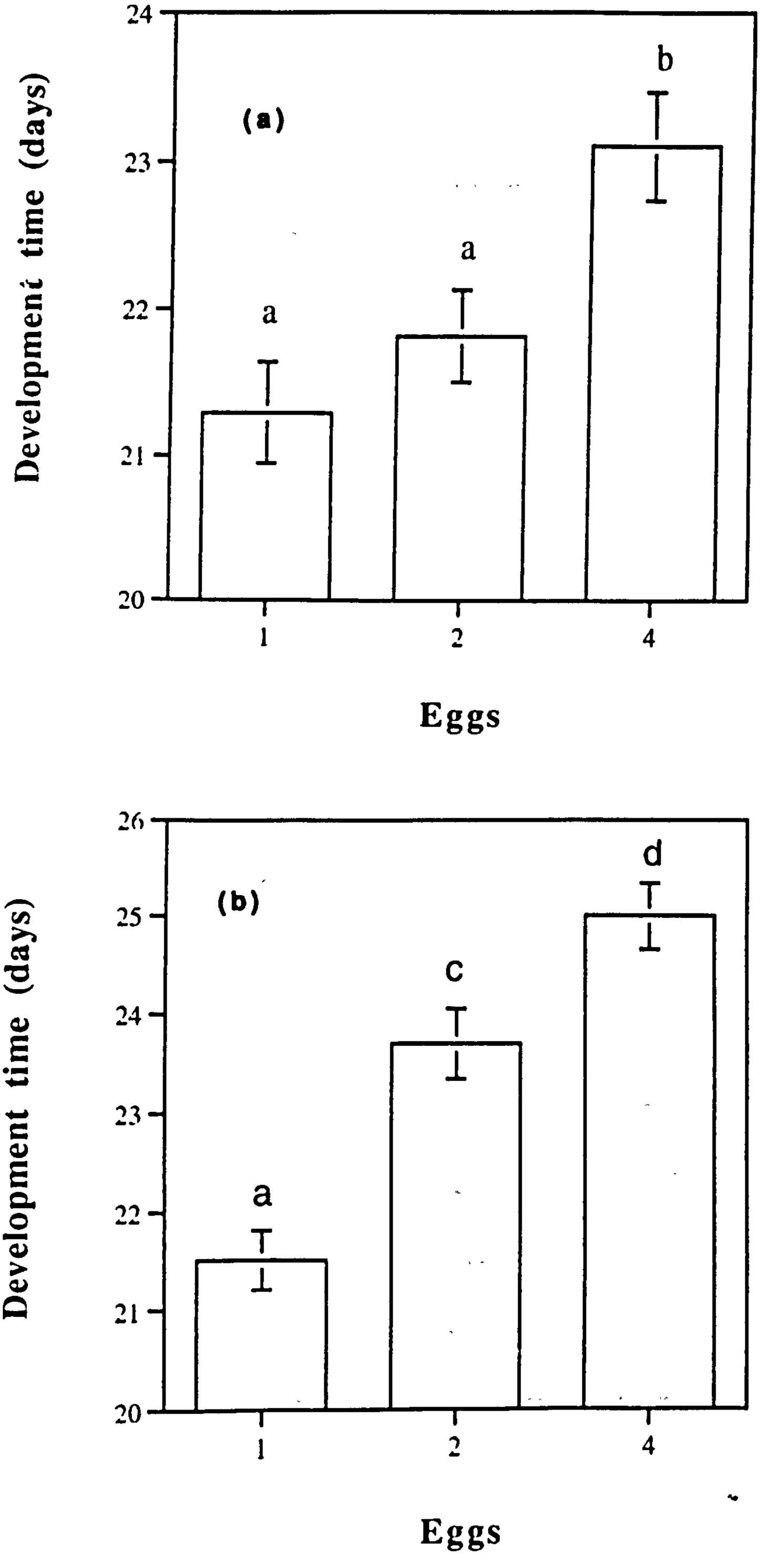
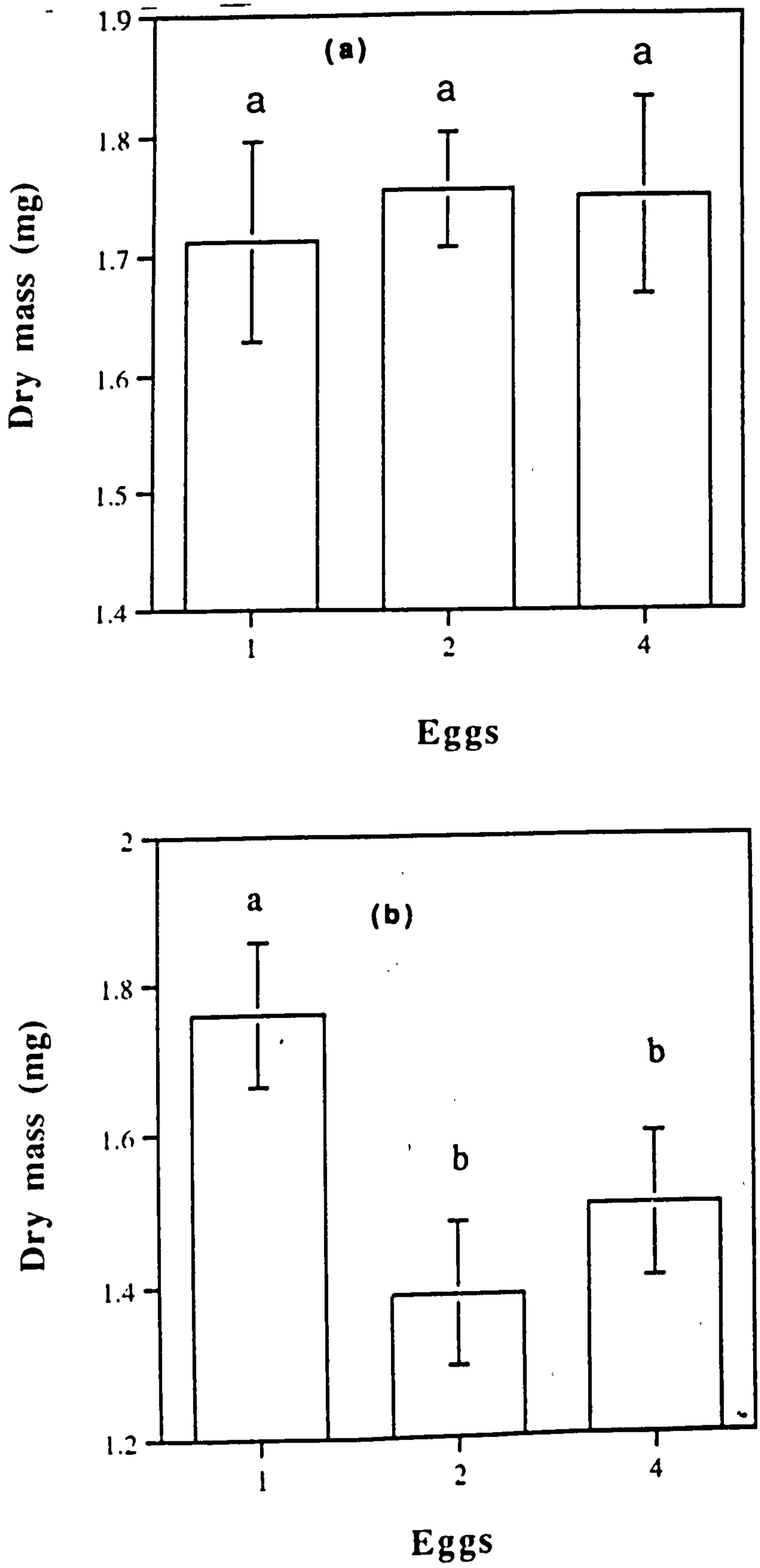


Fig. 4.3. The size of adult *Venturia* (adult dry mass in mg) reared from (a) L3 and (b) L5 hosts containing 1, 2 or 4 parasitoid eggs. Points with the same letter do not differ significantly ($P > 0.05$). Bars represent 95% confidence limits. Sample sizes are: L3 (1) 44, (2) 61, (4) 66; L5 (1) 44, (2) 44, (4) 32.



4.4 Discussion

The results of this investigation show that parasitoids reared from L3 and L5 hosts are affected differently by superparasitism. In parasitoids reared from both instars, superparasitism markedly influenced the development time, from egg to eclosion (Fig. 4.2). However, this effect was more marked in parasitoids reared from L5 hosts. Although the development times of *Venturia* from singly parasitized hosts was unaffected by instar, wasps from superparasitized L3 instars eclosed approximately 2 days earlier than wasps from L5 instars. Superparasitism influenced the size of eclosing wasps from L5, but not L3 hosts (Fig. 4.3). As with development time, the dry mass of eclosing wasps was apparently unaffected by instar in singly parasitized hosts, but in superparasitized L5 instars the size of eclosing wasps was significantly reduced (Fig. 4.3).

In solitary parasitoids, only one wasp can successfully develop and emerge from an individual host (Vinson, 1972; Waage, 1986; van Alphen & Visser, 1990), and supernumeraries may be eliminated through physical combat, as early instar larvae (Eller *et al.*, 1990; Speirs *et al.*, 1991). Parasitoid mortality was found to increase marginally with egg number in L5 hosts, and was consistently higher than in wasps reared from L3 hosts (Fig. 4.1). The increase in parasitoid mortality in L5 hosts could be the result of physical damage inflicted by *Venturia* larvae during fighting as suggested by Vinson & Sroka (1978) when they investigated a similar increase in parasitoid mortality with egg number for the braconid wasp *Cardiochiles nigriceps* attacking the tobacco budworm, *Heliothis virescens*. My results differ in that parasitoid mortality did not increase with egg number in superparasitized L3 hosts. Another factor, therefore, appears to be responsible. L5 hosts parasitized by *Venturia*, in contrast to earlier instars, usually pupate. Parasitoid larvae presumably ensure the suitability of earlier instars, through selective tissue feeding, thus preventing pupation (Chapter 3). The higher mortality of wasps developing in L5, as opposed to L3 hosts, irrespective of egg number per host, may indicate that some physiological incompatibility exists between *Venturia* and L5 hosts, which could be associated with pupation. This same incompatibility is a factor which could influence the developmental rate, as well as the growth potential (hence, the size) of wasps from superparasitized hosts. As the results clearly show that superparasitism affects L5 hosts more than L3 hosts, it suggests that they are less suitable. A similar physiological incompatibility has been found in other associations when parasitoids begin development in later instar compared to early instar hosts (Lewis, 1970; Jones & Lewis, 1971; Sato, 1980; Hopper & King, 1984; Tanaka *et al.*, 1984).

My results support data obtained in several other studies, suggesting that superparasitism by solitary parasitoids often delays the development of the progeny of these species. The egg to eclosion times of *Cardiochiles nigriceps* and *Microctonus vittatae* were both increased in superparasitized hosts (Vinson & Sroka, 1978; Wylie, 1983). Similarly, superparasitism retarded the development rate of *Telenomus remus* (Gerling, 1972) and *Biosteres longicaudatus* (Lawrence, 1988). McBrien & Mackauer (1990), investigating heterospecific larval competition between *Aphidius ervi* and *A. smithi*, also found that *A. ervi* required longer to develop in the presence of an older larva of *A. smithi,* even thought the latter was eventually killed by *A. ervi.* However, a recent study by Bai & Mackauer (1992) found that superparasitism had no measurable effect upon development time of *A. ervi,* but that wasps from superparasitized pea aphids were significantly larger than those from singly parasitized aphids. The authors suggested that this was because superparasitized aphids ingested more food, and incorporated it more efficiently, than singly-parasitized and unparasitized controls in that order (see also Cloutier & Mackauer, 1979, 1980). Thus, the effects of both multiparasitism and superparasitism may vary widely in different host-parasitoid associations.

Although I have shown that the effects of superparasitism may vary between associations, most of the data obtained to date applies to koinobiont parasitoids. As suggested by Bai & Mackauer (1992), the effects of superparasitism may be less evident in koinobionts than idiobionts, because koinobionts can mask any deleterious effects of larval competition during early development (when the host's growth potential may still be considerable) for more rapid development via compensatory feeding during later larval development. In these experiments, L5 hosts were post-feeding wandering larvae, hence their growth potential was nil. The resources available to *Venturia* attacking these L5 hosts are more or less predetermined, as in idiobiont-host associations (Chapter 3). It is therefore interesting that, in line with Bai & Mackauer's (1992) observations, superparasitism affected parasitoids from L5 hosts more adversely than from L3 hosts. The surviving *Venturia* larva may be able to compensate for any negative effects of superparasitism in growing L3 hosts, but cannot offset these factors so effectively in non-growing L5 hosts.

This account of differential suitability may be somewhat simplistic. The growth of endoparasitic koinobionts is governed by a number of complex biochemical interactions with potentially growing and developing hosts. Immature parasitoids may adjust their feeding rate in response to changes in host haemolymph protein levels or hormonal cues (Corbet, 1968; Smilowitz & Iwantsch, 1975). For example,

the ichneumonid parasitoid *Hyposoter exiguae* suspends development as a first instar until a hormonal cue from its host (*Trichoplusia ni*) triggers destructive feeding. Parasitism will not occur successfully after the ecdysone peak that signals pupation because the parasitoid fails to receive the correct hormonal stimuli (Smilowitz, 1974). Therefore, even a small delay in feeding caused by competition with other parasitoid larvae may seriously disrupt the normal development pattern of *Venturia,* because specific cues may have been missed in L5, but not L3 hosts.

These results, and those of other investigations, should be incorporated into models of superparasitism as an adaptive foraging strategy (for example, van der Hoeven & Hemerik, 1990; van Alphen & Visser, 1990; Speirs *et al.*, 1991). These models have thus far ignored the effects of superparasitism on the fitness of the surviving larva in solitary parasitoids. For *Venturia,* I have established that superparasitism not only alters host suitability in terms of progeny fitness, but that the effects of superparasitism may vary markedly between host instars with considerably different growth potential. As these consequences are variable and may be host instar-dependent, evolutionary models of superparasitism and host suitability need to incorporate the costs and benefit of superparasitism across a range of host types. This will allow a more comprehensive picture of host suitability to be obtained.

5. The effect of host nutrition on growth and development of *Venturia canescens*

5.1 Introduction

Parasitoids develop on a limited food source, with the quality and quantity of resources obtained from the host inevitably playing a crucial role in determining their reproductive success. A minimal amount of resources is necessary for successful development into a reproductive adult, while the type of food consumed by hosts will also influence the fitness of their parasitoids (Smith, 1957; Pimentel, 1966; Howell & Fisher, 1977; Thompson, 1979; Barbosa *et al.*, 1982; Vinson & Barbosa, 1987; Bloem & Duffey, 1990a,b). Consequently, host nutrition may profoundly influence the ability of the parasitoid to develop normally. However, most studies of host-parasitoid interactions have been carried out under conditions in which hosts were reared with excess food, and as a result their parasitoids were not limited by host nutrition during their development.

Whereas idiobiont parasitoids are able to assess quantitative differences in their hosts at oviposition, some workers (for example, Waage, 1982) believe that koinobionts may be unable to predict future host quality because it is determined by a set of unpredictable extrinsic factors such as the host's feeding rate, nutrition of its diet and the corresponding effects these have on host growth during the course of the interaction (Mackauer, 1986; King, 1989; Sequeira and Mackauer, 1992a). However, although koinobionts may frequently parasitize hosts which immediately provide insufficient resources for the development of their progeny, some koinobiont parasitoids compensate through regulating the development of their hosts or themselves enabling them to secure enough resources for their own development (Vinson, 1975; Stoltz & Vinson, 1979; Cloutier and Mackauer, 1979, 1980; Vinson & Iwantsch, 1980b; Strand *et al.*, 1988; Lawrence, 1990; Strand & Wong, 1991; Dushay & Beckage, 1993; Pennachio *et al.*, 1994).

Beckage & Riddiford (1983) investigated the effects of variable starvation of newly ecdysed final stage host larvae upon the per-cent emergence of the gregarious braconid parasitoid *Apanteles* (=*Cotesia*) *congregatus*. They found that the later that starvation is initiated, the higher the proportion of parasitoids that eclose, suggesting a period of 'indispensable host nutrition' occurs when the host must feed to satisfy the developmental requirements of the parasitoids. Although few investigations of the kind have been undertaken with solitary koinobionts, several recent studies have suggested that the nutritional demands of solitary species are less than those of

gregarious species. While attacking the same early host instars, larvae of the solitary parasitoid *Apanteles* (=*Cotesia*) *rubecula* emerge during the fourth instar of its host, *Pieris rapae*, whereas larvae of the gregarious *A. glomeratus* delay emergence until the fifth host instar. In this final instar the hosts consume and assimilate over 85% of their food intake (Slansky, 1978, 1986). Many solitary parasitoids, including *Venturia*, consume virtually all of their host before pupation. In such species it is unlikely that the nutritional demands are any less than those of gregarious species, and thus host nutrition may profoundly influence parasitoid fitness.

In chapter three I showed that parasitoid (*Venturia*) mortality, development time and size were all influenced by the instar of the host (*Plodia*) that was parasitized. When attacking early instar hosts, *Venturia* spent variable and prolonged periods as first instars, accelerating development only when the host larvae reached their final instar (see also Corbet, 1968). This physiological synchrony between parasitoid feeding and host size constitutes an important mechanism that allows koinobiont parasitoids to attack a wide range of host instars (Smilowitz & Iwantsch, 1973). However, in the previous experiment, hosts were reared on a standard diet under conditions of excess food, enabling parasitized hosts to develop rapidly and *Venturia* to exploit these good conditions. Consequently, there was very little variation in the fitness correlates of wasps emerging from hosts parasitized as L3-L5 instars. Under natural conditions it is likely that a number of interacting factors will potentially reduce host suitability from one instar to another by altering the speed at which they develop. A decline in temperature below the optimum for development, or a reduction in the quality of the hosts food source will correspondingly affect the performance of the developing parasitoid (Barbosa *et al.*, 1982).

Most studies examining the influence of host nutrition on parasitoid development have used phytophagous hosts, concentrating upon the role of plant-related factors such as toxins and allelochemicals that are sequestered by the host on parasitoid development and survival (Barbosa *et al.*, 1982). In this chapter I will examine a different aspect of this subject - the effect of varying the nutritional quality of host diet on development of *Venturia*. First, I will determine the effects on mortality, development time and adult parasitoid size, by varying the nutrition of parasitized 3rd and 5th instar hosts. These results may affect models of host quality based upon studies where hosts have been only reared with excess food.

Second, I determine if the progressive daily starvation of parasitized third instar *Plodia* larvae affects the survival and development.of *Venturia*. Moreover, by

weighing hosts at the commencement of starvation, I may be able to determine the precise developmental stage when *Plodia* provides *Venturia* with a minimal amount of resources for successful development, or that point of 'indispensable host nutrition' (Beckage & Riddiford, 1983). Furthermore, dry masses, development times, and mortalities of parasitoids were recorded, giving a comprehensive picture of the nutritional requirements of *Venturia* throughout the experimental period.

5.2 Materials and Methods

5.2.1 Host condition and parasitoid development

The aim of this experiment was to determine the influence of nutritional variability on the development of *Venturia* from L3 and L5 host reared as controls or under conditions which retard their growth and development.

Plodia used in the experiments were either late L3 instars or post-feeding late L5 instars. In order to obtain large hosts, I reared *Plodia* larvae in low densities (approximately 100 larvae per 25 grams of food medium). Small L5 hosts were obtained by culturing larvae at high densities (approximately 400 larvae per 25 grams of food medium).

(a) L5 hosts Hosts for parasitism were removed from high and low density culture jars. These were individually presented to single parasitoid females, which were allowed to parasitize once. Larvae were then placed in individual vials with food until parasitoid eclosion.

(b) L3 hosts These were also individually presented to wasps for parasitism (as above) and separated into 2 groups. Immediately after parasitism, the larvae from group 1 were placed in individual vials without food for 24 hours, and were then transferred to vials with nutritionally-deficient medium (wheat middlings without yeast and glycerol) for the following 8 days. On the 10th day after parasitism, the surviving larvae were provided with excess food (wheat middlings, yeast, and glycerol) until parasitoid eclosion. The hosts from the second group (=controls) were placed in vials with excess food immediately after parasitism.

To determine the number of encapsulations, two criteria were observed: all parasitized L5 hosts that produced a moth instead of a wasp were recorded as encapsulations; those hosts which produced neither wasp nor moth were dissected to

determine if they contained a developing or encapsulated parasitoid larva at the time of death. All emerging wasps were killed by freezing, oven dried for 3 days at 100°C, and weighed on a Cahn 29 microbalance. Development times and survivorship were also recorded.

5.2.2 Correlation of parasitoid success with duration of host starvation

The aim of this experiment was to determine the precise developmental stage at which *Plodia* provides *Venturia* with the minimum amount of resources for successful development.

L3 *Plodia* larvae were singly parasitized and then transferred to individual vials containing excess food for 4 days. Beginning on the fourth day after parasitism, host larvae were removed daily and weighed on a Cahn 29 microbalance to obtain their fresh weights. These larvae were then transferred to new vials and starved. This procedure was repeated on each of days 5 to 11; and vials were regularly monitored for the eclosion of adult wasps, *Plodia*, or death.

5.3 Results

5.3.1 Host condition and parasitoid development

(a) L5 instar hosts.

Parasitoid mortality varied significantly with treatment ($X^2 = 4.38$, d.f. = 1, $P < 0.05$; Table 5.1). Nine of 53 control hosts failed to produce adult parasitoids: five died as pupae (all contained dead final instar *Venturia* larvae) while four wasp larvae were encapsulated. Fifty-eight out of 61 poorly-nourished hosts produced adult wasps; 3 wasp larvae were encapsulated.

The development time of parasitoids from L5 hosts differed significantly between the two host-nutrition treatments ($t = 3.66$, d.f. = 100, $P < 0.001$; Table 5.1). Parasitoids from poorly-nourished hosts reared in high densities eclosed just under 1 day before those from the larger hosts reared at low densities (Table 1). The size of wasps emerging from L5 hosts also varied significantly between the two host treatments ($t = 5.41$, d.f. = 100, $P < 0.001$; Table 1). Wasps which developed in the control hosts attained a mean dry mass approximately 400 µg greater than those from the poorly nourished hosts.

(b) L3 instar hosts.

Parasitoid mortality varied significantly with treatment ($X^2 = 49.78$, d.f. = 1, $P < 0.001$; Table 1). Ninety-eight of 150 poorly nourished hosts perished during the 9 days of starvation. Once transferred to excess food, however (day 10), all L3 larvae developed rapidly and produced adult wasps, with no further mortality or encapsulations recorded.

Parasitoid development time varied significantly between wasps emerging from the two host treatments ($t = 32.27$, d.f. = 94, $P < 0.001$; Table 1). *Venturia* adults eclosed from well-fed hosts approximately 12 days prior to those which had developed from poorly nourished hosts. There was, however, no significant effect of treatment on the size of emerging adult wasps ($t = 1.796$, d.f. = 94, $P > 0.05$; Table 1).

Table 5.1. Growth and development of *Venturia canescens* reared from well-fed and starved L3 and L5 instars of *Plodia interpunctella*. Figures in brackets denote standard error (S.E.); ** and * indicate that within each instar group wasps emerging from hosts reared on nutritionally deficient food are significantly different at $P < 0.001$ and $P < 0.05$ respectively.

Host instar	Host feeding regime	Sample size	Dvt. time (d)	Dry mass (mg)	Mort-ality (%)
L3	Excess food	47	21.30 (0.17)	1.71 (0.04)	6.43
L3	Starved	150	33.10 (0.12)**	1.63 (0.03)	65.35**
L5	Excess food	53	21.52 (0.15)	1.76 (0.05)	16.98
L5	Starved	61	20.88 (0.10)**	1.36 (0.05)**	4.92 *

5.3.2 Correlation of parasitoid success with duration of host starvation

Parasitoid mortality varied significantly with the duration of host starvation (X^2 = 99.31, d.f. = 6, $P < 0.001$). No *Venturia* developed successfully from hosts (mostly L4) starved from the 4th day after parasitism and only one emerged the following day. However, from the 6th to 11th days after parasitism, over 60% of hosts produced adult wasps (Figure 5.2a).

The difference in host larval fresh weight between hosts producing adult parasitoids, and those in which the host died during development (both after the initiation of starvation) was significant (one-way ANOVA, $F = 133.27$, d.f. = 1, 138, $P < 0.0001$). The mean weight of hosts at starvation from which a parasitoid eclosed was 12.84 mg, equivalent to the weight of late 5th instar *Plodia* larvae. The mean weight of hosts which died after starvation was 4.74 mg, or the approximate weight of mid-4th to early 5th instar *Plodia*. Figure 5.1 shows the weight distribution of hosts which either produced adult wasps or died after the onset of starvation. The point of overlap between the 2 categories occurs at between 7.0 and 9.0 mg, and is the 'critical minimal resource threshold' for successful parasitoid development. Under excess food, parasitized 3rd instar hosts reach this critical weight as early 5th instars.

Figure 2b shows the mean fresh weight (FW) of hosts at the commencement of starvation, beginning 4 days after parasitism. Host FW increased daily reaching a maximum on about the 8th day after parasitism. At this stage, the larvae ceased feeding and entered the wandering phase.

The egg-to-adult development time of parasitoids varied significantly with the day on which host starvation began (one-way ANOVA, $F = 43.78$, d.f. = 6, 85, $P < 0.001$). Parasitoids develop and eclose earlier in hosts that are starved for longer (Figure 5.2c). Wasps from hosts starved from the 6th day after parasitism emerged about 4 days before those hosts in which starvation was delayed until 11 days after parasitism.

Eclosing parasitoid dry mass also varied significantly with the length of host starvation (one-way ANOVA, $F = 10.02$, d.f. = 6, 85, $P < 0.001$). The mean size of *Venturia* increased daily between the 5th and 8th day after parasitism and levelled off

Fig. 5.1. Weight distributions of *Plodia* larvae producing adult *Venturia* (unshaded bars) or in which hosts died, producing neither parasitoids nor adult moths (shaded bars). Hosts were parasitized as mid 3rd (M3) larval instars. From the 4th to 11th day after parasitism, a number of hosts were randomly removed daily and subjected to starvation thereafter. Their fresh weights at the onset of host starvation are indicated on the horizontal axis. Total sample size = 142.

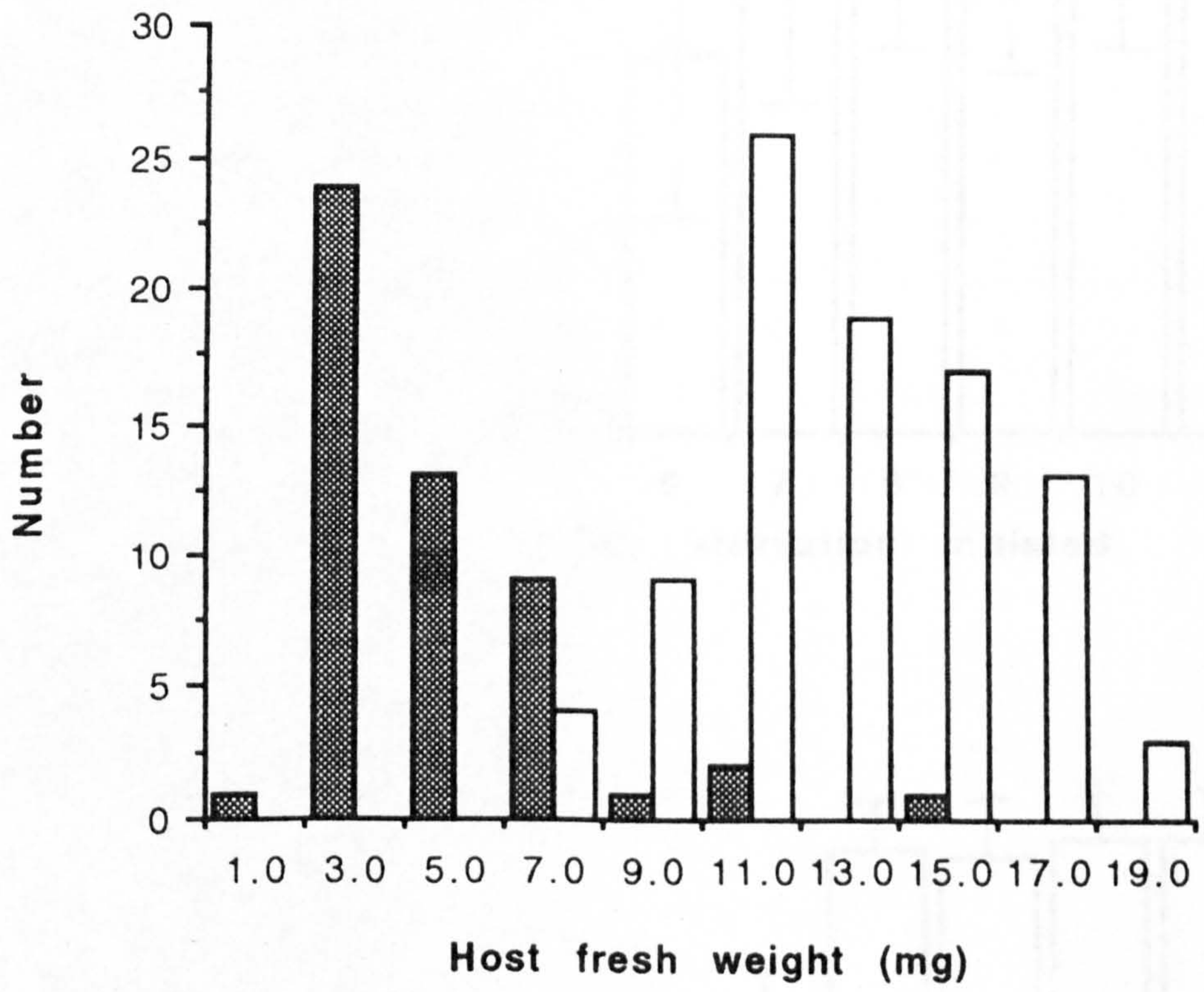


Fig. 5.2. The correlation of parasitoid success with duration of host starvation. (a). Percentage successful parasitoid emergence (± 95% confidence intervals). Sample sizes are: day 4- 20, day 5 - 18, day 6 - 18, day 7 - 18, day 8 - 19, day 9 - 17, day 10 - 19, day 11 - 13. (b) Mean daily fresh weight of *Plodia* (± 95% confidence intervals). Sample sizes as in 2(a). (c) Development time in days, from oviposition to adult eclosion (± 95% confidence intervals). Sample sizes are: day 5 - 1, day 6 - 11, day 7 - 14, day 8 - 18, day 9 - 17, day 10 - 18, day 11 - 12. (d) Size of adult *Venturia* (dry mass in mg; ± 95% confidence intervals). Sample sizes are as in Fig. 2(c).

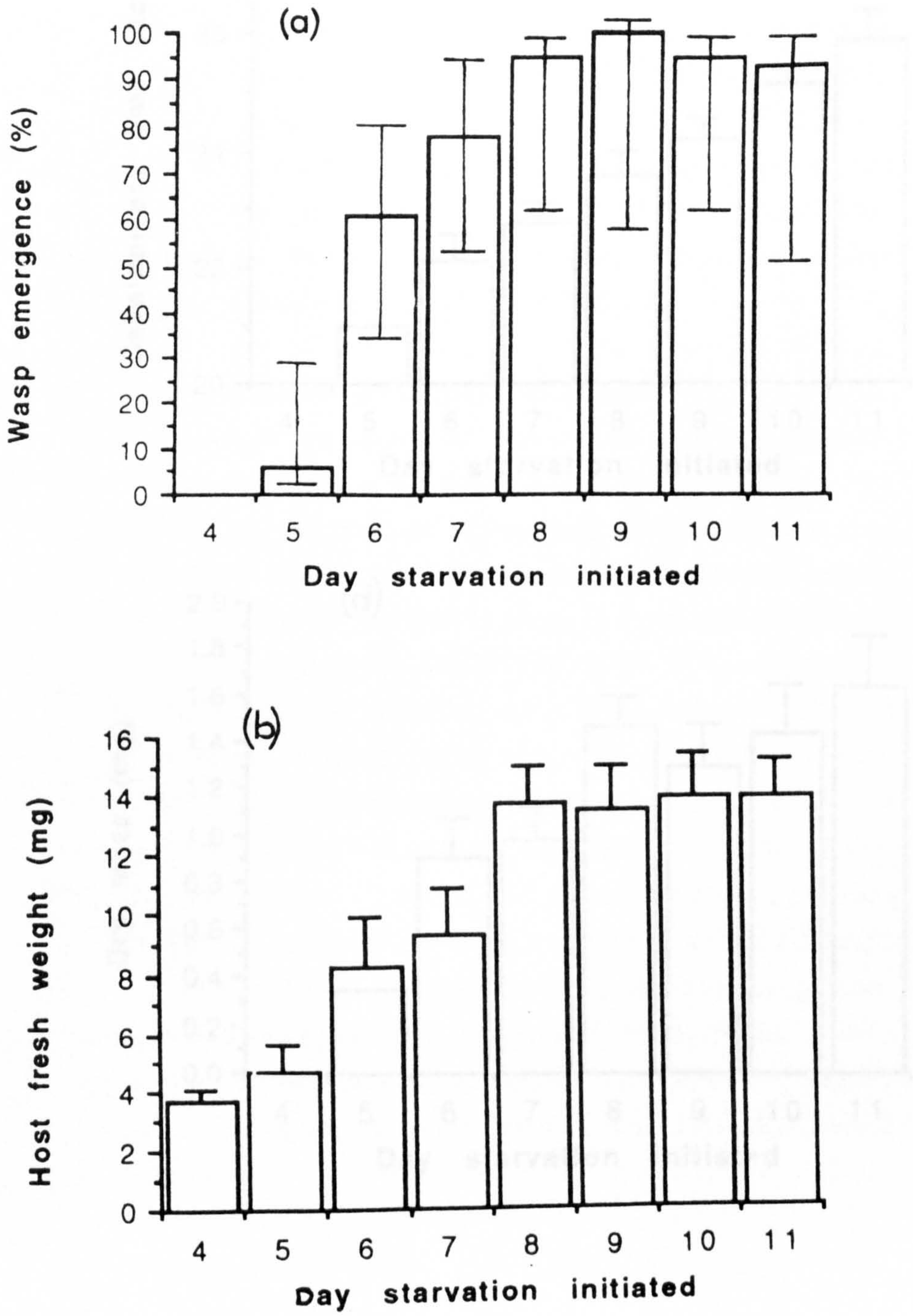
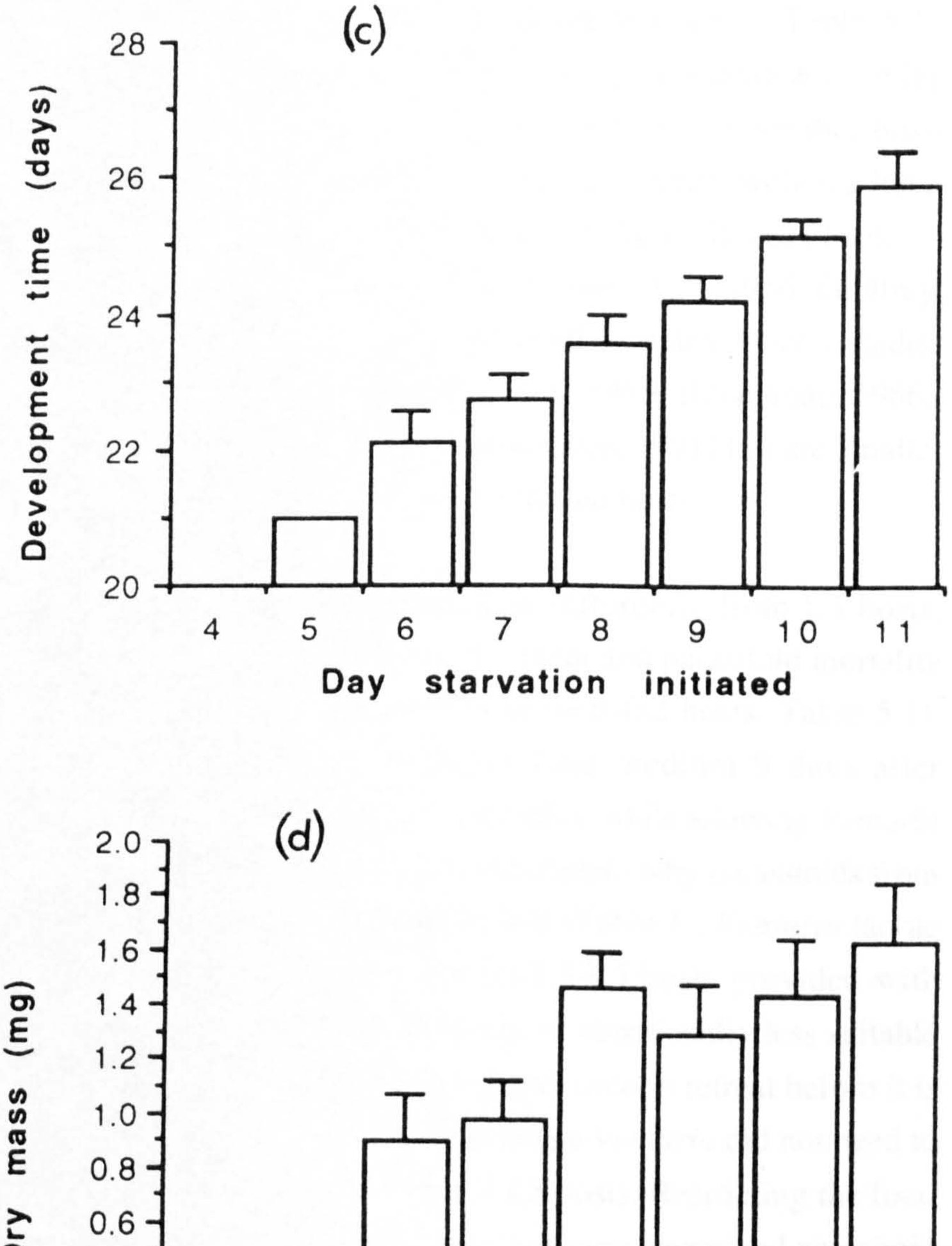


Fig. 5.2 (continued).



thereafter (Figure 2d). The largest wasps, with a mean dry mass of 1.632 mg, eclosed on the final day (11) of host starvation.

5.4 Discussion

In this investigation I found that variations in host condition influenced parasitoid development in a number of ways. Wasps from starved L5 hosts were smaller than those from well-nourished hosts but developed faster (Table 5.1). Starved hosts contained less resources than well-fed larvae, presumably accounting for these size differences. However, parasitoids developed faster on smaller hosts probably because they were consumed in less time than the larger, well-fed hosts (Godfray, 1994). Parasitoid mortality was also higher in healthy L5 larvae (Table 1). Hosts in poor condition often have a reduced cellular defence (Salt, 1956; Godfray, 1994) which may account for these differences in parasitoid mortality. Recent studies have found that parasitoids survive better (Wajnberg *et al.*, 1985; Bouletreau, 1986), develop faster (Wajnberg *et al.*, 1990; Kouame & Mackauer, 1991) but are smaller (Wajnberg *et al.*, 1990) when developing in poorly nourished hosts

Host starvation affected parasitoid development differently from L3 hosts. *Venturia* took over 10 days longer to complete development and parasitoid mortality was almost 70% in starved hosts (compared to 6% in well-fed hosts; Table 5.1). Transferring the surviving starved hosts to excess food medium 9 days after parasitism enabled these hosts to develop normally thereafter while allowing *Venturia* to compensate for early resource deficiency. This could explain why parasitoids from both L3 host treatments did not vary significantly in size (Table 1). *Venturia* larvae show arrested development in second instar, but not L3-L5 hosts provided with excess food (Chapter 3). This developmental delay allows nutritionally less suitable hosts to grow after parasitism and to construct a pre-pupal cocoon retreat before it is destroyed. *Plodia* larvae grow rapidly when well-fed, hence *Venturia* did not need to arrest development to obtain sufficient food from L3-L5 hosts. Restricting the food of large, nutritionally sufficient final instar (L5) hosts, however, decreased parasitoid development time, but limiting the food available to small, L3 hosts lengthened parasitoid development by increasing the time spent in early stages. Similar results have been recorded in koinobionts whose development (like *Venturia*) is closely synchronized with that of the host (eg. Weseloh, 1984; reviewed by Mackauer & Sequeira, 1993 and Godfray, 1994).

In the second experiment I investigated the correlation of parasitoid success with duration of host starvation and found that percentage parasitoid eclosion varied with length of host starvation in hosts parasitized as L3. All hosts starved 4 days after parasitism perished and failed to produce an adult wasp, while only one wasp emerged from hosts starved from the 5th day after parasitism (Fig. 5.2a). However, as the duration of starvation decreased, the percentage of wasp emergence (Fig. 5.2a), parasitoid development time (Fig. 5.2c) and adult wasp size (Fig. 5.2d) all increased. Hosts given access to food for longer periods were themselves larger (Fig. 5.2b), accounting for the corresponding increase in parasitoid size and development time.

The critical host resource threshold for *Venturia* to develop successfully occurred when hosts reached their mid-5th instar, and weighed between 7 and 9 mg (Fig. 5.1). Hosts starved the longest (beginning on days 4 and 5 after parasitism) had not reached this size and therefore *Venturia* were unable to develop from them. Corbet (1968) showed that *Venturia* (= *Nemeritis*) larvae suspend development as a first instar until a physiological cue, perhaps hormonal, triggers the parasitoid to moult and commence destructive feeding. Parasitism presumably cannot be successfully completed in pre-5th instars because the parasitoid fails to receive the correct hormonal stimuli.

The contention that solitary parasitoids markedly suppress the growth and development of their hosts (Tanaka *et al.*, 1984; Sato *et al.*, 1986; Tanaka *et al.*, 1992), thus leading to the assumption that gregarious parasitoids have greater nutritional demands than solitary parasitoids (Slansky, 1986), is misleading. The physiological and nutritional demands of parasitoids vary in accordance with a number of host-related factors (eg. immunology, growth potential) and many solitary koinobionts require their hosts to grow as large as healthy larvae before they are destroyed (Gauld, 1988; Chapter 3). Although *Venturia* parasitizes a wide range of host instars, they cannot develop successfully unless the host continues to feed, grow and reach the size of a healthy (unparasitized) final instar. Many gregarious koinobiont parasitoids alter host metabolism by increasing the assimilation efficiencies or consumption rates of hosts when they are heavily parasitized (Fuhrer & Keja, 1976; Slansky, 1978; Vinson & Iwantsch, 1980b). However, some solitary koinobionts also strongly alter the energy metabolism of their host during endoparasitism (Beckage & Riddiford, 1983). For example, aphids superparasitized by *Aphidius smithi* feed faster and assimilate nutrients more effectively than singly parasitized and unparasitized aphids in that order (Cloutier & Mackauer, 1979,

1980). The assimilation efficiency of *Trichoplusia ni* is also increased throughout parasitism by the ichneumonid, *Hyposoter exiguae* (Thompson, 1982).

The assumption that solitary parasitoids have lower nutritional requirements than gregarious species has largely been based upon a limited number of studies. In these associations, the parasitoid is able to develop in early-instar hosts whose growth is arrested by the parasitoid (host regulation) (Vinson, 1975; Thompson, 1982, 1983; Beckage & Templeton, 1985) at a particular size or stage that is much smaller than the growth potential of healthy (unparasitized) hosts (eg. *Campoletis sonorensis* (Vinson, 1972); *Hyposoter exiguae* (Smilowitz & Iwantsch, 1973)). This pronounced reduction in the growth of parasitized hosts presumably occurs because medium sized hosts have a higher nutritional and developmental suitability than large or small hosts. In contrast, the nutritional requirements of *Venturia,* relative to the growth potential of unparasitized hosts, are greater than in these other associations, irrespective of instar attacked. This is because a suitable host must attain a mass which is equivalent to that of an unparasitized mid-5th instar. This could explain why hosts parasitized as early instars grow 80% as large as controls (Chapter 3).

The results of similar investigations need to incorporate the effects of host nutrition upon parasitoid development. I have shown that development of *Venturia* is greatly influenced by the condition of the host as affected by variations in host diet. Thus the contention that solitary parasitoids are less influenced by host nutrition than gregarious parasitoids (Vinson & Iwantsch, 1980b) may not be correct in all cases. Parasitoid survival, development time and size were all influenced by the condition of the host during the interaction and these effects varied with host instar at parasitism. Size is an important correlate of fitness because it may affect an individual's reproductive success through variations in fecundity, longevity and searching efficiency (Salt, 1940; Vinson and Iwantsch, 1980a; Bellows, 1985; Visser, 1994) while differences in development time can affect fitness by varying the intrinsic rate of increase (Lewontin, 1965). It would be valuable to investigate the developmental interactions between parasitoids and their hosts under a variety of nutritional regimes which may occur under natural conditions. In this way we can evaluate the effects of host nutrition on parasitoid fitness and incorporate them into models of host suitability.

6. Host species and its influence on the development of *Venturia canescens*

6.1. Introduction

The growth and development of insect parasitoids is often markedly influenced by the host species from which they develop. Host-related variations in certain fitness correlates such as size and survivorship have been observed in many associations (Lewis & Vinson, 1971; Legner & Thompson, 1977; Rotheray *et al.*, 1984; Moratorio, 1987; Sequeira & Mackauer, 1992a,b). Salt (1940) showed that the size of emerging adult *Trichogramma evanescens* varies with host species. Similarly, Corrigan & Lashomb (1990) found that the eulophid wasp *Edovum puttleri* was larger and produced more oocytes when reared from eggs of *Leptinotarsa texana* than *L. decemlineata*. Therefore, host quality as affected by host species can influence the biology of parasitoids.

Most studies on host species suitability, however, have been undertaken using idiobiont parasitoids (Haeselbarth, 1979; Askew & Shaw, 1986) where host resources are ostensibly static during the interaction, and parasitoid size is often a function of host species size (for example, Salt, 1940, Arthur & Wylie, 1959, Rotheray *et al,* 1984; Chapters 3-5). In koinobiont-host associations the amountsof resources for parasitoid growth and development are not fixed and parasitoid development depends largely upon host feeding rate and capacity for growth during the interaction (Mackauer, 1986; Godfray, 1994; Chapter 5). We may therefore expect host instar and species to affect koinobionts differently than idiobionts, because the amount of host resources available is not predictable at oviposition.

In Chapter three I showed that the growth of *Venturia* is delayed in early instar *Plodia* with accelerated development occurring only after the host has completed its final larval moult. Although in the laboratory *Venturia* is commonly reared on *Plodia* and a similar host, *Anagasta kuehniella*, Salt (1964, 1975) found that it will also parasitize other hosts which vary considerably in their rate of development and growth potential. Therefore, the aim of this investigation is to determine the effects of host species and instar on fitness related traits in *Venturia*. Few studies have simultaneously investigated the influence of instar and species on koinobiont development. I will examine the development of *Venturia* from L2-L5 instars of *Plodia* and *Corcyra* as well as from L5 *Anagasta*. When reared below 30°C, *Corcyra* develops at a slower rate than *Plodia* (Subramanyam & Hagstrum, 1993) although

diet influences the development of both species (Cox *et al.*, 1981; Mbata & Osuji, 1983). This study reports the influence of host species and instar on the development of *Venturia*, with particular reference to adult size, development rate and mortality.

6.2. Materials and methods

6.2.1 Parasitoid mortality, development time and adult size

L2-L5 *Plodia* and *Corcyra* larvae were isolated from cultures according to head capsule dimensions (Table 6.1) and were individually presented to parasitoids. The development of *Venturia* from post-feeding wandering L5 larvae of another pyralid species, *Anagasta kuehniella,* was compared with the data obtained from *Plodia* and *Corcyra. Anagasta* grows slightly larger than *Plodia* when reared on the same diet (Taylor, 1988).

Wasps were allowed to oviposit once in each host that were then transferred to glass vials containing approximately one gram of their respective food media. Parasitized hosts were closely monitored daily for the emergence of adult wasps or moths. Following eclosion, parasitoids were killed by freezing, and then placed into an oven at 100°C for 3 days in order to obtain dry mass data. Wasps were subsequently weighed on a Cahn 29 electrobalance and hind tibia measurements were made using a calibrated stereomicroscope. Development time was recorded as the number of days from oviposition to parasitoid eclosion.

Encapsulation was recorded when a parasitized host produced an adult moth instead of a wasp. If neither wasp nor moth had emerged within 50 (*Plodia, Anagasta*) or 70 (*Corcyra*) days of oviposition, dead host larvae or pupae were removed from vials and dissected in order to determine at what stage the parasitoid had died within the host.

6.2.2 The development of *Venturia* in late L5 *Anagasta*, *Plodia* and *Corcyra* larvae

To determine if the size of post-feeding L5 host size affects parasitoid development, the data obtained from L5 *Corcyra* and *Plodia* (above) was compared with that from a third host, *Anagasta.* These larvae were parasitized by *Venturia* according to the protocol above, and mortality, development time and adult wasp size were recorded.

6.2.3 Relationship between adult wasp size and egg load

In order to test the relationship between adult wasp size and egg load, a number of 5-day old wasps reared from both host species were killed by freezing, placed on a dampened slide and dissected by grasping the metasoma with forceps and pulling the ovipositor distally with another pair of forceps. This enabled the paired lateral oviducts to be removed. Ovulated eggs were counted by cutting the oviducts at the calyx gland just below the ovaries, and teasing them carefully into the suspension. Adult wasp size was determined by measuring the hind tibia length under a calibrated stereomicroscope.

6.2.4 Relationship between non-growing L5 host size and parasitoid size

In order to determine if the size of adult wasps is affected by host size in final instar *Corcyra* and *Plodia,* a number of L5 hosts from each species of a range of sizes were taken from cultures, weighed to within 0.1 mg on a Cahn 29 microbalance and singly parasitized by *Venturia.* Some L5 *Corcyra* and *Plodia* may not have completed their growth at the time of parasitism, so all parasitized larvae, irrespective of size or species were starved by placing the larvae singly in vials without food after parasitism. Eclosing wasps were killed by freezing, and their hind tibia measured under a stereomicroscope.

6.2.5 Head capsule widths of parasitized L2-L4 *Corcyra* and unparasitized (control) larvae

In Chapter three I showed that the growth of L2 and L3 *Plodia* is reduced in parasitized hosts compared with unparasitized larvae, but that hosts parasitized as L4 grew as large as healthy larvae. In order to determine the influence of parasitism on the growth of *Corcyra*, a number of L2, L3 and L4 hosts were taken from cultures, parasitized singly by *Venturia* and placed in vials with approximately 2 g of food medium. A separate group of unparasitized L2 hosts (= controls) were isolated from cultures and similarly placed in vials with approximately 2 g of food medium. Upon eclosion of parasitoids (from L2-L4 hosts) or adult moths (from controls) the *Corcyra* cocoon was carefully cut open and the final larval head capsule at time of death or pupation was removed and measured under a stereomicroscope.

6.3 Results

6.3.1 Parasitoid mortality, development time and adult size

Mortality was consistently higher in all but L2 instar *Corcyra* compared to *Plodia* instars. Percentage encapsulation was highest from L5 *Corcyra*, with 76 moths emerging from 172 parasitized hosts and a further 49 producing neither wasp nor moth. *Venturia* were able to develop with greater success in L2-L4 *Corcyra*, where mortality was less than 40%. *Plodia* suffered less than 20% mortality in L3-L5 hosts. However, this increased to 44% in L2 hosts, most of these larvae dying within 2 days of oviposition. A 3-way contingency table was used to analyse mortality data, with instar, host species and whether parasitoid development was successful or not (parasitoid mortality) as factors. The overall test of independence was rejected ($G = 214.53$, d.f. = 10, $P < 0.01$; Fig. 6.1a) and there were significant interactions between host species and mortality ($G = 12.27$, d.f. = 1, $P < 0.01$) and instar and mortality ($G = 16.77$, d.f. = 1, $P < 0.001$).

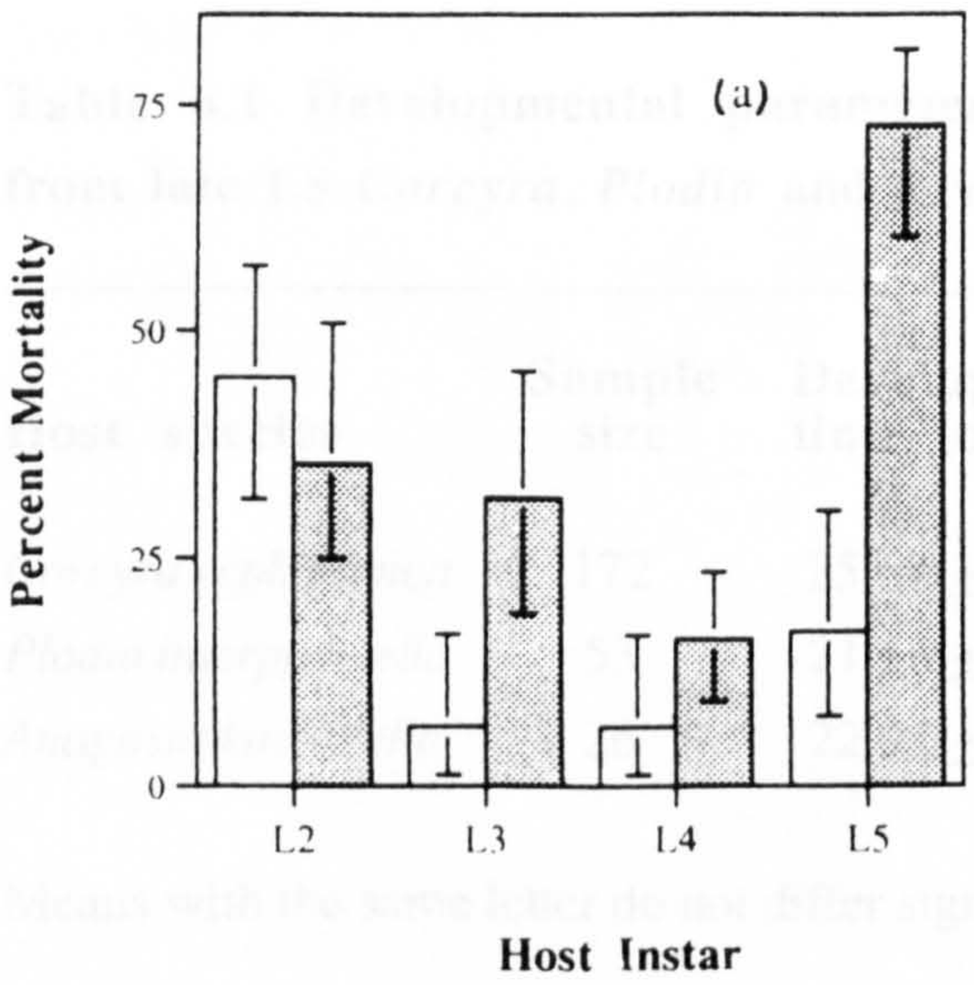
A two-way ANOVA on development time, with host species and instar as factors, revealed a significant interaction between species and instar ($F = 33.0$, d.f. = 3, 348, $P < 0.001$; Fig. 6.1b). The egg-to-adult development time of *Venturia* from *Plodia* was fairly uniform in L3-L5 instars, but wasps from L2 hosts took some 4 days longer to complete development to eclosion. However, parasitoid development time decreased steadily with host instar at parasitism from *Corcyra*, ranging from about 38 days (L2) down to 25 days (L5). In all instars, parasitoid development was longer from *Corcyra* than *Plodia* (Fig. 6.1b).

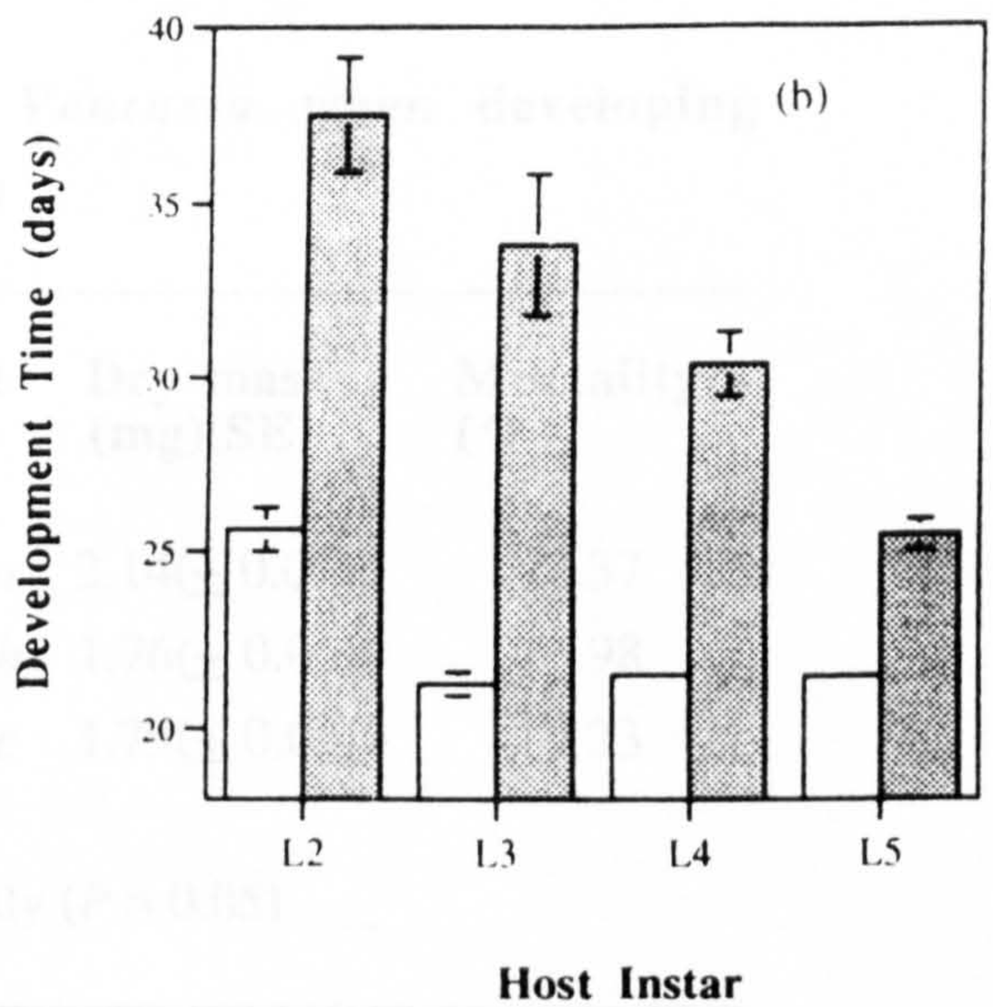
A two-way ANOVA on adult wasp size also revealed a significant interaction between species and instar ($F = 8.30$, d.f. = 3, 348, $P < 0.001$; Fig. 6.1c). The size of adult wasps increased from L2-L4 *Plodia* instars but decreased marginally in L5 hosts. Conversely, *Corcyra* produced wasps were fairly uniform in size irrespective of instar at parasitism, and were also larger than parasitoids emerging from the same *Plodia* instars.

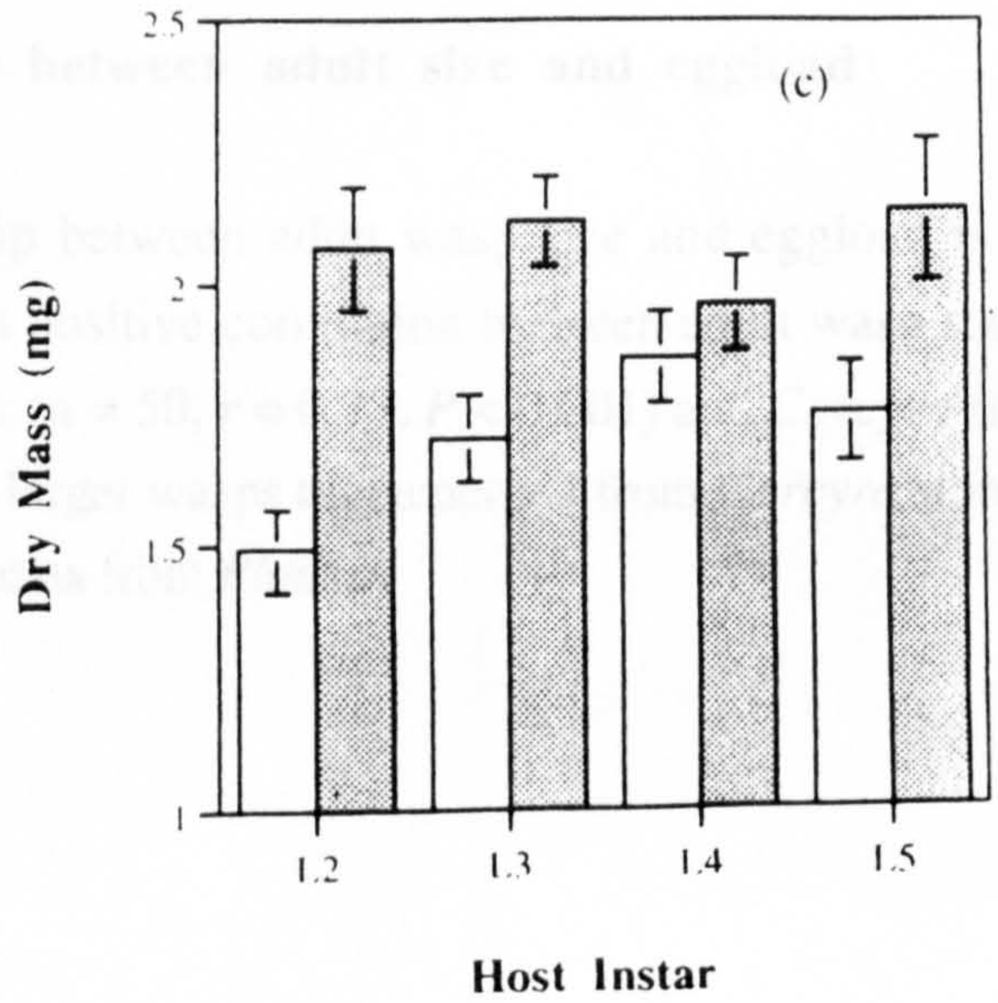
6.3.2 The development of Venturia in late L5 *Anagasta*, *Plodia* and *Corcyra* larvae

Parasitoid mortality varied significantly between the 3 hosts ($X^2 = 49.22$, d.f. = 2, $P < 0.01$). *Venturia* from L5 *Corcyra* suffered over 70% mortality, with less than

Fig. 6.1 (a). Percentage mortality of *Venturia* from hosts parasitized as L2-L5 *Corcyra* (stippled bars) and *Plodia* (open bars). Line bars represent confidence intervals (±95%). Sample sizes are - *Corcyra:* L2 = 58, L3 = 51, L4 = 80, L5 = 172; *Plodia:* L2 = 67, L3 = 47, L4 = 47, L5 = 53. (b). The egg-to-adult development time in days of *Venturia* emerging from hosts parasitized as L2-L5 larval *Corcyra* (stippled bars) and *Plodia* (open bars). Line bars represent confidence intervals (± 95%). Sample sizes are as in Fig. 1a. (c). The size of newly eclosed adult *Venturia* as defined by dry mass in mg, emerging from hosts parasitized as second (L2) through fifth (L5) larval instars of *Corcyra* (stippled bars) and *Plodia* (open bars). Line bars represent confidence intervals (± 95%). Sample sizes are - *Corcyra:* L2 = 38, L3 = 35, L4 = 67, L5 = 47; *Plodia:* L2 = 37, L3 = 44, L4 = 44, L5 = 44.







20% of wasps from L5 *Anagasta* and *Plodia* perishing during development (either by encapsulation or at a later stage).

The egg-to-adult development time of *Venturia* varied significantly between the 3 hosts (one-way ANOVA, F =11.89, d.f. = 2, 109, $P < 0.001$; Table 6.1). Between hosts, the development time also differed significantly (Tukey's pairwise comparisons, $P < 0.05$) with *Plodia*-produced wasps taking the least time to complete development and *Corcyra*-produced wasps the longest (Table 6.1). Wasps from *Anagasta* eclosed more than a day after wasps from *Plodia.*

One-way ANOVA also revealed that parasitoid size varied significantly between the 3 hosts (F = 124.48, d.f. = 2, 109, $P < 0.001$; Table 6.1). Wasps from *Anagasta* and *Plodia* did not differ significantly in size, but were much smaller than wasps emerging from *Corcyra* (Tukey's pairwise comparisons, $P < 0.05$).

Table 6.1 Developmental parameters of *Venturia* when developing from late L5 *Corcyra*, *Plodia* and *Anagasta*

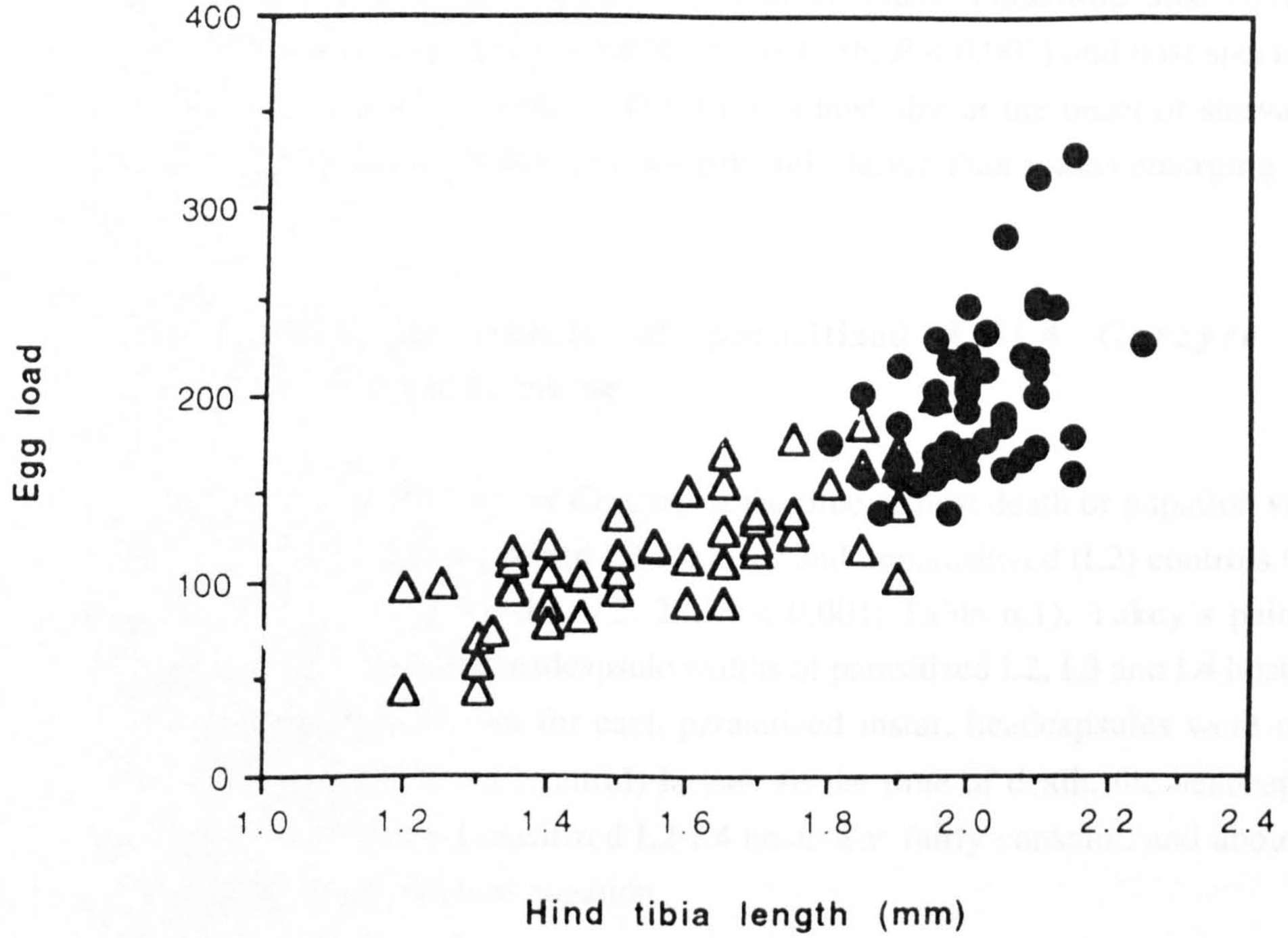
Host species	Sample size	Development time (d)(SE)	Dry mass (mg)(SE)	Mortality (%)
Corcyra cephalonica	172	25.68(± 0.21)*a*	2.14(± 0.07)*a*	72.37
Plodia interpunctella	53	21.56(± 0.15)*b*	1.76(± 0.05)*b*	16.98
Anagasta kuehniella	26	22.95(± 0.20)*c*	1.79(± 0.09)*b*	19.23

Means with the same letter do not differ significantly ($P > 0.05$).

6.3.3 Relationship between adult size and eggload

The relationship between adult wasp size and eggload is shown in Fig. 2. There is a significant positive correlation between adult wasp size and eggload for *Venturia* from *Plodia* (n = 50, $r = 0.73$, $P < 0.001$) and *Corcyra* (n = 50, $r = 0.45$, $P < 0.01$; Fig.6.2). The larger wasps that emerged from *Corcyra* stored more eggs than their smaller counterparts from *Plodia.*

Fig. 6.2. The relationship between adult *Venturia* size, measured as hind tibia length, and the number of mature eggs carried in the lateral oviducts when five days old from *Corcyra* (circles) and *Plodia* (triangles).



6.3.4 Relationship between non-growing L5 host size and parasitoid size

A two-tailed t-test was performed to determine if a significant difference existed in the slopes of the 2 regression lines of parasitoid size for the *Plodia/Corcyra* starved data. The difference was not significant ($t = 0.216$, n = 39, $P > 0.05$). This enabled us to perform an ANCOVA to determine if parasitoid size (hind tibia length) varied significantly between host species of a given mass. Parasitoid size covaried significantly with host size ($F = 66.00$, d.f. = 1, 36, $P < 0.001$) and host species ($F = 17.32$, d.f. = 1, 36, $P < 0.001$). For a given host size at the onset of starvation, wasps emerging from *Plodia* were significantly larger than wasps emerging from *Corcyra* (Fig. 6.3).

6.3.5 Headcapsule widths of parasitized L2-L4 *Corcyra* and unparasitized (control) larvae

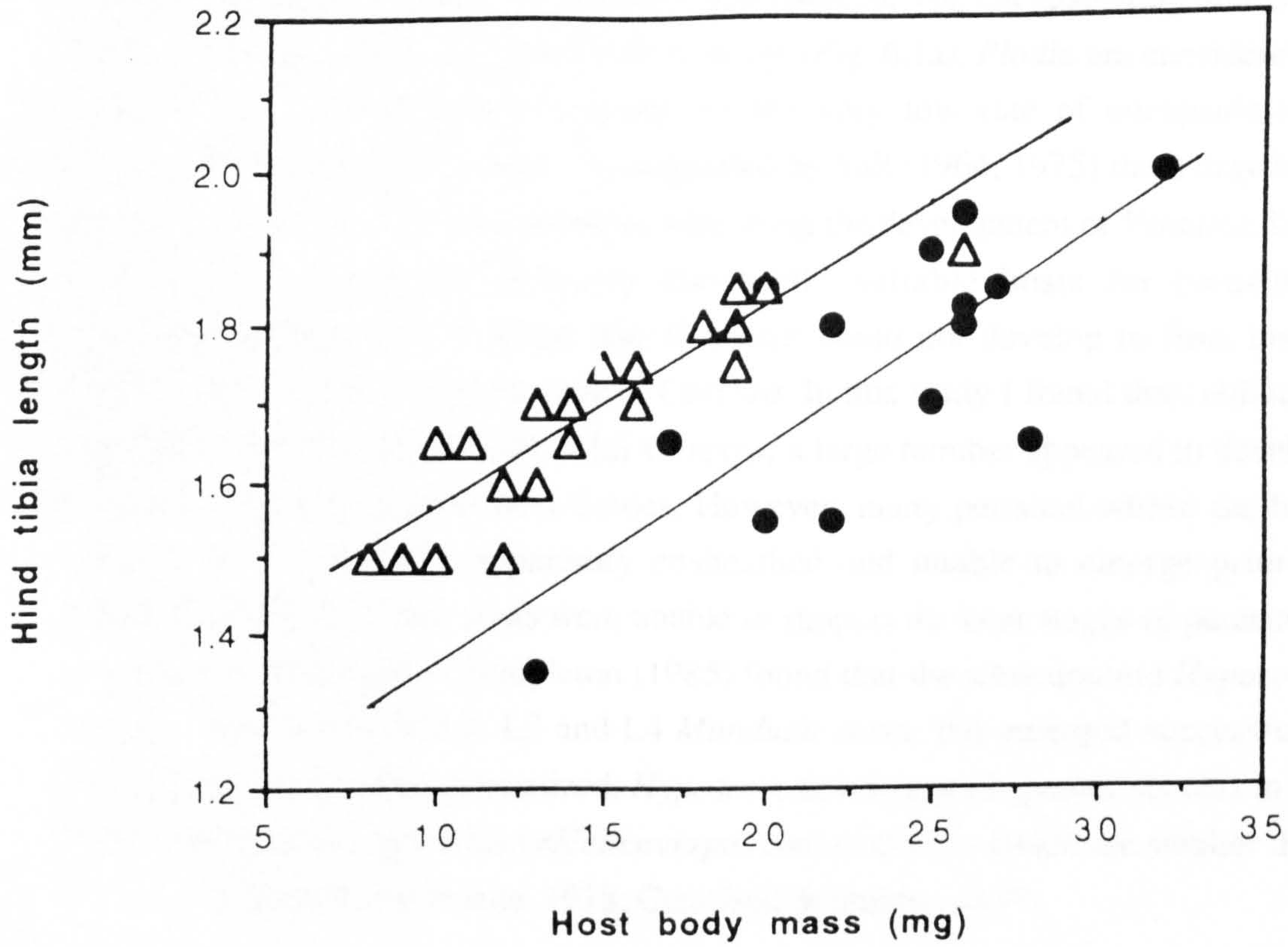
The headcapsule sizes of *Corcyra* at the time of host death or pupation varied significantly between parasitized L2-L4 hosts and unparasitized (L2) controls (one-way ANOVA, $F = 25.54$, d.f. = 3, 28, $P < 0.001$; Table 6.1). Tukey's pairwise comparisons revealed that headcapsule widths of parasitized L2, L3 and L4 hosts did not differ significantly, but for each parasitized instar, headcapsules were much smaller than unparasitized (control) larvae. At the time of death, the headcapsule width of *Corcyra* from parasitized L2-L4 hosts was fairly constant, and about 20-30% smaller than controls at pupation.

Table 6.2. Head capsule widths of various larval instars of *Corcyra* when parasitized by *Venturia*

Instar parasitized	Sample size	Head capsule width ($x \pm$ SE in mm)
L2	8	0.95 ± 0.04 *a*
L3	4	1.03 ± 0.01 *a*
L4	6	1.03 ± 0.05 *a*
Unparasitized	14	1.31 ± 0.03 *b*

Means with the same letter do not differ significantly ($P > 0.05$).

Fig. 6.3. The relationship between adult *Venturia* size, measured as hind tibia length, emerging from different sizes (body mass, mg) of starved L5 *Corcyra* (circles) and *Plodia* (triangles).



6.4 Discussion

Parasitoid mortality varied considerably between the two hosts (Fig. 6.1a). From *Plodia*, it was highest in L2 instars, probably due to the physical damage inflicted at oviposition, when the minute larva frequently became attached to the parasitoid ovipositor (Chapter 3). L2 *Corcyra* are larger (approximately the same size as L3 *Plodia*) and consequently mortality was reduced. The encapsulating ability of *Corcyra*, but not *Plodia*, increased with host age (Fig. 6.1a). *Plodia* are considerably smaller hosts and this could account for the very low rate of encapsulation, regardless of instar at parasitism. As suggested by Salt (1964, 1975) there may be a maximum size of host larvae capable of supporting the development of *Venturia*. Late fifth instar *Corcyra* are probably marginally suitable hosts for parasitoid development; Salt (1964) found that *Venturia* could not develop in final instar *Galleria mellonella*, a larger host than *Corcyra*. In this study I found that, although many wasps were encapsulated in L5 *Corcyra*, a large number appeared to develop normally, consuming most host tissues. However, many perished within the host cuticle where they were apparently ensheathed and unable to emerge prior to pupation. Evidently these hosts were unable to support the later stages of parasitoid development. Beckage & Templeton (1985) found that the ichneumonid *Hyposoter exiguae* usually perished in L3 and L4 *Manduca sexta*, but emerged successfully when earlier instars were parasitized. *Hyposoter* develops with greater success in L4 *Trichoplusia ni* and *Heliothis* (=*Helicoverpa*) *zea*, two hosts which are smaller than *Manduca* (Jowyk & Smilowitz, 1978; Campbell & Duffey, 1979).

Measurements of the headcapsule widths of L5 *Corcyra* with emerged parasitoids showed that they were significantly smaller than the headcapsules of unparasitized larvae of the same instar, irrespective of whether parasitism had occurred in L2, L3 or L4 hosts (Table 6.2). This illustrates active regulation of host growth by *Venturia*, possibly the consequence of selective larval feeding on certain host tissues (Strand *et al.*, 1988) or secretions from the parasitoid larva (Vinson & Iwantsch, 1980b) although there may be input from the ovipositing female wasp (Dushay & Beckage, 1993). In contrast, *Venturia* does not arrest the development of L4 *Plodia* (Chapter 3) indicating that the parasitoid regulates host growth and development in accordance with its own metabolic and nutritional requirements (Mackauer & Sequeira, 1993). The headcapsule size range of L5 *Plodia* (0.85-1.15 mm) is similar to that of L4 *Corcyra* (1.00-1.20 mm; Chapter 2) suggesting that late L4 or early L5 *Corcyra* provide sufficient resources for parasitoid development.

The egg-to-adult development time of *Venturia* also varied with host species (Fig. 6.1b) and was consistently greater from all *Corcyra* instars. Parasitoid development occurred most quickly from L3-L5 *Plodia* instars, probably in response to rapid host development after parasitism (Chapter 3). *Venturia*, in common with many larval endoparasitoids, delays destructive feeding until the host is a final instar, ensuring enough resources are available for their own development. The development of *Venturia* is extended in poorly nourished L3 *Plodia* because these hosts take longer than well-fed hosts to reach their final instar (Chapter 5). Similarly, the slower growth rate of *Corcyra* was reflected in the increased development time of *Venturia* from pre-L5 instars.

The size of emerging parasitoids was consistently higher in all *Corcyra* instars (Fig. 6.1c). When both hosts are provided with excess food, the growth potential of *Corcyra* is much greater than that of *Plodia,* with post-feeding wandering *Corcyra* larvae often twice as large (mass, fresh weight) as the corresponding stage *Plodia* larvae (Chapter 2). Hence, when *Venturia* commence destructive feeding, potentially more resources are available from *Corcyra* than *Plodia,* accounting for the differences in size of eclosing wasps. However, parasitoid development proceeded faster on *Plodia* presumably because they are smaller and therefore consumed in less time than *Corcyra* (Godfray, 1994).

Anagasta-produced wasps took significantly longer to develop from L5 hosts than wasps from *Plodia* of the same instar, even though the parasitoids were similar in size (Table 6.1). This suggests that *Venturia* may utilize nutrients from *Anagasta* less effectively than from *Plodia,* with a cost being an increase in the development time of the parasitoid. Similarly, within starved, final instars of *Plodia* and *Corcyra,* parasitoid size was strongly correlated with host weight (Fig. 6.3). However, for a given host size, *Plodia* produced much larger wasps than *Corcyra,* showing that *Venturia* appears to be able to convert host tissue more effectively from *Plodia*. The reduced suitability of *Corcyra* may be due to differences in nutritional quality rather than quantity or it may be linked to host immunology, since *Venturia* suffered higher mortality in L5 *Corcyra* than *Plodia.* Sandlan (1982), investigating interspecific patterns of host suitability for the pupal idiobiont wasp *Coccygomimus* (= *Pimpla*) *turionellae,* also found that factors other than host weight affected parasitoid development. He suggested that differences in relative amounts of various nutrients amongst host species affected the growth of the parasitoid. It is worth noting that the parent wasps were derived from stock reared for many generations on

Plodia alone, which could account for the differences in the efficiency of host utilization by *Venturia.*

Host size may affect the reproductive success of *Venturia* in a number of ways. Size was positively correlated with eggload in wasps emerging from both hosts (Fig. 6.2). However, eggload is not necessarily an accurate measure of reproductive potential for *Venturia,* because it is synovigenic (Flanders, 1950) and is able to mature several times as many eggs as can be stored in its oviducts at a given time when conditions are favourable (Chapters 2 & 8). Size may also influence longevity, mobility and colonizing ability (Sandlan, 1982; Godfray, 1994).

I have shown that *Venturia* adopts a different developmental strategy in *Corcyra* compared to that in *Plodia.* A certain minimum host size is probably required to support the development of *Venturia* (Chapter 5). In starved L5 *Plodia* this was found to be when the host reached its mid-5th instar, or in the weight range of 6-8 mg. Different host species are expected to exhibit species-specific growth and development patterns that would result in their attaining the critical size for parasitoid maturation at different times during development. This occurs earlier in a large host (*Corcyra*) compared with a smaller host (*Plodia*) and could account for the lower suitability of *Corcyra* that have been parasitized well beyond the critical size threshold. The earlier regulation of host growth in *Corcyra* compared with *Plodia* also shows that *Venturia* is able to adaptively respond to differences in the patterns of host development by preventing further host growth when conditions are most favourable (Smilowitz & Iwantsch, 1973; Shaw, 1981; Gunasena *et al.*, 1989).

As the suitability of a host should primarily depend upon its ability to support parasitoid development, I suggest that *Corcyra* is less suitable than *Plodia* as a host because *Venturia* suffered higher mortality from them, particularly from final instars. This is particularly important since it is likely that later instars are easier to find for a wasp that predominantly locates hosts through probe searching (Rogers, 1972). The larvae of lepidopterous pests of stored products spend most of their development concealed in the food medium, and therefore larger, later instars are more likely to be encountered. Thus, the persistence of the parasitoid may be severely affected if the most accessible stage is largely invulnerable to parasitism.

Few studies have investigated instar-dependent variations in parasitoid growth and development for koinobionts attacking different host species that vary considerably in growth rate and potential. I have shown that interspecific host

differences in size and growth rate markedly affect the growth and development of *Venturia*. Further studies are needed to determine the efficacy of *Venturia* parasitizing both hosts under natural conditions, where environmental heterogeneity may influence and perhaps alter suitability. The mechanisms of stage-specific patterns of host regulation and parasitoid development should also be examined in greater detail, to determine the extent to which polyphagous parasitoids such as *Venturia* can adapt to differences in the biology of their hosts.

7. Influence of host behaviour and size on acceptance by *Venturia canescens*

7.1 Introduction

Parasitoids attack hosts that vary considerably in their response and vulnerability to parasitism. The number of parasitoids which attack a host species may vary from one or two to over 100 (Price, 1972; Gross, 1993). Certain characteristics of the host may reduce the probability of parasitism by providing protection from parasitoids before, during, and after encounters. These traits are described as primary and secondary host defences (Robinson, 1969). Primary defences are those which decrease the chances of being located by foraging parasitoids (or predators) irrespective of their proximity to hosts (Edmunds, 1974) and include such factors as Batesian mimicry, crypsis, and other factors including micro-refuges (Stamp, 1981; Allen, 1990; Godfray, 1994). An elimination of cues released by the host which attract parasitoids is also a primary defensive mechanism.

Once a host is contacted, secondary defences are utilized by the host and act in either of two ways. The first is through the use of behavioural or morphological defences that reduce the probability of oviposition and primarily operate through evasive and/or aggressive tactics employed by the host to ward off parasitoid attack. These include biting, writhing, thrashing, regurgitation of fluids aimed at the parasitoid, head or abdominal flicking and rearing, rapid crawling or burrowing and by "freezing" (=catalepsis) (Prop, 1960; Myers *et al.*, 1978; Rotheray, 1981; Stamp, 1982; Taylor, 1988; Allen, 1990; Gerling *et al.*, 1990). The hardened integument of egg, larval, and pupal host stages may provide physical protection against parasitoids (Cole, 1959; Gross, 1993; Guershon & Gerling, 1994). Physiological mechanisms constitute the other secondary host defences If the parasitoid is able to successfully parasitize the host, the developing wasp eggs and early-instar larvae may die through encapsulation or their inability to assimilate host tissues containing toxins or allelochemicals sequestered by the host from its foodplant (Barbosa *et al.*, 1982; Slansky, 1986)

Few studies have specifically investigated the influence of host behaviour on the acceptance of the host by parasitoids. Host acceptance is the third step in a successful host-parasitoid association (see Chapter 1) and is the process whereby the parasitoid attempts to parasitize a host after its presence is detected (Salt, 1938;

Doutt, 1959; Vinson, 1976, 1985; Arthur, 1981; Allen, 1990). Observed patterns of acceptance have frequently assumed certain degrees of parasitoid preference for specific host stages (Lindgren *et al.*, 1970; Duodu & Davis, 1974; Smilowitz & Iwantsch, 1975; Sathe & Nikam, 1985; Hopper, 1986) although these patterns could reflect the outcome of behavioural interactions between hosts and parasitoids (Gardner *et al.*, 1984; Gerling *et al.*, 1990; Allen, 1990; Kouame & Mackauer, 1991; Reznik *et al.*, 1992). While some host stages may be entirely suitable for parasitoid development, their active resistance to parasitism may prevent successful oviposition. Allen (1990) investigated behavioural interactions between 2 braconid parasitoids, *Cotesia urabae* and *Dolicogenidea eucalypti* and 3 stages of their gregarious host, the gum leaf skeletonizer, *Uraba lugens*. The ovipositional success of both parasitoids decreased with host size: larger hosts reared, thrashed, and occasionally injured parasitoids by biting their appendages. Gerling *et al.* (1990) also found that early instars of the pea aphid were more susceptible to attack from the wasp *Aphelinus asychis* than later instars which aggressively resisted parasitism. Cornell *et al.* (1987) found that the response of gregarious web-spinning buckmoth caterpillars, *Hemileuca lucina* to simulated parasitoid and predator attack varied with instar. Early instars exhibited defensive behaviour much more than escape behaviours, while this situation was reversed in later instars. The authors suggest that this was due to a decline in the tendency to aggregate as larvae develop.

An understanding of insect defences may also help us to elucidate the evolution of parasitoid oviposition behaviour. The long-term responses of parasitoids to host defences may determine instar and species preference (Taylor, 1988) the species composition of parasitoid complexes and guilds (Gross & Price, 1988; Gross, 1993) and may also select for parasitoid counter defences in both koinobiont and idiobiont parasitoids (Calvert & van den Bosch, 1972; Gerling *et al.*, 1990; Gross, 1993). For example, some koinobionts temporarily paralyze hosts prior to oviposition (Melton & Browning, 1986), indicating the effectiveness of host behavioural defences; others oviposit rapidly, or physically hold the host with their appendages during oviposition (Roberts, 1933; Steffan, 1961; Jones & Lewis, 1971).

The foraging behaviour of *Venturia* within patches is characterized by a pattern somewhere between random and non-random searching (Waage, 1978). When foraging on heavily infested patches, the wasp jabs its ovipositor into the medium much like the needle of a sewing machine ("probe-searching) (van Alphen & Vet, 1986). When a host is detected moving just below the food surface, the behaviour of the parasitoid becomes more directed and it begins stabbing excitedly in the

vicinity of the vibration until the host is encountered (Williams, 1951). In laboratory populations, L5 "wandering" larvae of *Plodia* and *Corcyra* often crawl over the surface of food medium where they are presumably seeking pupation sites (Chapter 2). In heavily infested jars, even earlier instars may be driven from the food (personal observations). Contacts between surface-roving hosts and *Venturia* were commonly observed in culture and these hosts were vigorously attacked by the parasitoids. A similar pattern of behaviour was recorded in another ichneumonid, *Diadegma chrysostictos,* that was reared in culture on *Plodia.*

It is hardly surprising that the parasitoids detect and attack free-moving hosts because stored product pest moths infest many foods besides cereal products where they are likely to be more exposed and thus susceptible to a wider variety of predators and koinobiont parasitoids. *Plodia* and *Corcyra* also occur on dried fruits, vegetables and peanuts (Cox & Bell, 1991) which do not provide the same three-dimensional "enemy -free space" afforded the hosts in cereal products. Hosts developing on these foods are therefore liable to be exposed through much of their larval life. In these situations, probe-searching would not be a cost effective foraging strategy and selection would favour a strategy oriented towards antennal host location (van Alphen & Vet, 1986). The ichneumonid wasp *Eriborus trochantoratus,* a parasitoid of *Corcyra* in South-East Asia, does not probe-search and will only attack free-moving exposed hosts. It was found that *Corcyra* infests bulkier, non-cereal foods in this region (R. Butcher, personal communication).

Although parasitoids were seen to attack exposed hosts in culture, hosts did not respond passively but actively resisted parasitism, displaying a variety of aggressive, evasive and passive tactics after being contacted. Therefore, an investigation was commenced to examine the host-acceptance behaviour between *Venturia* and two of its hosts, *Corcyra* and *Plodia.* As discussed in Chapter 6, full-grown late L5 *Corcyra* larvae are much larger than the corresponding stage of L5 *Plodia,* and previous observations have shown them to be somewhat more aggressive to the presence of foraging adult *Venturia.*

The specific aims are:

(1) to compare the responses of L3-L5 *Corcyra* and *Plodia* to simulated parasitoid antennal palpation using a two-haired brush;

(2) to quantify the influence of host size (large or small L5), species (*Plodia* or *Corcyra),* and condition (alive or dead) on the foraging success of *Venturia;*

(3) to compare how the defensive behaviours of L5 *Plodia* and *Corcyra* larvae influence host acceptance and the host-parasitoid interaction with *Venturia.*

7.2 Materials and Methods

7.2.1 Response of L3-L5 *Plodia* and *Corcyra* to simulated antennation by *Venturia*

Twenty randomly chosen L3, L4 and L5 larvae from each host species were removed from cultures and placed individually into an experimental arena (Petri dish base diameter = 10 cm). Two artificial stimuli were selected which simulate parasitoid antennal palpation (Stamp, 1986; Cornell *et al.*, 1987). A small, two-haired brush was used to simulate antennal touch. The stimulus was applied mid-dorsally to each host larva twice at ten second intervals unless the larva responded earlier; if the larva did not respond after the second stimulus was applied, a reading of "no response" was recorded. The responses of *Plodia* and *Corcyra* to these stimuli were subdivided into a number of categories.

1. Escape responses

These are behaviours that allow a host to free itself from an attacking parasitoid and to move away from a second attack by the same wasp. The specific responses are:

1. *Writhe:* rapid crawling forward or reverse from stimulus.
2. *Thrash:* vigorous wriggling in response to stimulus, but neither forward nor reverse; it may facilitate rapid burrowing into medium when contacted.

2. Passive defences

These are behaviours that allow a host to avoid detection, even when antennally contacted. These responses are:

1. *Still:* ceasing movement entirely and remaining horizontal in response to stimulus.
2. *Curl:* larva contracts head and abdomen in response to stimulus.

3. Aggressive defences.

These are behaviours that physically drive off attacking parasitoids.

1. *Headrear* : the head and anterior portion of the larva are raised and arched towards the posterior portion of the body in response to stimulus.
2. *Flick* : the head and anterior portion of the larva are swung quickly in response to stimulus, causing it to jump.
3. *Bite* : the larva lifts its head towards the stimulus and opens its mandibles.

7.2.2 Influence of host behaviour on foraging success by *Venturia*: effect of host size, species and state.

This experiment is designed to test the hypothesis that host state, size and species influence the level of host acceptance by *Venturia*. Groups of ten L5 *Plodia* and *Corcyra* were removed from culture according to size. Small wandering *Plodia* were reared in high density jars exceeding 400 larvae per 25 grams of food medium; large wandering *Plodia* were reared in low density jars containing less than 200 hosts per 25 g of food medium. The small larvae were selected with fresh weights approximately 50% that of the large larvae (8-10 mg as opposed to 18-20 mg). Both groups of *Corcyra* larvae were removed from the same culture jars, with the small larvae being some 2-3 days younger and 50-60% smaller than the large larvae. In order to ensure that larvae within each size/species class were similar for all replicates, hosts were pre-weighed on a Cahn 29 electrobalance. Additionally, 5 larvae from each class were frozen, and allowed to thaw for 15 minutes prior to the commencement of the experiment ("dead" class) while the others made up the "living" class. Thus, there were 8 groups of 5 larvae for each block, made up of classes combining large and small, alive and dead individuals of *Plodia* and *Corcyra*.

Five larvae from one of the groups were randomly selected and placed into a plastic box (17.5 x 11 x 5cm) with 15 adult parasitoids for 10 minutes. During this time, several aspects of parasitoid behaviour following contact with a host was recorded. The following categories were observed:

(i) contact and examination (CE): the parasitoid physically contacted a host larva and palpated it antennally. At contact the tips of the antennae were curved downwards and pressed onto the host, which signified "examination". If, during examination, contact with the host was lost, a second contact was considered only if the time elapsed between the contacts exceeded approximately 20 seconds.

(ii) ovipositor thrusting (OT): the parasitoid arched its abdomen, unsheathing the ovipositor and jabbing it at an individual host larva.

(iii) ovipositor insertion (OI): during the process of jabbing the ovipositor contacted and was inserted into the host

Oviposition was not determined because of the large number of contacts and re-encounters with individual hosts that inevitably led to superparasitism in each group. Some hosts may have been attacked several times during the course of observations. There was a 10 minute interval after the completion of observations on each group. The experiment consisted of five randomized blocks, with 15 different parasitoids being used for each block. Each of the replicates was carried out on successive days.

7.2.3 Influence of host behaviour on foraging success by *Venturia*: host strategies on contaminated food medium.

This experiment was designed to test the effectiveness of defensive and evasive strategies shown by L5 *Plodia* and *Corcyra* when contacted by foraging wasps on contaminated food medium. This substrate contains food and host-derived semiochemicals and kairomones which "release" probing behaviour by *Venturia* (Waage, 1978).

One-hundred *Plodia* and fifty *Corcyra* larvae were randomly removed from culture, and placed into a plastic box (25 x 12 x 9cm; the "arena") layered with 5 mm of well-mixed contaminated food medium obtained from both *Plodia* and *Corcyra* cultures which had been sieved to remove larger material.

Five parasitoids were then placed onto the substrate of the arena; when at least one of the wasps began to probe the medium, observations were commenced. When a host was contacted antennally by *Venturia*, the behaviour of the host was noted (as per experiment 1), as well as the outcome of the interaction (ovipositor insertion or host escape). Using a stop-clock, the handling time was recorded, which was interpreted as the time between antennal palpitation of the host and either ovipositor insertion or host escape (when the parasitoid lost contact with the host and re-commenced random probing of the medium). Encounters with hosts that burrowed into the medium (hence, through ovipositor insertion only) were ignored; only those occurring on the surface were incorporated into this experiment.

7.3 Results

7.3.1 Response of L3-L5 *Plodia* and *Corcyra* to simulated antennation by *Venturia*

In response to simulated antennation, host behaviour varied with species and instar (Fig. 7.1). As larvae developed, some behaviours increased while others decreased or disappeared. The behaviours were divided into sedentary, escape and aggressive responses (Figs.7.1 & 7.2). *Corcyra* was the more aggressive host, although in both species there was a tendency to adopt more passive, evasive tactics ("run" or "freeze") in the final (L5) instar. A 3-way contingency table was used to analyse this data, with host species *(Plodia, Corcyra)*, instar (L3-L5) and response (run, still, aggressive-defensive and no response) as factors. The overall test of

Fig. 7.1. Distribution of sedentary, escape and aggressive behaviours exhibited by *Plodia* (open bars) and *Corcyra* (stippled bars) in response to touch stimulus. Means with 95% confidence intervals are shown. Sample size was 60 for each species: (a) escape responses; (b) sedentary responses; (c) aggressive responses; (d) no response.

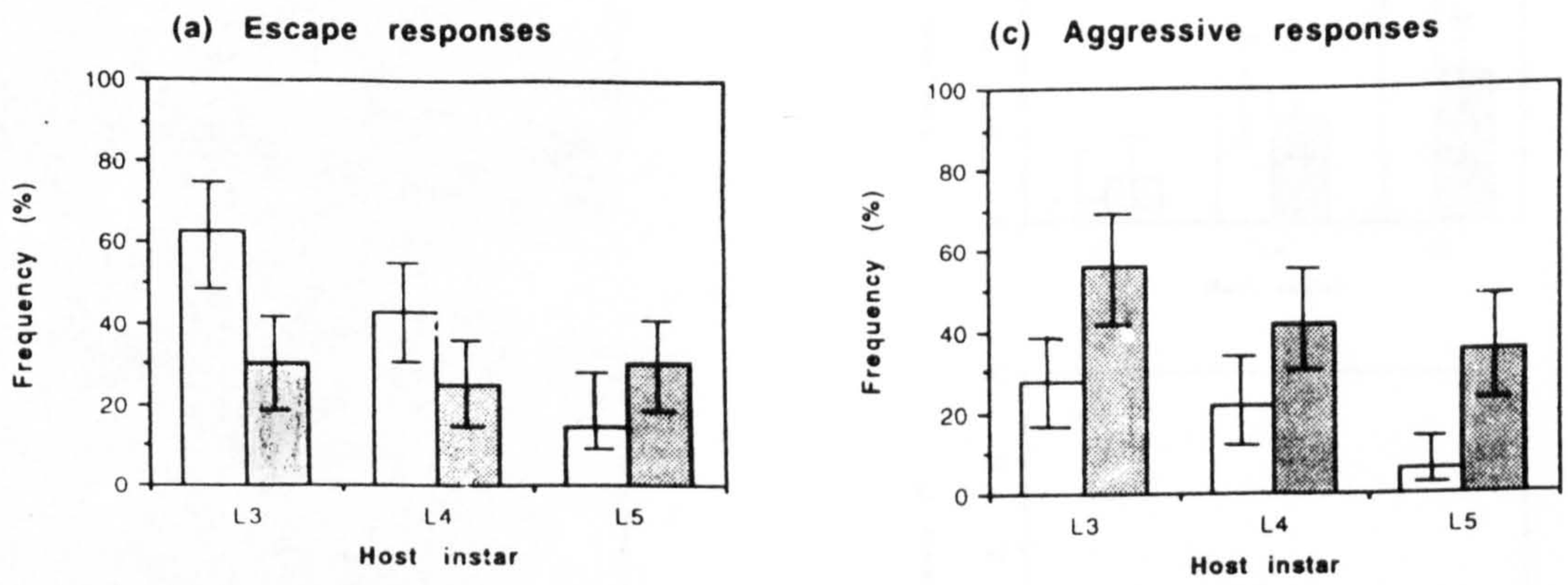
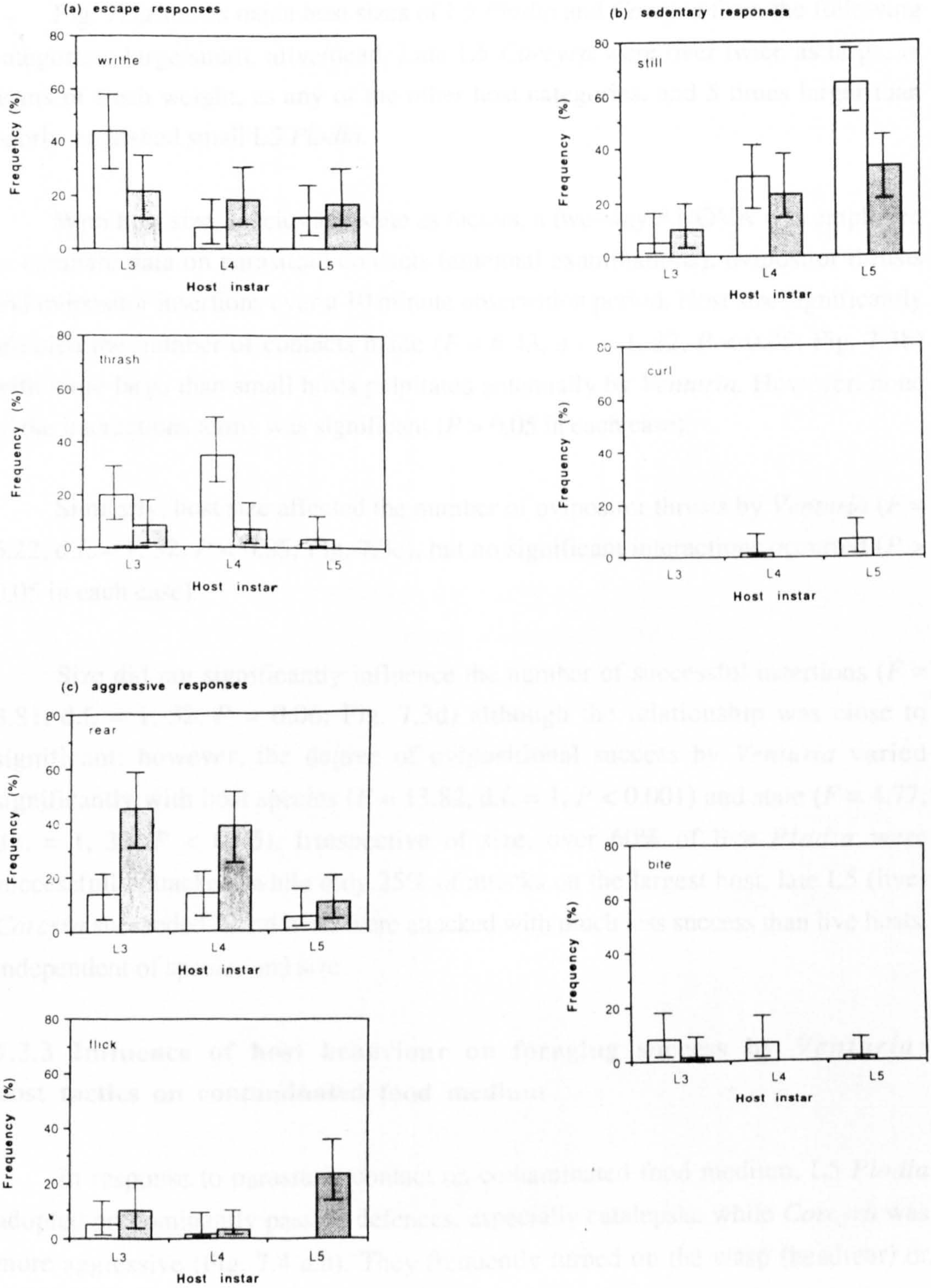


Fig. 7.2. Distribution of individual larval behaviours of *Plodia* (open bars) and *Corcyra* (stippled bars) in response to touching using a two-haired brush. The behaviours are expressed as the percentage of the total responses to the stimulus in instars L3 to L5. Means with 95% confidence intervals are shown. Sample size was 60 for each species: (a) escape responses; (b) sedentary responses; (c) aggressive responses.



independence was rejected (G = 113.80, d.f. = 17, $P < 0.01$). There were also significant interactions between response and species (G = 35.42, d.f. = 3, $P <$ 0.01) and response and instar (G = 58.76, d.f. = 6, $P < 0.01$).

7.3.2 Influence of host behaviour on foraging success by *Venturia*: effect of host size, species and state.

Fig. 7.3a shows mean host sizes of L5 *Plodia* and *Corcyra* from the following categories: large/small, alive/dead. Late L5 *Corcyra* were over twice as large, in terms of fresh weight, as any of the other host categories, and 5 times larger than poorly-nourished small L5 *Plodia*.

With host size, species and state as factors, a two-way ANOVA was employed to compare data on parasitoid contacts (antennal examinations), ovipositor thrusts and ovipositor insertions over a 10 minute observation period. Host size significantly affected the number of contacts made (F = 6.43, d.f. = 1, 32, $P < 0.05$; Fig. 7.3b) with more large than small hosts palpitated antennally by *Venturia*. However, none of the interactions terms was significant ($P > 0.05$ in each case).

Similarly, host size affected the number of ovipositor thrusts by *Venturia* (F = 6.22, d.f. = 1, 32, $P < 0.05$; Fig. 7.3c), but no significant interactions occurred ($P >$ 0.05 in each case).

Size did not significantly influence the number of successful insertions (F = 3.81, d.f. = 1, 32, P = 0.06; Fig. 7.3d) although the relationship was close to significant; however, the degree of ovipositional success by *Venturia* varied significantly with host species (F = 13.82, d.f. = 1, $P < 0.001$) and state (F = 4.77, d.f. = 1, 32, $P < 0.05$). Irrespective of size, over 60% of live *Plodia* were successfully attacked, while only 25% of attacks on the largest host, late L5 (live) *Corcyra* succeeded. Dead hosts were attacked with much less success than live hosts, independent of species and size.

7.3.3 Influence of host behaviour on foraging success by *Venturia*: host tactics on contaminated food medium

In response to parasitoid contact on contaminated food medium, L5 *Plodia* adopted predominantly passive defences, especially catalepsis, while *Corcyra* was more aggressive (Fig. 7.4 a,b). They frequently turned on the wasp (headrear) or

Fig. 7.3. The effect of larval size (mg) species and state on the host acceptance behaviour of *Venturia*. Open bars = live host groups; stippled bars = dead host groups. Means with standard error bars are shown. The graphs are as follows: (a) host weight; (b) number of host contacts per observation period; (c) percentage of hosts contacted by parasitoids followed by ovipositor thrusts; (d) percentage of hosts contacted by parasitoids followed by successful ovipositor insertion.

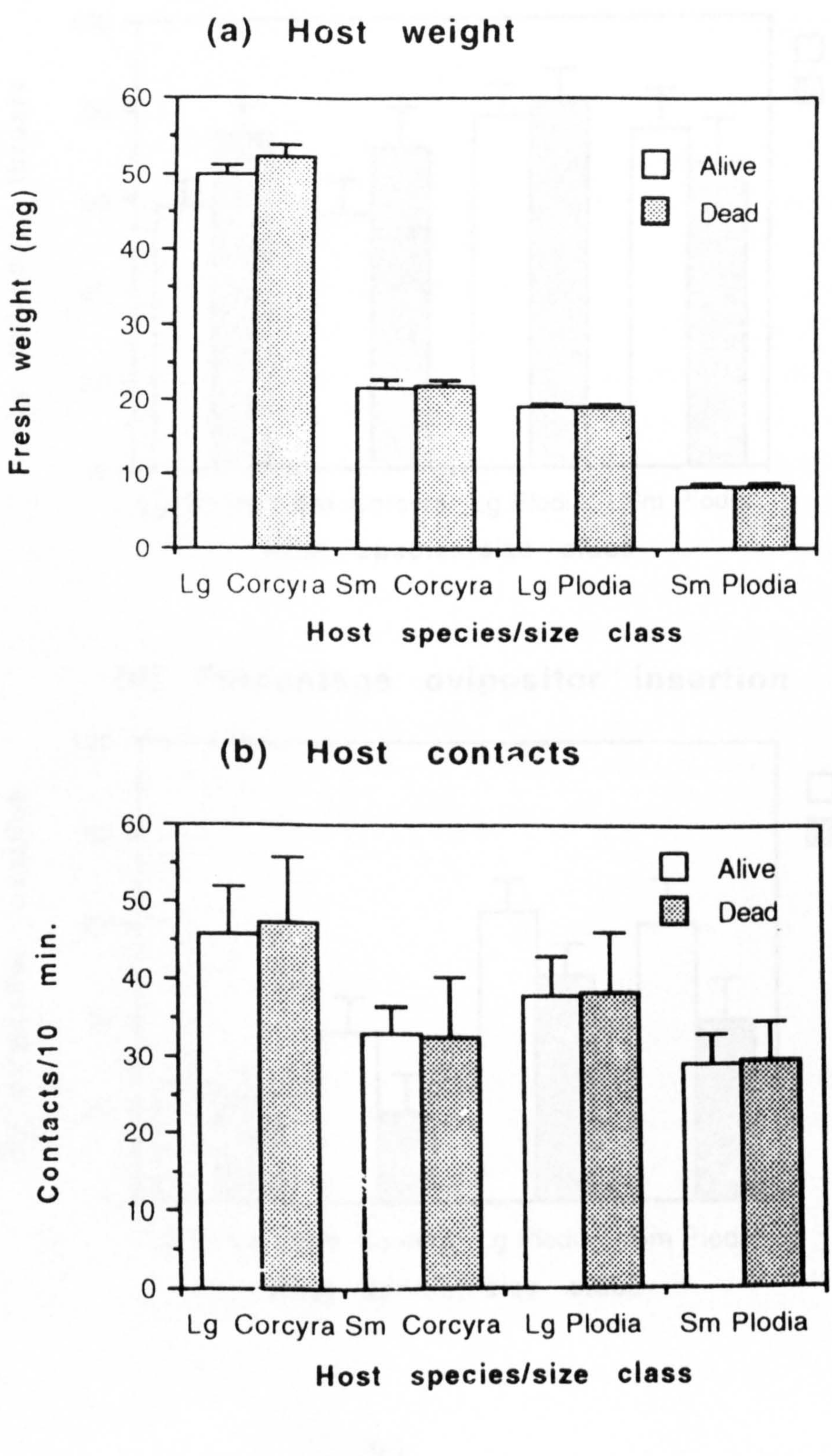
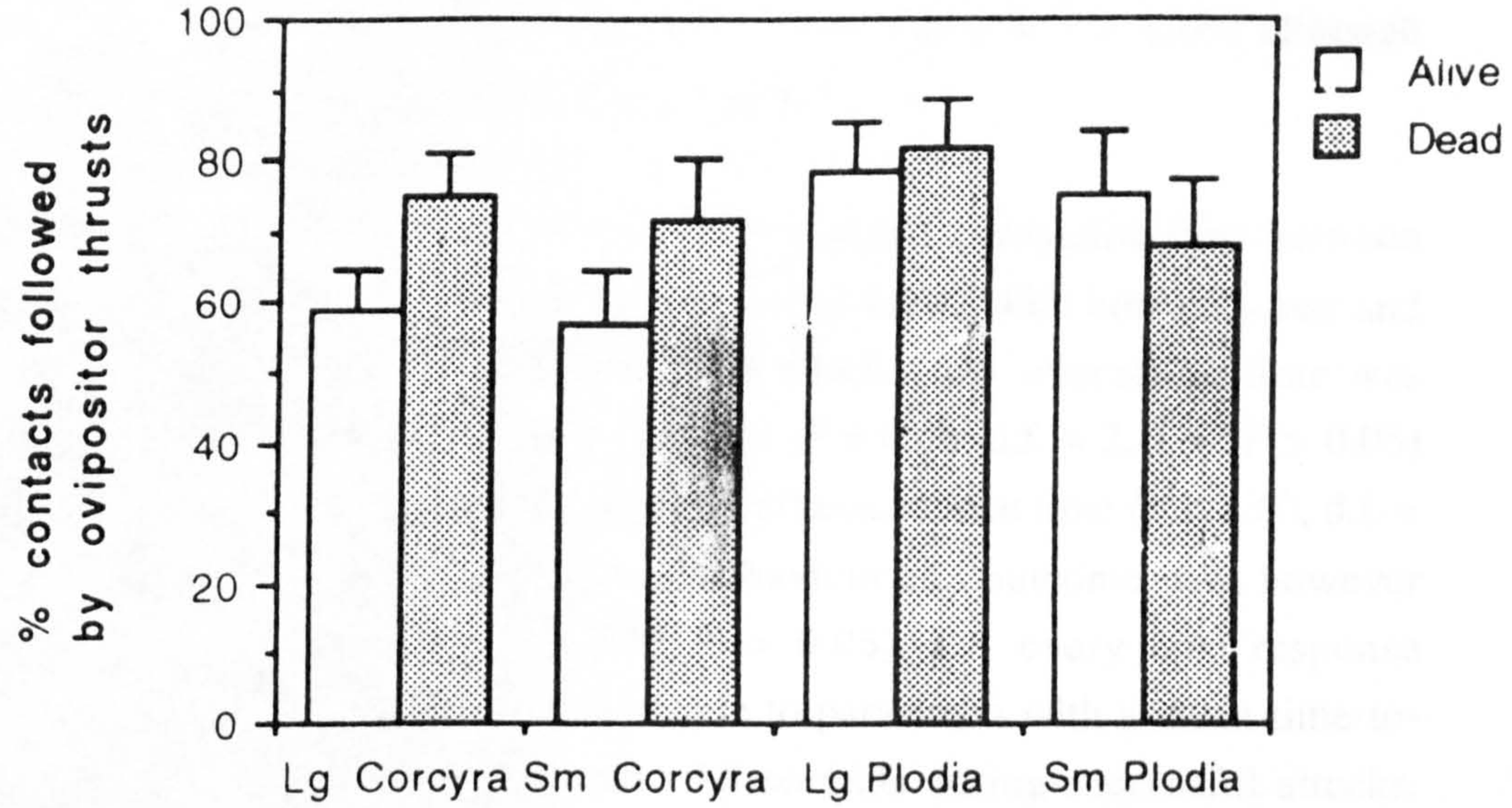
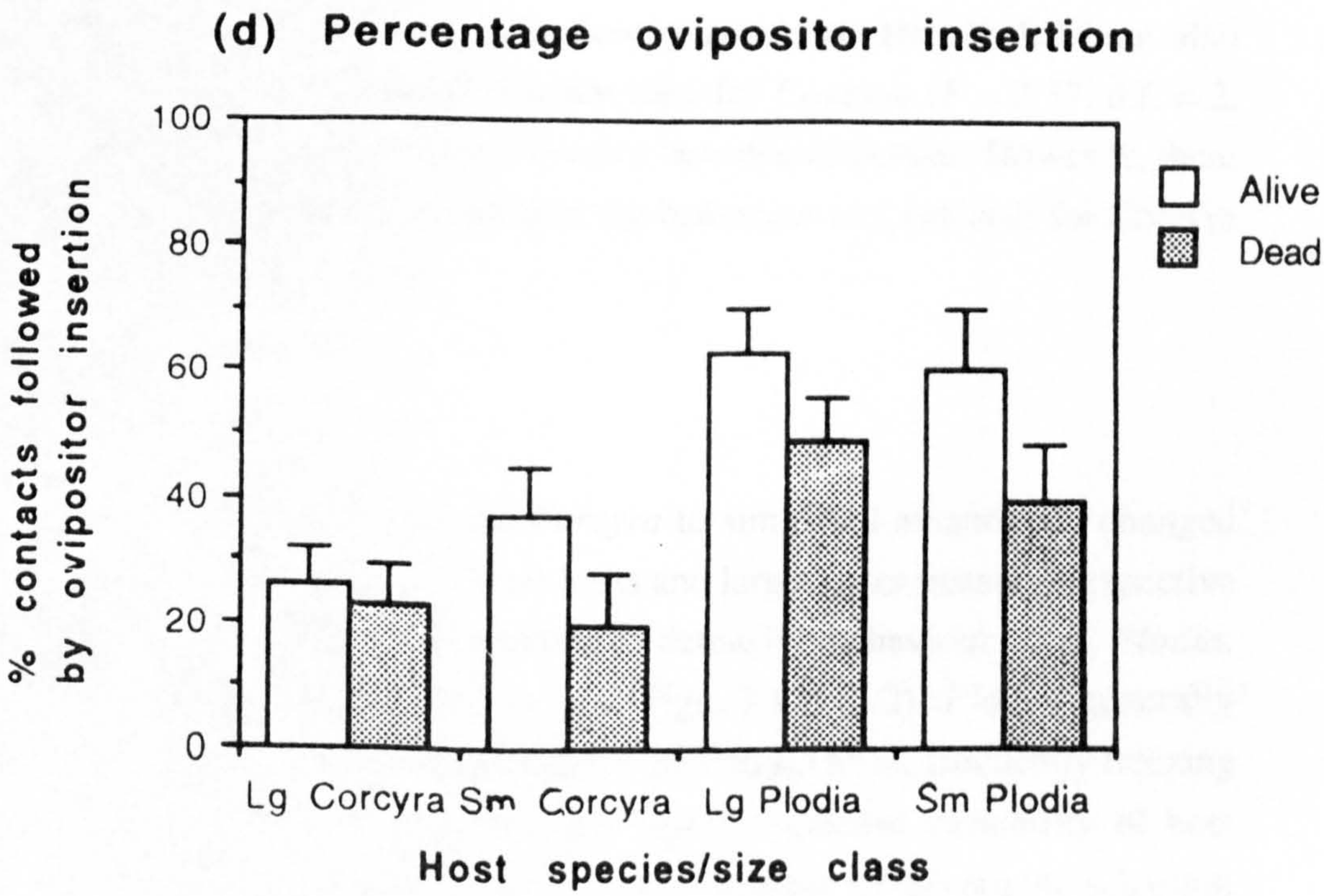


Fig. 7.3 (continued).





flicked their heads back violently, throwing off the parasitoid while enabling the larva to jump a centimetre or more.

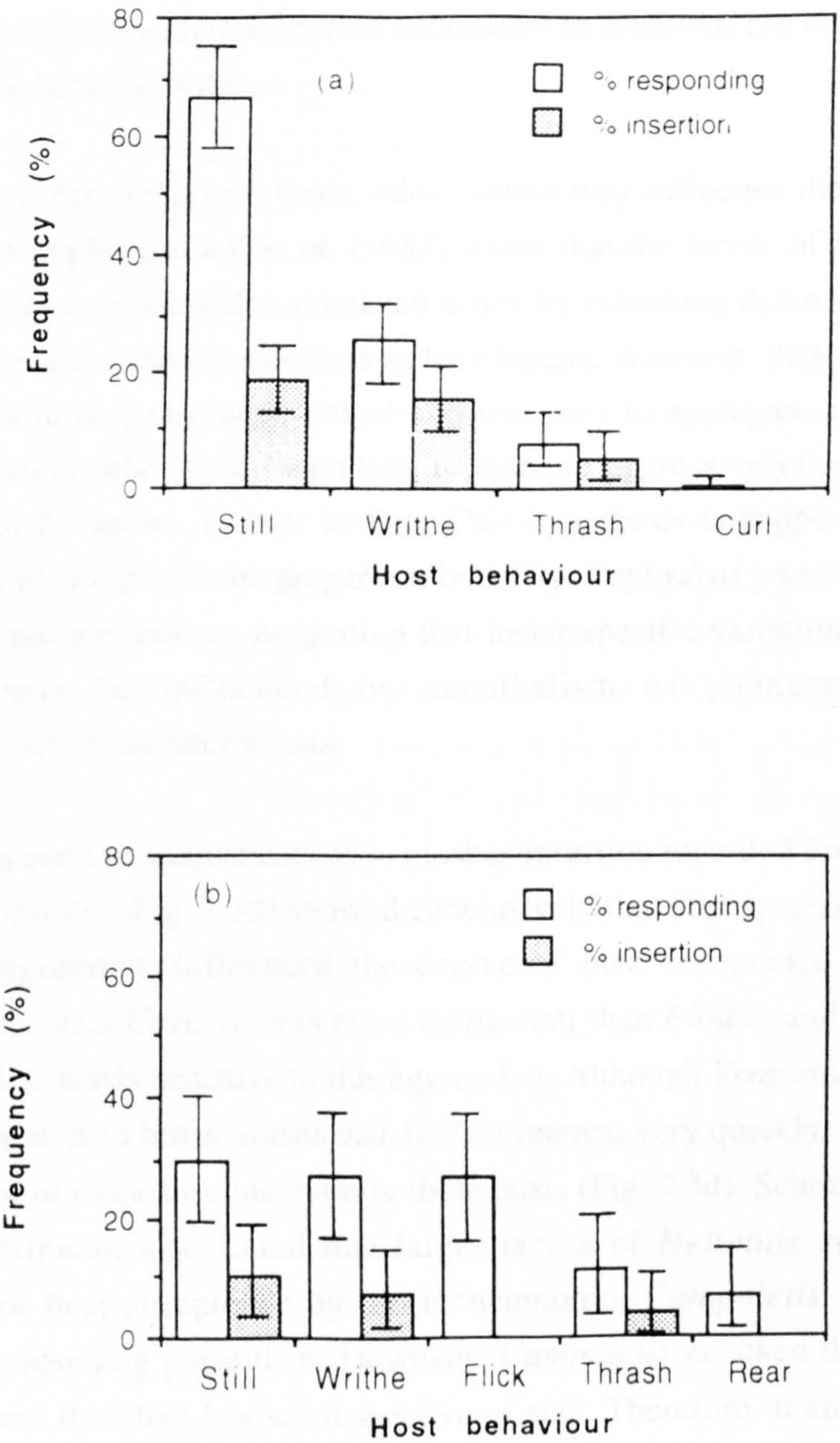
A 2 x 2 contingency table was used to determine if there was an association between host species and response after antennation by *Venturia.* A significant relationship occurred between response and species ($X^2 = 72.60$, d.f. = 5, $P < 0.01$). Further analysis revealed that the association between host response and the success of the strategy against parasitoid attack is significant for both species (*Plodia:* $X^2 = 18.46$, d.f. = 3, $P < 0.01$; *Corcyra:* $X^2 = 11.01$, d.f. = 4, $P < 0.05$) although the relationship is stronger with *Plodia* than *Corcyra.*

A two-way ANOVA was used to determine if the interaction time between parasitoid and host (contact to parasitism or escape) varied with host response and whether or not an attack was successful. For *Plodia,* the interaction time was unaffected by the host's behaviour after contact ($F = 0.28$, d.f. = 2, 170, $P > 0.05$) but the outcome of the interaction significantly influenced total time ($F = 4.60$, d.f. = 1, 170, $P < 0.05$). The interaction between behaviour and outcome was, however not significant ($F = 0.34$, d.f. = 2, 170, $P > 0.05$). For every host response category, time to escape was greater than time to parasitism with a mean time-to-escape of 4.6 seconds for the former and 3.8 seconds during successful attacks. Similarly, for *Corcyra,* the total time during successful attacks was significantly less than when the host escaped ($F = 7.87$, d.f. = 1, 64, $P < 0.01$). The difference in time was greater than it was for *Plodia,* with a mean time of 4.7 seconds for escaping hosts and 3.4 seconds for hosts that were parasitized. Host behaviour also significantly influenced the total interaction time for *Corcyra* ($F = 2.57$, d.f. = 2, 64,$P < 0.05$). Thus, the interaction time varied between responses. However, there was not a significant interactive effect between behaviour and outcome for Corcyra ($F = 0.36$, d.f. = 2, 64, $P > 0.05$).

7.4 Discussion

The response of both *Plodia* and *Corcyra* to simulated antennation changed markedly between small, mid-instar (L3) hosts and larger, later instars. Irrespective of instar, *Corcyra* exhibited more aggressive defensive behaviours than *Plodia,* although this tendency decreased with age (Figs. 7.1 & 7.2). *Plodia* generally adopted evasive strategies, which were most evident in L5 hosts, frequently freezing in response to the stimulus. The instar and species-specific variability of host response to touch suggests the influence of a number of divergent selection

Fig. 7.4. Distribution of larval behaviours and outcome of the interaction between *Venturia* and its hosts, *Plodia* and *Corcyra* after parasitoid antennal contact on an experimental patch. The behaviours are expressed as the percentage of total responses (open bars) and the percentage of successful attacks (stippled bars). Means with 95% confidence intervals are shown. The graphs are as follows: (a) *Plodia*; (b) *Corcyra*. Sample sizes: *Plodia* = 176, *Corcyra* = 70.



pressures. Healthy, late 5th instar *Corcyra* are larger than the corresponding stage of *Plodia,* and may be able to ward off parasitoid or predator attack more successfully by displaying either/or a combination of aggressive and evasive tactics. Pre-5th instars of both species are usually confined to the food medium, where they are afforded some protection from parasitism and predation in enemy-free refuges. However, when host densities are high, the greatest threat to survival may come from conspecific larvae, in the form of cannibalism (Fox, 1975). Large, late instar hosts readily attack smaller hosts in these situations so that aggressive, rather than passive defences may be a more effective deterrent for younger hosts against attack from older conspecifics. This could account for the higher levels of aggression displayed by pre-L5 *Plodia* and *Corcyra* larvae. Dial & Adler (1985) found that behaviours associated with intraspecific encounters by *Heliothis zea* reflected the risk of cannibalism between instars.

However, for gregarious hosts, other factors may influence their response to attack. For example, Cornell *et al.* (1987) found that the larvae of the buckmoth, *Hemileuca lucina*, responded to simulated attack by exhibiting defensive behaviours as early instars and escape behaviours as later instars. However, they suggested that these changes in response were linked to a tendency to aggregate as early instars (thus, stimulating other group members to respond aggressively) and to disperse from the host foodplant as later instars. This hypothesis is supported by Stamp (1982, 1984) working with the gregarious butterfly, *Euphydras phaeton. Plodia* and *Corcyra* are not gregarious, suggesting that instar-specific variations in defensive behaviour may be influenced by cannibalism as younger instars and predators/parasitoids as later instars.

Comparisons of frequencies of ovipositor insertion recorded for live and dead *Plodia* and *Corcyra* (Fig. 7.3d) showed conclusively that host species, as correlated with host aggression, influenced the degree of host acceptance by *Venturia.* Irrespective of size, *Corcyra* was more belligerent than *Plodia*, and *Venturia* may have been particularly sensitive to this aggression. Although *Venturia* readily jabbed its ovipositor at dead hosts, wasps usually lost interest very quickly, accounting for the lower rate of ovipositor insertion in these hosts (Fig. 7.3d). Schmidt (1974), in a similar experiment, also found that larger larvae of *Heliothis zea* limited the expression of host acceptance by the ichneumonid, *Campoletis sonorensis* by aggressively resisting parasitism. However, *Campoletis* attacked dead hosts with greater success than live hosts, irrespective of size. Therefore, it appears that host movement is a more important factor in releasing and sustaining attack behaviour for

Venturia than it is for *Campoletis*. Differences in the acceptance of dead hosts by the two parasitoids may linked with variations in host ecology. *Venturia* locates concealed hosts in medium where vibration and movement are important cues in detection; alternatively, *Campoletis* attacks more dispersed hosts exposed on the larval foodplant. Here, detection is less likely to be influenced by movement than by antennal contact, thus non-moving hosts may be readily attacked. Although I did not record the elapsed time between initial contact and ovipositor insertion, *Venturia* clearly spent more time examining dead hosts than live hosts before moving on the next phase. This suggests that host movement "releases" ovipositor thrusting behaviour in *Venturia*.

Irrespective of host size, L5 *Corcyra* larvae were much more aggressive than *Plodia* larvae and adopted a number of defensive tactics when contacted by wasps, including head and tail flicking, rearing and vigorous wriggling. Consequently, *Venturia* were much more likely to ignore *Corcyra* or to lose contact while jabbing at them. *Plodia*, on the other hand, were consistently the more passive host species and tended to exhibit more evasive tactics such as rapid crawling or catalepsis after antennal palpitation by *Venturia*. These, however, were generally unsuccessful, with over 60% of attacks resulting in a successful ovipositor insertion (Fig. 7.3d).

Parasitoid foraging success also varied in accordance with host species and behaviour on contaminated food medium (Fig. 7.4). *Venturia* were most successful in attacking *Plodia* larvae that attempted to escape by writhing after contact, and had least success against larvae that went still (Fig 7.4a). *Corcyra* exhibited a wider range of responses than *Plodia*, and was less vulnerable to attack (Fig 7.4b). Several studies showed that 'freezing' was a less effective defence against parasitoids than active resistance after contact (e.g. Loan, 1964; Herrebout, 1969; Rotheray, 1981) and suggested that two opposing selection pressures influenced host defensive behaviour. The first, from predators, selected for crypsis and catalepsis, the second from parasitoids selected for vigorous activity (Rotheray, 1981). However, against *Venturia*, host's freezing after antennation may have been afforded protection because wasps could not detect their presence on heavily contaminated medium. The sensory receptors of *Venturia*, like other parasitoids which detect hosts by their odour, may be overwhelmed by background volatile signals emanating from the food effectively camouflaging the hosts (Vinson, 1985). It is interesting that wasps easily detect and attack hosts isolated from contaminated food, even when they go still after contact.

Independent of response, the total interaction time between contact and escape was significantly greater than between contact and parasitism. *Venturia* obviously ignored a host after successfully parasitizing it; however, hosts attempting to escape were pursued with vigour until contact was lost or the attack succeeded. Because large, aggressive hosts (e.g. *Corcyra*) or *Plodia* that go still are more likely to escape parasitism, a wasp must balance her potential gain in fitness of pursuing an escaping host against her potential cost in terms of lost time if the attack fails (Gerling *et al.*, 1990; Kouame & Mackauer, 1991).

7.4.1 Adaptations for host location by parasitoids

A comparative approach has been widely used to define correlations between a species behaviour and an environmental factor indicative of adaptation (eg. Lack, 1971; Ridley, 1982; Thornhill, 1984) although, until recently, this approach has been ignored in understanding the evolution of parasitoid host-location. Vet & van Alphen (1985) and Vet & Bakker (1985) compared the searching behaviour of dipteran parasitoids within patches, and distinguished three main searching modes:
(a) vibrotaxis (movement of the host is the cue to detection).
(b) ovipositor searching (hosts are detected by regular probing of the substrate while the parasitoid walks).
(c) by antennal palpitation (moving and/or still hosts are detected after antennal contact).
Some parasitoid species use only one of these modes, while others (including *Venturia* and a closely related ichneumonid, *Diadegma chrysostictos*) show more complex behaviour patterns consisting of all three modes.

Comparative studies of *Drosophila* parasitoids have shown a tendency for alysiine wasps (Braconidae) to search by vibrotaxis (e.g. *Asobara tabida*) (van Alphen & Vet, 1986) whereas *Leptopilina* spp. (Eucoilidae) spend more time locating hosts by probe-searching (Vet & Bakker, 1985). The eucoilid wasp, *Tanycarpa punctata* locates older host larvae by drumming the substrate with their antennal tips and detecting the hind spiracles of the larvae which usually protrude from the surface (van Alphen & Vet, 1986).

The adaptive significance of these searching strategies is that they enable koinobionts to maximise encounter rates with their hosts in accordance with differences in the behaviour and ecology of the preferred host stage attacked (van Alphen & Vet, 1986). For koinobionts like *Venturia*, that parasitize a wide range of

host instars, searching specialization may be detrimental because it may favour the location of one host instar over another. Two main conditions, however, may significantly influence the degree of searching specialization. First, a particular developmental stage of a host species may be attacked by many parasitoid species (Gross & Price, 1988). Thus, due to heavy competition for a host, there may be selection for host "partitioning", based on polymorphic aspects of host behaviour (Carton & David, 1985). Parasitoids may become adapted to locate hosts by refining their searching strategy resulting in a particular specialization described. Because host behaviour and ecology may vary with instar, these parasitoids then become adapted to a limited range of instars. For example, *Asobara tabida* (Alysiinae), which searches exclusively by vibrotaxis, only parasitizes L2 *Drosophila melanogaster;* first instars do not produce sufficient vibrations and third instars invariably encapsulate *Asobara* eggs (A.R. Kraaijeveld, personal communication).

Venturia successfully attacks several host instars utilizing all three of the modes described in response to differences in the behaviour and ecology of *Corcyra* and *Plodia* that vary with host stage (with L1-L4 hosts predominantly confined to the food medium and L5 larvae frequently crawling on the surface during the so-called "wandering phase"). The dynamic response of *Venturia* to these changes allows it to exploit several host instars with maximum efficiency. For smaller, concealed pre-L5 hosts, *Venturia* searches both vibrotactically and by random probing of the substrate. Ovipositor searching is a better mode when searching at high host densities, while vibrotaxis is a more economical strategy at low densities (van Alphen & Vet, 1986). Contacts with wandering hosts on the substrate require an entirely different strategy for a foraging wasp. In the case of *Corcyra,* these hosts may be considerably larger than the parasitoid. For koinobionts like *Venturia,* that do not paralyse the host, large hosts represent a real risk because they can injure parasitoids by biting, vigorous thrashing, or trapping them in fluid droplets exuded from the host gut (Slansky, 1986; Allen, 1990; Gross, 1993). *Venturia* frequently ignored L5 *Corcyra* after antennal contact, whereas the smaller, less aggressive host *Plodia* was readily attacked. This observed pattern of preference by *Venturia* for *Plodia* may be more a consequence of behavioural interactions between hosts and parasitoids than preference in the strict sense of the definition (Gerling *et al.*, 1990). However, where both hosts occur together, the much more vigorous defensive action of *Corcyra* might actively discourage *Venturia* from attacking it when an alternative is present, or could lead to the evolution of a preference for *Plodia* as an adaptation to the greater risk incurred in attacking *Corcyra* (Taylor, 1988). Ignoring aggressive L5 *Corcyra*

may also benefit *Venturia* because these hosts are less suitable than L2-L4 instars (Chapter 6), hence egg wastage may be reduced.

7.4.2 Parasitoid counter-adaptations to host defences

An important and relatively unstudied aspect of host defences is their potential influence on the evolution of parasitoid oviposition behaviours. In previous chapters I have suggested that koinobiosis may have evolved in response to specific factors including a lower probability of survival in larger hosts due to superparasitism (both conspecific and heterospecific) (Askew, 1975; Slansky, 1986) and a reduced risk of being discovered in host pupae, compared with host larvae (Gauld, 1988). However, it is probable that host defences have selected for parasitoid counter oviposition strategies.

Some host insects drop from their foodplant when a nearby parasitoid is detected, descending on a silken thread and climbing back to the plant to resume feeding when the threat has passed (Godfray, 1994). Yeargan & Braman (1986) found that the braconid wasp *Diolcogaster facetosa* detects the threads of its host, the green cloverworm (*Plathypena scabra*) and slides headfirst down the thread, rapidly ovipositing in the host when it is contacted. The flimsy thread of first instar hosts cannot support the weight of both host and parasitoid, so that L2 and L3 hosts are most successfully parasitized. Even more fascinating is the oviposition behaviour of *Mesochorus discitergus* (Ichneumonidae), a hyperparasitoid of the braconid *Cotesia marginiventris*, itself a primary parasitoid of *P. scabra*. *Mesochorus* captures suspended second instar hosts by hanging on to the edge of the host foodplant with its hind tarsi and reeling in the caterpillar by pulling the silken thread upwards. Later, heavier host instars are attacked in a similar fashion as *Diolcogaster*, and oviposition occurs if the host contains *Cotesia*, the primary parasitoid (Yeargan & Braman, 1989).

Many koinobiont parasitoids oviposit into specific regions of the host body (Bussart, 1937; Gerdin & Hedqvist, 1985; Wylie, 1985). Calvert & van den Bosch (1972) found that the braconid wasp, *Monoctonus paulensis*, oviposited only within the fused thoracio-abdominal ganglia of its host, the pea aphid *Acyrthosiphon pisum*. In many cases, specific oviposition sites are utilized to circumvent morphological host defences (e.g. armour) that prevent ovipositor insertion over the general body surface of the host (Gross, 1993). Salt (1968), however, suggested that many parasitoids oviposit in specific regions of the host because these are less-well

protected immunologically. This contention is supported by the fact that many early-instar parasitoid larvae, which are more susceptible to internal host defences, migrate to specific regions of the host after they hatch from the egg. First instar *Venturia,* for example, like many other ichneumonids, use their caudal appendage for this purpose (Salt, 1968).

The effectiveness of a host's aggressive behaviour against parasitoids has been overcome in several distinct ways by koinobionts. Some temporarily paralyse the host before laying an egg (Calvert & van den Bosch, 1972; Melton & Browning, 1986) while others physically hold the host still during oviposition (Waloff, 1967; Glen, 1977). Another major adaptation of koinobionts compared to idiobionts is the ability of many species to oviposit rapidly (Allen, 1990; Gross, 1993). Rapid oviposition requires the parasitoid to generally produce small, yolk-deficient (hydropic) eggs that can be mobilized quickly. Idiobiont parasitoids on the other hand, usually produce yolky (anhydropic) eggs that are much larger, relative to the body mass of the parasitoid, and consequently a single egg may take a considerable time to lay; in the case of *Pleolophus indistinctus* (Ichneumonidae), up to two hours per egg (Price, 1970). Idiobionts, therefore, virtually always paralyse the host before ovipositing (or are restricted to attacking inactive or less active host stages) (Jervis & Kidd, 1986; Vinson & Iwantsch, 1980b).

Venturia utilizes a number of strategies to attack hosts of various sizes both in the medium and on the food surface. When attacking smaller hosts on the substrate, *Venturia* first locates them antennally and frequently hold them still while ovipositing. After detection, larger hosts on the surface are vigorously pursued and attacked very rapidly, the total sequence from contact to oviposition lasting only a few seconds. In the food medium, a host can be parasitized by *Venturia* in a fraction of a second and before the host has any time to respond defensively.

Although few studies have thus far been undertaken on the effectiveness of host defences against parasitoids, it is clear that hosts actively resist parasitism and that the outcome of these interactions have a significant effect upon host acceptance and preference by parasitoids. However, many investigations have ignored the consequences of host behavioural defences on certain aspects of the host selection process as well as models of the population dynamics of hosts and parasitoids. Therefore, understanding levels of host acceptance and preference by parasitoids can be enhanced by accounting for the influence that host defensive behaviour has on parasitoid oviposition success.

Chapter 8. Resource variability and lifetime reproductive success in *Venturia canescens*

8.1 Introduction

The reproductive success of parasitoids is governed by a number of constraints including the abundance of suitable hosts, the fecundity of the parasitoid, the presence of a source of nutrition for the adult female parasitoid and the mortality of the host during the parasitoid's larval stages (Price, 1975; Vinson, 1985), thus their reproductive perfomance may be limited by such factors as the distance between host patches, the host-finding ability of the parasitoid and the longevity of the parasitoid that influences the number of hosts that can be encountered (Visser, 1994).

Many empirical studies of parasitoid lifetime reproductive success have simply provided the insects with excess hosts and a continuous supply of food after eclosion, thus ignoring the true heterogeneity of natural systems. In this regard their results shed little light upon the factors that influence parasitoid fitness, because the insects are in a relatively constraint-free environment. At eclosion, a female parasitoid may find herself in an alien habitat or one where there are no suitable hosts because the host population has shifted spatially, or has been recently exploited to extinction. Thus, the major problem facing a parasitoid, in addition to finding a mate, is the location of oviposition sites and food. As both of these resources may themselves likely be spatially separated, the reproductive success of the parasitoid will probably be determined by a series of trade-offs that lead to a reduction in progeny production or an adjustment in the fecundity schedule.

The theory of trade-offs between competing life history characters states that a negative correlation exists between major components of fitness in animals as a consequence of the constraints on the rate at which essential resources can be obtained and allocated for vital functions (Reznick 1985; Bai & Smith, 1993). Trade-offs are often expressed by the negative correlation between age and reproductive rate (Charlesworth, 1980; Clutton-Brock, 1988) or between longevity and fecundity (Roitberg, 1989). The theory of life-history trade-offs has been widely tested in many organisms, but few empirical studies have been carried out with parasitoids, and in those that have, several important parameters have been ignored. For example, studies by Mackauer (1982) and Kopelman & Chabora (1992) demonstrated that the parasitoids *Aphelinus semiflavus* and *Leptopilina boulardi* adjust their daily rate of progeny production (fecundity schedules) in accordance with variations in host

density (Mackauer, 1983) or host availability (Kopelman & Chabora, 1992). However, in both studies the female wasps were provided with a continuous supply of food (honey solution) that greatly extended their longevity and period of oviposition. Bai & Smith (1993) also found that the egg parasitoid, *Trichogramma minutum*, adjusted its fecundity schedule according to host density, but these insects were also provided with a constant food source that enabled them to extend their period of progeny production. None of these studies, however, varied the duration of food access to the female parasitoids, hence it was not determined what (if any) effect this has on their lifetime reproductive success.

In nature, there are three main food sources used by adult parasitoids: hosts, honeydew and certain plant exudates, such as nectar. The latter is an extremely important source of adult nutrition because it may significantly influence parasitoid longevity and fecundity, thus increasing parasitism (Allen & Smith, 1958; Leius, 1963; Syme, 1975: Jervis & Kidd, 1986). However, as discussed above, hosts may be located a considerable distance from suitable food sources, thus the costs and benefits of leaving host patches to search for food is likely to depend upon many factors, including the risk of mortality incurred when dispersing to search for (and return from) the food source, the quality of the host patch and the physiological condition of the parasitoid. Therefore, in empirical investigations, the presence or absence of a source of adult parasitoid nutrition is likely to have an influence upon its lifetime reproductive success.

Many theoretical models have been developed (e.g. Cook & Hubbard, 1977; Charnov, 1979, 1982; Charnov & Skinner, 1985; Mangel, 1987, 89a,b) that provide rules for parasitoids on how to forage most profitably (on the assumption that parasitoids forage in ways to maximise their lifetime reproductive success). Most of these studies have predicted that individual parasitoid behaviour varies in response to changes in its physiological state (e.g. egg load, hunger level) brought about by differences in environmental quality (e.g. the number and distribution of potential host types). However, few of these studies have determined the influence of these interacting states on the lifetime reproductive success of parasitoids. The models also predict that being large or small may have consequences for the fitness of individual wasps (e.g. Hurlbutt, 1987; van den Assem *et al.*, 1989). Few investigations have, however, determined the influence of differences in body size on total progeny production in studies of lifetime reproductive success.

Egg load counts have often been used to determine fecundity, with larger wasps being assumed to have a higher fitness because they carry more eggs than smaller wasps (e.g. Corrigan & Lashomb, 1985; Liu, 1985; Donaldson & Walter, 1988; Rosenheim & Rosen, 1992; see also Chapter three). Virtually all of these parasitoids, however, are synovigenic, and can mature several times as many eggs as can be stored in their oviducts at a given time (Lawrence *et al.*, 1982; Rosenheim & Rosen, 1992). In Chapters three and six I showed that, in *Venturia*, egg compliment is positively correlated with parasitoid size in wasps reared from two hosts, *Plodia* and *Corcyra*. *Corcyra*-produced wasps are much larger than *Plodia*-produced wasps, regardless of instar at parasitism, thus wasps emerging from *Corcyra* stored up to twice as many eggs at capacity (5 days after eclosion) as wasps from *Plodia*. Trudeau & Gordon (1990) found that *Venturia* reared from *Anagasta cautella* was able to store up to 250 eggs at capacity. However, early work by Beling (1932) and Ahmad (1936), using *Anagasta kuehniella* as host, revealed that the realized reproductive potential of *Venturia*, even when provided with a constant food source and excess hosts, was considerably less than these egg loads suggest, with 50-75 progeny produced. Since these early studies there has been no attempt to determine the reproductive success of *Venturia* in the laboratory.

Bai & Smith (1993) suggested that a major trade-off may occur between longevity and fecundity in parasitoids, where organisms partition their resource investment between reproductive tissue and body tissue (Kirkwood, 1981; Roff, 1984). When resources are limited, there may be insufficient available for both purposes, hence a trade-off results. Thus, assuming that the energy expended per unit of time is constant for two conspecific female parasitoids, the wasp that invests a greater proportion of her resource budget for reproduction will have proportionately less to invest for maintenance, and her life expectancy may be shorter than that of the other wasp as a result. Some recent studies have shown that there is a negative correlation between reproduction and survival in parasitoids (e.g. Hohmann *et al.*, 1989; Orr & Boethel, 1990), although Bai & Smith (1993) failed to find such a correlation between these two life-history parameters in the egg parasitoid, *Trichogramma minutum*. Therefore, trade-offs between fecundity and survival occur in some host-parasitoid associations but not in others.

In this chapter I will examine the influence of host (L5 *Plodia*) and food (honey solution) availability on lifetime reproductive success in *Venturia*. I will test the hypotheses that *Venturia* adjusts its fecundity schedule in response to differences in host and food access, and that there is a further trade-off between longevity and

fecundity. The *Venturia-Plodia* association makes a model empirical system because there is no need to mate wasps at emergence, thus removing an extra level of complexity from the protocol, and, under natural conditions, wasps may emerge into an environment where hosts may have shifted spatially, and suitable sources of nutrition (e.g. nectar) are located a considerable distance from hosts. Therefore, in nature *Venturia* probably encounters a series of trade-offs that determine its reproductive success. The aim of this investigation is to determine the lifetime reproductive success of *Venturia* under different constraints imposed by exposing parasitoids to variable periods of host and food access. The results will show if there are trade-offs between early and late reproduction, and reproduction and survival. I will discuss the findings relevant to the theory of life-history evolution.

8.2 Methods

8.2.1. Lifetime reproductive success of *Venturia* in response to temporal variations in food and host access

Parasitoids were isolated from culture as pupae and placed in glass vials. For each treatment, the following procedure was applied. The contents of a culture jar containing 20-22 day old late L5 *Plodia* larvae was emptied onto a coarse sieve which was placed over 2 finer sieves and a container base. The contaminated medium was shaken vigorously to enable finer food medium to be filtered from the host-containing material, which remained in the top (coarse) sieve. This sieve was then placed over a second base, with a heat lamp being situated 5-10 cm over the medium. This drove the larvae down through the coarse sieve and into the base, where they could be easily removed. Using a pair of soft forceps, hosts were placed into small plastic tubs in groups of 50.

Larvae were chilled in a freezer for approximately 5 minutes at approximately -10°C and were then placed in groups of 100 onto a patch, consisting of a 10 cm diameter petri dish filled to within 5 mm of the surface with plaster of Paris. Approximately 2 g of finely milled wheat bran was evenly spread over the patch containing hosts, and this was covered by nylon bolting cloth which was firmly secured by two elastic bands. The patches were than left in a plastic box for 24 hours before being presented to parasitoids. During the experiments, each wasp had access to two patches (200 larvae) daily that were placed into a large plastic boxes (25 x 12 x 9 cm) and contained sufficient bran to reach the top rim of each patch. All wasps used in this study were 0-12 hours old at the commencement of the experiment, and their

hind tibia measurements were taken at time of death using a stereomicroscope (accuracy 0.05mm).

Host/food access treatments

To test the hypothesis that parasitoids can adjust their fecundity schedule according to host availability and food access, the following treatments were used:

(1) Temporal host availability

(a) 24 h host access: parasitoids were exposed to 200 hosts for 24 hours after which they were immediately transferred to another box containing two fresh patches containing 200 more hosts. This process was again repeated daily until wasp death.

(b) 2 h host access: parasitoids were presented with 200 hosts for two hours daily, then were isolated without hosts in another box (see below) for the following 22 hours. This process was repeated daily until wasp death.

(c) 0.5 h host access: parasitoids were presented with 200 hosts for 30 minutes daily, then were isolated without hosts in another box (see below) for the following 23.5 hours. This process was repeated daily until wasp death.

(2) Food availability

(a) 24 h food access: regardless of host availability, wasps had continuous access to 50% honey solution absorbed into a ball of cotton wool.

(b) 24 h access, 48h starvation: parasitoids had access to 50% honey solution (as above) for 24 hours, followed by 48 hours starvation. This pattern of food access was repeated until the parasitoid died.

(c) Starvation: parasitoids had no access to honey solution at any time until death.

Thus, each block consisted of three host availability and three food availability treatments with nine wasps per block. The treatment order in each block was randomized. Each block was replicated 10 times, thus 90 wasps were used in the experiment.

Each day approximately 1-2 hours after the automatic photoperiod light switched on (0900-1000 hrs), all hosts were removed from the patches and transferred to clear glass jars containing excess food (larvae were post-feeding L5 instars and used the food as a substrate for pupation). Jars were labelled and left for 30 days in order to allow all adult moths and parasitoids to emerge. Jars were frozen at -10°C and all individual insects contained in them were counted.

The number of hosts (200) presented to parasitoids daily was not limiting because *Venturia* is synovigenic (Flanders, 1950) and the number of ovulated eggs (those available for oviposition) was determined beforehand (see Chapter 2). Furthermore, many hosts always escaped parasitism. Parasitoids with 0.5h or 2h daily host access, when not exposed to host larvae, were maintained in large plastic boxes (as used in experiments) containing a shallow (2mm) layer of uncontaminated wheat bran with or without honey solution, according to treatment.

Due to the experimental design, hosts from each of three temporal parasitoid access groups were retained on patches for different lengths of time, from 48 hours (constant host access treatment) down to 24.5 hours (limited host access treatment). During the course of the experiment I found that total insect mortality was higher in the constant host access treatments, where hosts spent considerably longer times confined on patches with other host larvae. Therefore, to see if this was due to increased stress or possibly because of increased parasitoid ovipositor insertions, controls were set up retaining hosts on patches for the same lengths of time described above but with no parasitoid access. Hosts were placed on patches in groups of 100 for 24.5, 26 and 48 hours, after which time they were transferred to jars containing food medium. Jars were frozen for 24 hours 30 days later, sufficient time to allow all adult moths to emerge, and the moths were counted on a white tray using soft forceps.

8.3. Results

8.3.1 Relationship between host patch residence time and survival (control 1).

The total number of emerged adult *Plodia* from patches kept isolated for 48, 26 or 24.5 hours (the same length of time on patches as in the experiment) did not vary significantly with time (one-way ANOVA, $F = 0.22$, d.f. = 2, 27, $P > 0.05$). A mean of 138.2 hosts (69.1%) retained on patches for 48 hours emerged as adult moths, whereas hosts retained on patches for 26 hours produced 135.7 moths (67.9%) and hosts returned for 24.5 hours produced 133.1 moths (66.5%).

8.3.2 Relationship between adult wasp size and longevity when parasitoids are deprived of hosts (control 2).

For parasitoids deprived of hosts, there was a significant positive correlation between size and longevity when wasps were provided with constant food ($r = 0.66$, n = 10, $P < 0.05$) and 24h with food and 48h starvation ($r = 0.70$, n = 10, $P < 0.05$), although not in starved hosts ($r = 0.36$, n = 10, $P > 0.05$). Fig. 8.1 shows the longevity of *Venturia* in relation to adult wasp size in host-deprived wasps with access to food for variable periods of time.

8.3.3 Relationship between adult wasp size, block, host and food access and longevity.

The sample variances of the longevity data for the different food/host access treatments were initially analysed using an F-max test for homogeneity of variance. The largest and smallest variances were found to be significantly different ($P < 0.05$), so the data were log-transformed. A further *F*-max test revealed that the difference in the extreme variances of the log-transformed data was not significantly different ($P > 0.05$). Prior to the analysis of covariance, the assumption of homegeneity of slopes was tested for both longevity (8.3.3) and progeny production (8.3.4, below). This assumption was not met for both log-transformed longevity ($F = 0.71$, d.f. = 8, 67, $P > 0.05$) and log-transformed progeny production ($F = 0.89$, d.f. = 8, 67, $P > 0.05$). A two-way ANCOVA for parasitoid longevity, with length of host and food access as factors, revealed that longevity varied significantly with food access ($F = 338.32.41$, d.f. = 2, 66, $P < 0.001$; Table 8.1) and between blocks ($F = 3.36$, d.f. = 9, 66, $P < 0.01$; Table 8.1). Constantly-fed wasps lived considerably longer than starved wasps or those provided with limited access to food. However, longevity did not vary significantly in response to duration of host access ($F = 0.25$, d.f. = 2, 66, $P > 0.05$; Table 8.1) and the interaction between food and host access was also not significant ($F = 0.91$, d.f. = 4, 66, $P > 0.05$; Table 8.1). Therefore, within each feeding treatment, parasitoid longevity was largely unaffected by temporal variations of host access. Fig. 8.3 shows longevity distributions for *Venturia* under the different feeding regimes. Parasitoid longevity is fairly normally distributed in the 24h and starvation treatments (Fig. 8.3a & c). Parasitoid longevity also covaried significantly with adult wasp size ($F = 4.24$, d.f. = 1, 66, $P < 0.05$; Table 8.1). Thus, adult parasitoid lifespan is strongly influenced by the size of the wasp, with larger wasps generally living longer than smaller conspecifics. Fig. 8.2 shows the longevity of *Venturia* as a function of adult wasp size from all 9 food and host access treatments.

Fig. 8.1. The longevity of *Venturia* in relation to adult wasp size when parasitoids are deprived of hosts, but provided with food for different periods of time. The graphs are: (a) 24h (constant) food access, (b) alternate 24h food access, 48h starvation, (c) starvation. The Y-axis on graphs (b) & (c) reflect the shorter longevities of wasps in these treatments compared with (a). N = 10 wasps for each food availability treatment.

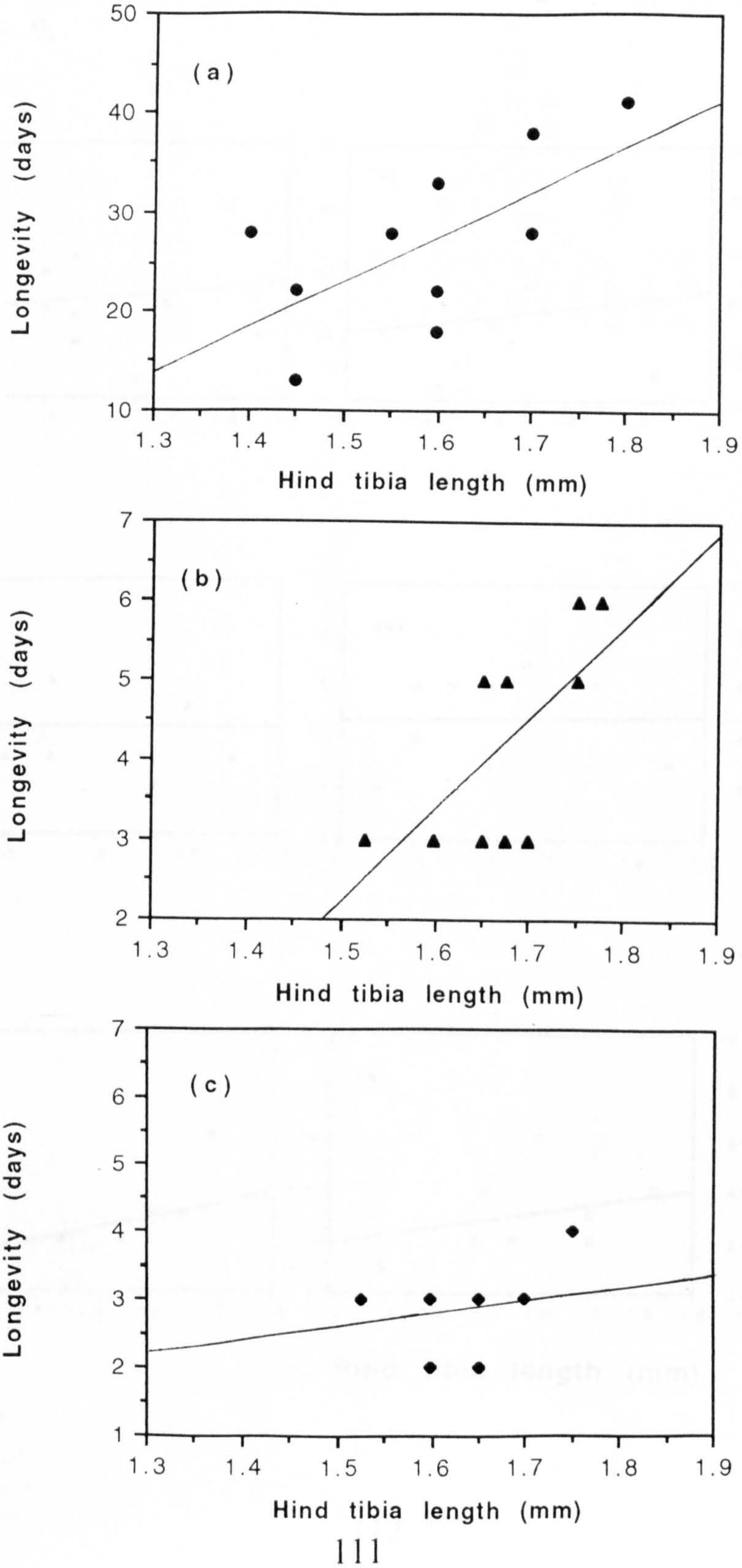


Fig. 8.2. The longevity of *Venturia* in relation to adult wasp size when parasitoids are provided with food and hosts for different periods of time. Graphs a-c = 24h (constant) food access, d-f = alternate 24h food access, 48h starvation, g-i = starvation. Within each feeding treatment, triangles = 0.5h host access daily, squares = 2h host access daily, triangles = 24h (constant) host access. Sample size = 10 wasps, except for the following: (d) = 8, (f) = 9, (g) = 9, (h) = 9.

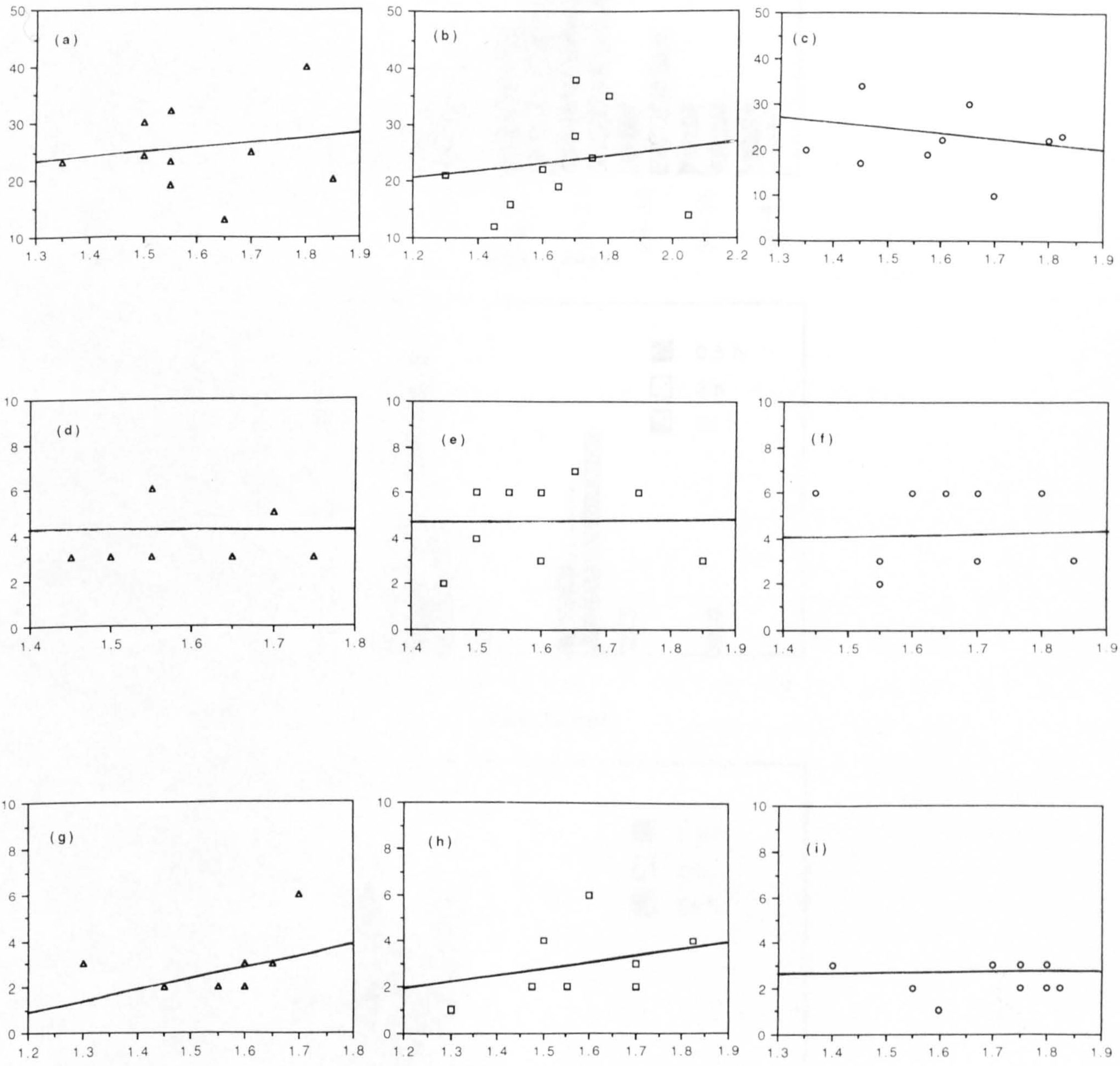


Fig. 8.3. Longevity distributions of *Venturia* in response to differences in food and host access. The graphs are: (a) 24h food access, (b) alternate 24h food access, 48h starvation, (c) starvation. Black bars = wasps with 0.5h host access daily, hatched bars = wasps with 2h access daily, stippled bars = wasps with 24h (constant) host access. N = 10 wasps for each food/host access combination.

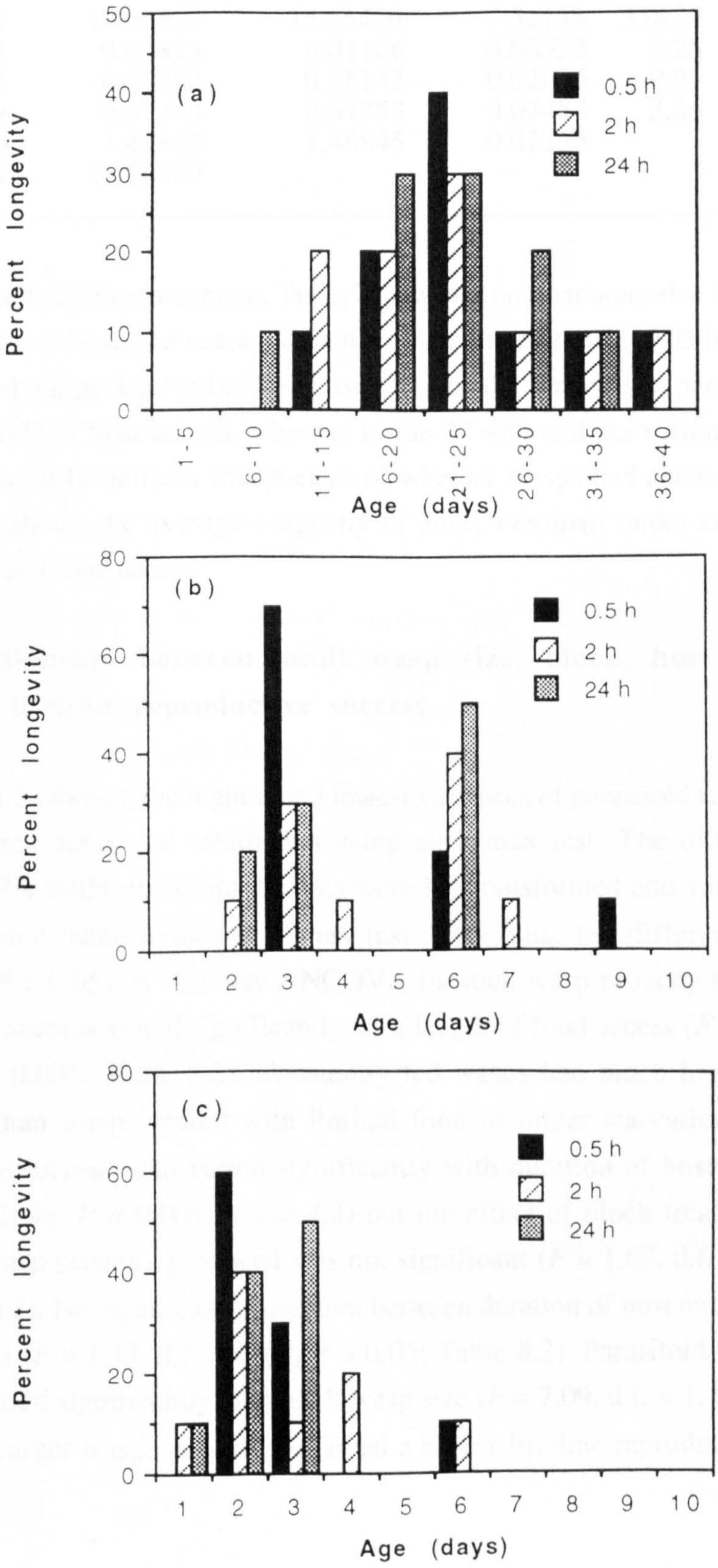


Table 8.1. Analysis of variance (with adult size as covariate) for longevity in *Venturia*.

Source	DF	SeqSS	AdjSS	AdjMS	F	P
Size	1	0.08324	0.9428	0.9428	4.24	0.043
Food	2	14.94599	15.05476	7.52738	338.32	0.000
Host	2	0.01825	0.01106	0.00553	0.25	0.781
Food*Host	4	0.07282	0.08142	0.02036	0.91	0.461
Block	9	0.67353	0.67353	0.07484	3.36	0.002
Error	66	1.46845	1.46845	0.02225		
Total	84	17.26229				

Within each feeding treatment, Tukey's pairwise comparisons also revealed that length of access to hosts did not significantly affect longevity ($P > 0.05$ in each case). Constantly-fed wasps deprived of hosts lived marginally longer than parasitoids with variable periods of host access, whereas in the 24-48h and starvation treatments, longevity was fairly uniform irrespective of whether wasps had access to hosts or not. Fig. 8.4 shows the average longevity of adult *Venturia* under conditions of variable host and food access.

8.3.4. Relationship between adult wasp size, block, host and food access and lifetime reproductive success.

As in 8.3.2 (above), the highest and lowest variances of parasitoid fecundity data were compared across all treatments using an F-max test. The difference was significant ($P < 0.05$), therefore the data were log-transformed and variances were again compared using a second *F*-max test. This time, the difference was not significant ($P > 0.05$). A two-way ANCOVA for total wasp progeny revealed that reproductive success varied significantly with length of food access ($F = 27.83$, d.f. = 2, 66, $P < 0.001$; Table 8.2). Constantly-fed wasps had much higher realized fecundities than wasps reared with limited food or under starvation (Fig. 8.3). Reproductive success also varied significantly with duration of host access ($F = 6.65$, d.f. = 2, 66, $P < 0.001$; Table 8.2) but the effect of block treatment on the number of wasp progeny produced was not significant ($F = 1.69$, d.f. = 9, 66, $P > 0.05$; Table 8.2). No significant interaction between duration of host and food access was observed ($F = 1.12$, d.f. = 4, 66, $P > 0.05$; Table 8.2). Parasitoid reproductive success covaried significantly with adult wasp size ($F = 7.09$, d.f. = 1, 66, $P < 0.01$; Table 8.2). Larger wasps generally enjoyed a higher lifetime reproductive success

Fig. 8.4. Mean longevity for adult *Venturia* when provided with food and hosts for different periods of time. Data was obtained by back transformation of log-transformed means. Line bars represent 95% confidence intervals. Open bars = constant food access, stippled bars = alternate 24 h food access, 48 h starvation, hatched bars = starvation. N = 10 wasps for each food/host treatment.

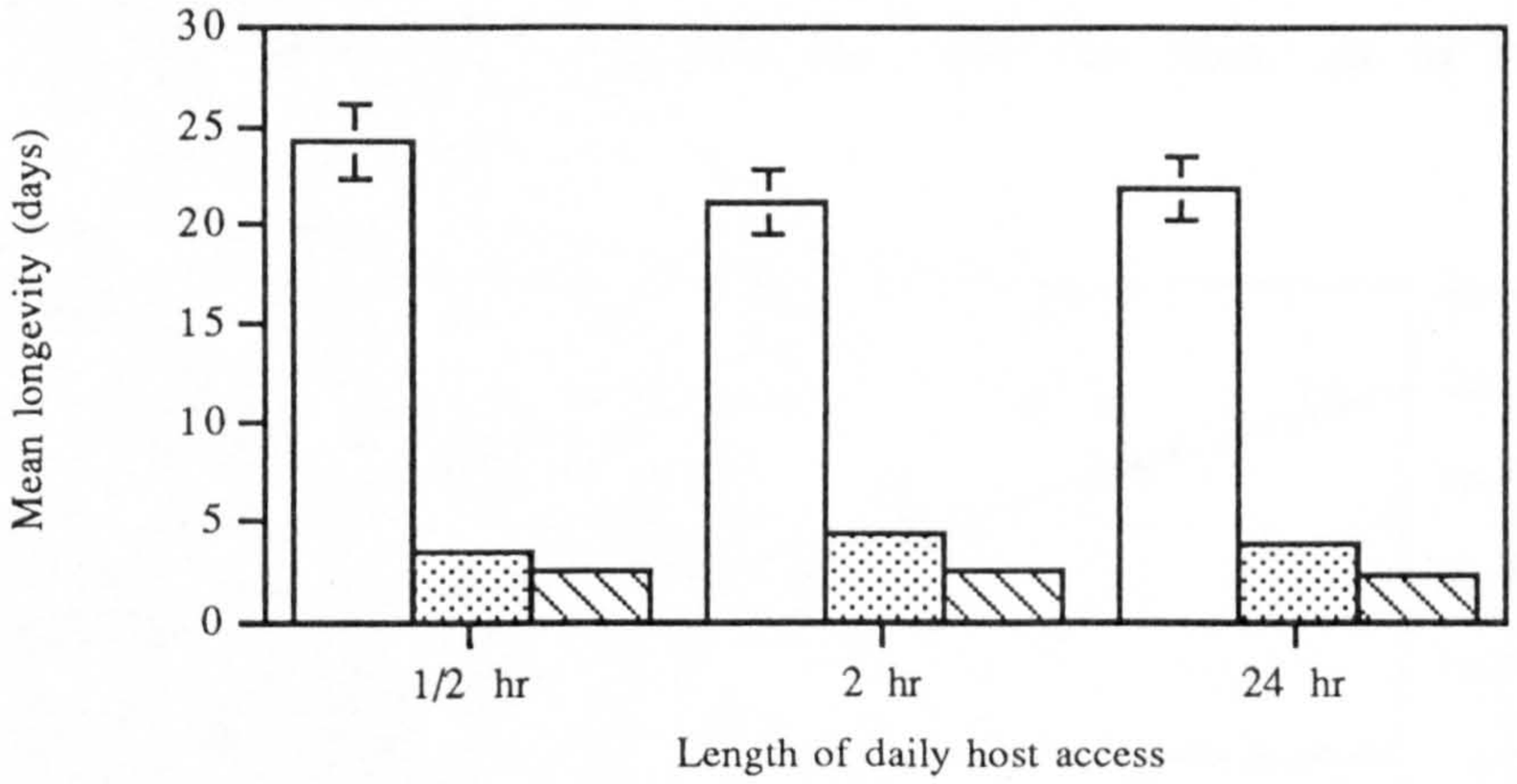


Fig. 8.5. Mean lifetime reproductive success for adult *Venturia* when provided with food and hosts for different periods of time. Data was obtained by back transformation of log-transformed means. Line bars represent 95% confidence intervals. Open bars = constant food access, stippled bars = alternate 24 h food access, 48 h starvation, hatched bars = starvation. N = 10 wasps for each food/host treatment.

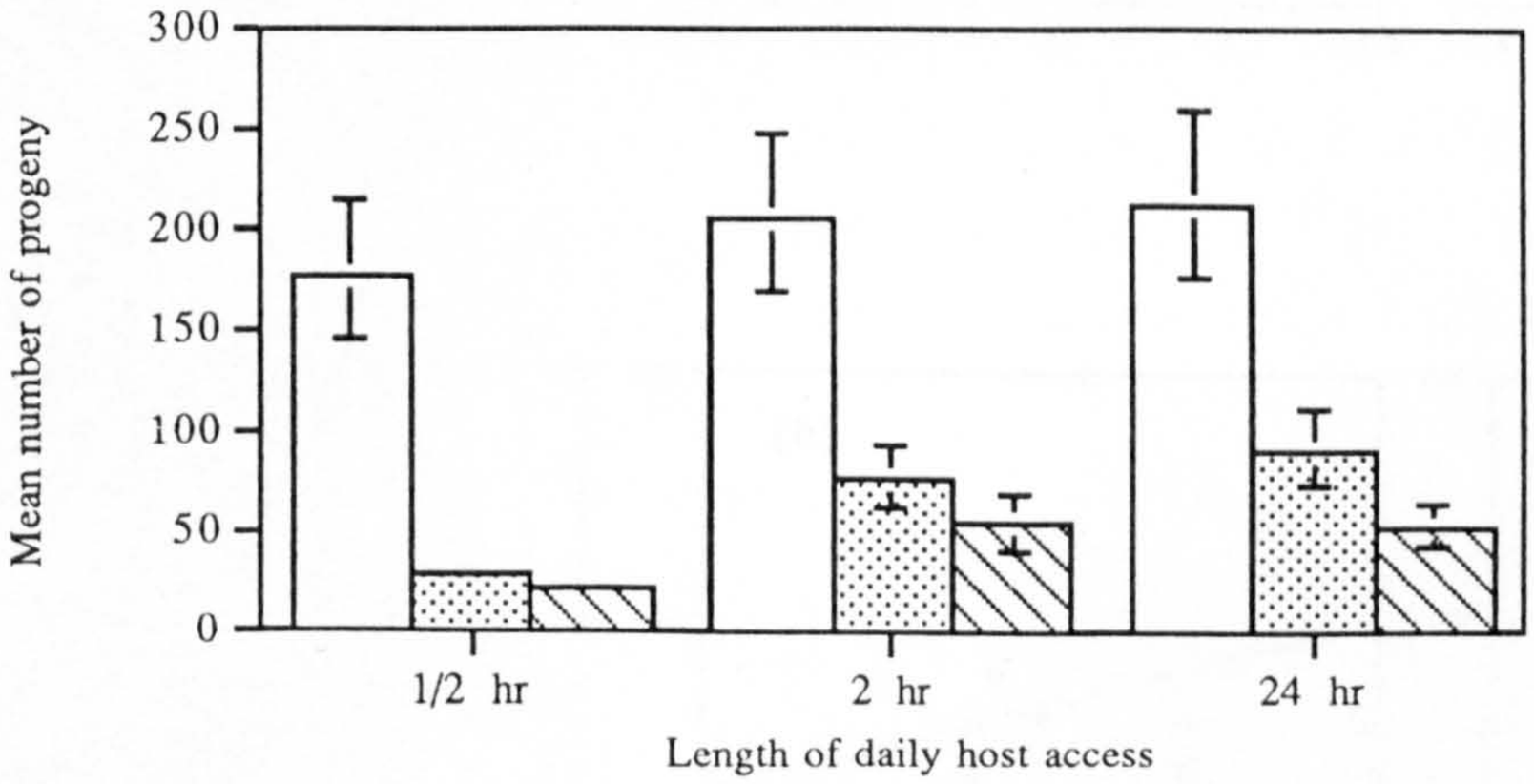
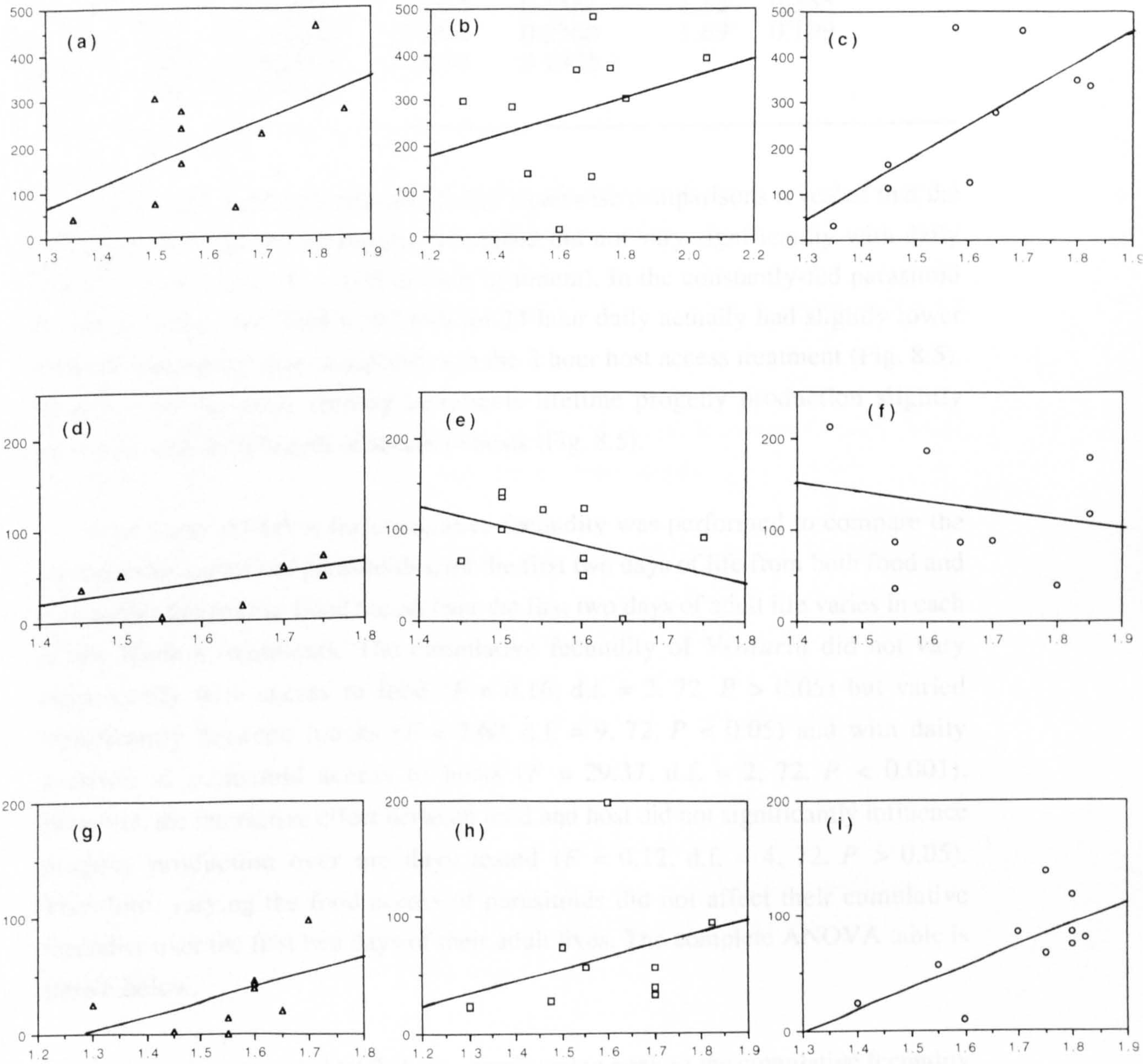


Fig. 8.6. The lifetime reproductive success of *Venturia* in relation to adult wasp size when parasitoids are provided with food and hosts for different periods of time. Graphs a-c = 24h (constant) food access, d-f = alternate 24h food access, 48h starvation, g-i = starvation. Within each feeding treatment, triangles = 0.5h host access daily, squares = 2h host access daily, triangles = 24h (constant) host access. Sample sizes are the same as in Fig. 8.2.



than smaller wasps. The lifetime reproductive success of *Venturia* in relation to adult wasp size from all 9 host and food access treatments is shown in Fig. 8.6.

Table 8.2. Analysis of variance (with adult size as covariate) for lifetime reproductive success in *Venturia*.

Source	DF	SeqSS	AdjSS	AdjMS	F	P
Size	1	1.7289	0.9890	0.9890	7.09	0.010
Food	2	7.6251	7.7661	3.8830	27.83	0.000
Host	2	1.8262	1.8558	0.9297	6.65	0.002
Food*Host	4	0.6792	0.6243	0.1561	1.12	0.355
Block	9	2.1244	2.1244	0.2360	1.69	0.109
Error	66	9.2074	9.2074	0.1395		
Total	84	23.1912				

Within each feeding treatment, Tukey's pairwise comparisons revealed that the total number of parasitoid progeny produced did not vary significantly with daily length of host access ($P > 0.05$ in each treatment). In the constantly-fed parasitoid treatment, wasps provided with hosts for 24 hour daily actually had slightly lower realized fecundities than conspecifics in the 2 hour host access treatment (Fig. 8.5). However, in the other feeding treatments lifetime progeny production slightly increased with daily length of access to hosts (Fig. 8.5).

A two-way ANOVA for cumulative fecundity was performed to compare the reproductive success of parasitoids over the first two days of life from both food and host access treatments. Food access over the first two days of adult life varies in each of the feeding treatments. The cumulative fecundity of *Venturia* did not vary significantly with access to food ($F = 0.16$, d.f. = 2, 72, $P > 0.05$) but varied significantly between blocks ($F = 2.60$, d.f. = 9, 72, $P < 0.05$) and with daily duration of parasitoid access to hosts ($F = 29.37$, d.f. = 2, 72, $P < 0.001$). However, the interactive effect between food and host did not significantly influence progeny production over the days tested ($F = 0.12$, d.f. = 4, 72, $P > 0.05$). Therefore, varying the food access of parasitoids did not affect their cumulative fecundity over the first two days of their adult lives. The complete ANOVA table is shown below.

A separate two-way ANOVA was employed to analyse the cumulative fecundity of constantly-fed (24h) parasitoids in response to host access (0.5h, 2h, 24h) over the first 5 days of life; the other food access treatments (24/48h, starvation) were

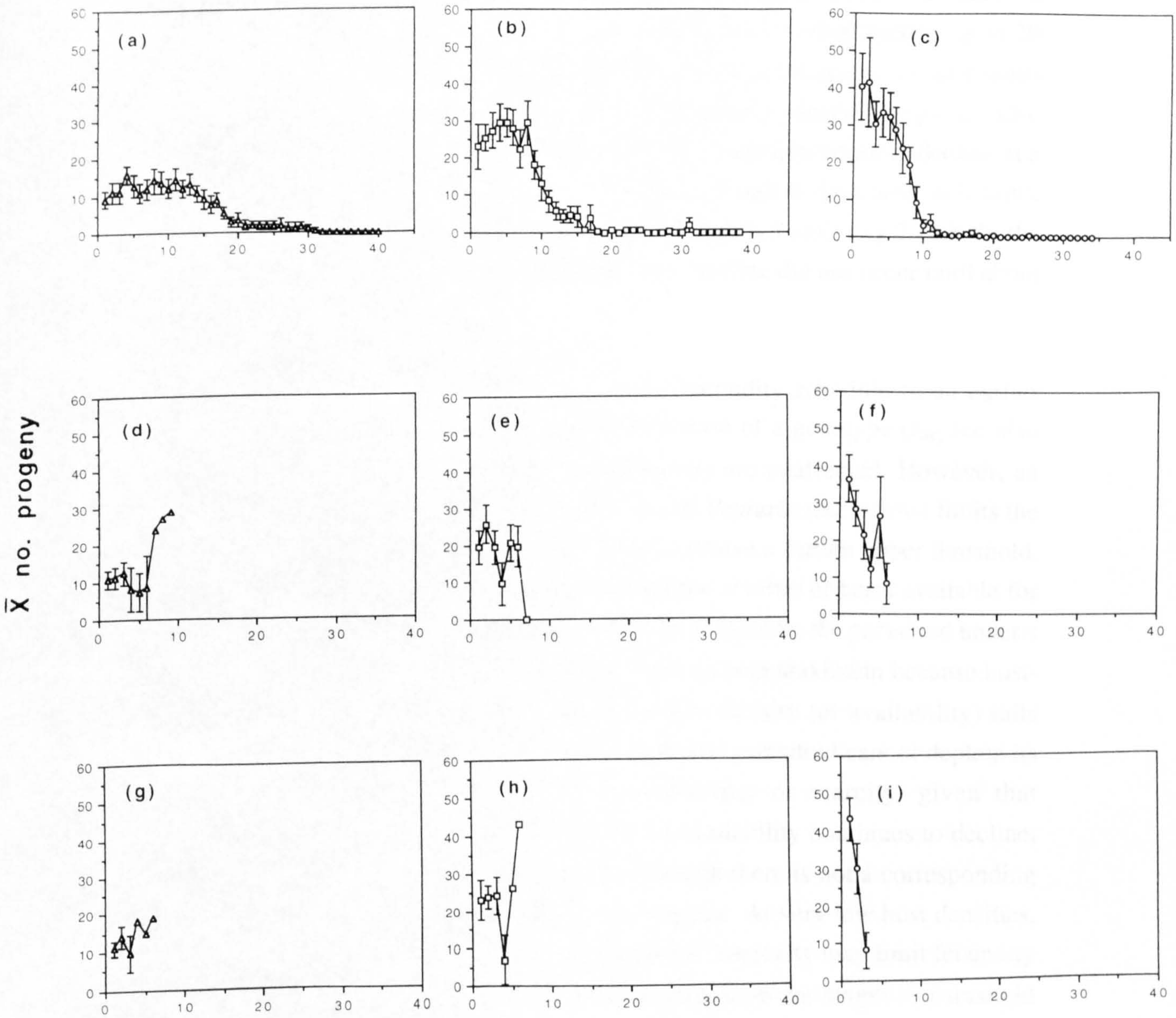
excluded from the analysis because most parasitoids died during the first 5 days of adult life. An initial F-max test revealed that the difference in extreme variances was not significant ($P > 0.05$). Total progeny production for 24h wasps varied significantly with duration of daily host access ($F = 6.94$, d.f. = 2, 18, $P < 0.01$; Fig. 8.7a-c) but not between blocks ($F = 1.21$, d.f. = 9, 18, $P > 0.05$). Constantly fed wasps with access to hosts for only 1/2 hour per day produced an average of 60.1 progeny over the first 5 days, or 28.3% of their total lifetime fecundity; wasps with 2 hours access to hosts daily produced an average of 135.5 progeny over this time (48.6%) and parasitoids constantly exposed to hosts produced an average of 167.6 progeny (64.5%) over the same time period. Tukey's pairwise comparisons revealed that the difference in cumulative fecundity was only significant ($P < 0.05$) between the limited and constant host access treatments. The ANOVA table is shown below.

Fig. 8.7 shows the age-specific fecundity of *Venturia* under variable periods of host and food access. *Venturia* clearly adjusts its fecundity schedule to a later period of adult life when host access is limited and food access is unlimited (Fig. 8.7a), but depletes its egg compliment progressively earlier in life as hst access is increased (Figs. 8.7a & b).

8.3.5. Relationship between block, food and time treatments and total insect emergence (parasitoids and hosts combined).

As in the above analyses, the highest and lowest variances for the total insect data were compared using an F-max test for homogeneity of variances. The difference was not significant ($P > 0.05$), allowing two-way ANOVA to be carried out. A two-way ANOVA for mean total insects emerged (for each wasp treatment) showed that insect number did not vary significantly with length of access to hosts ($F = 2.60$, d.f. = 2, 81, $P < 0.05$) or with length of access to food ($F = 1.74$, d.f. = 2, 81, $P > 0.05$) and the interaction between food and time was also not significant ($F = 0.29$, d.f. = 4, 72, $P > 0.05$; Table 8.6). The mean total number of insects (wasps and moths) that emerged from the constant host access (24 hour) treatment was 130.33 (or 65.2%), which increased to 136.50 (68.3%) and 136.44 (68.2%) for the 2 hour and 1/2 hour access treatments, respectively.

Fig. 8.7. Age-specific fecundity of adult *Venturia* provided with food and hosts for different periods of time. Bars represent standard error of the mean. Graphs a-c = 24h (constant) food access, d-f = alternate 24h food access, 48h starvation, and g-i = starvation. Within each feeding treatment, triangles = 0.5h host access daily, squares = 2h host access daily, and circles = 24h (constant) host access. For sample sizes at a given age, please refer to Appendix (i).



8.4. Discussion.

The results of this investigation clearly demonstrate that a dynamic relationship exists between duration of host access and oviposition rate. Parasitoids provided with constant food responded to variable periods of host access by adjusting their daily rate of oviposition (Fig. 8.7a-c). Parasitoids adjusted their fecundity schedule in accordance with host availability, with wasps provided unlimited access to hosts showing a heavily skewed pattern of early adult reproduction (Fig. 8.7c), while wasps with limited host access distributed their progeny fairly evenly throughout their adult lives (Fig. 8.7a). Consequently, parasitoids with unlimited food and host access displayed a prolonged period of post-reproductive survival lasting up to 20 days in some individuals (Fig. 8.7c), whereas restricting host access to parasitoids resulted in a decrease in the length of post-reproductive survival (Figs. 8.7a,b). When wasps were constantly supplied with hosts, reproduction began to decline at a relatively early stage in their adult lives, (between 4 and 6 days after eclosion), whereas in the medium host access group this was delayed until day 7 or 8. In the limited host access group, a noticeable reproductive decline did not occur until about the 15th day after eclosion (Fig. 8.7a).

Lewontin (1965) showed that a shift in the fecundity schedule to an earlier reproductive age enlarges the intrinsic rate of increase of a genotype (r_m; see also Lessells, 1991) even if total fecundity and longevity are unaffected. However, an economical egg maturation strategy characteristic of *Venturia* (see below) limits the ability of the parasitoid to respond to host densities above a certain upper threshold. This upper threshold implies a host density where the number of hosts available for oviposition exceeds the potential number that can be utilized by the parasitoid under a given set of environmental conditions; at this point, r_m is at maximum because host-density is non-limiting for the parasitoid. If the host density (or availability) falls below the upper threshold, r_m will decline because the parasitoid cannot deplete its egg reserves in response to limited host availability or scarcity, given that superparasitism is avoided. When host density or availability continues to decline, oviposition shifts to a later reproductive age, although there is not a corresponding loss in total fecundity and superparasitism remains low. At very low host densities, or given extremely limited access to hosts, parasitoid longevity may limit fecundity and superparasitism may increase further, depending upon the length of parasitoid access to hosts. In this experiment, *Venturia* had sufficient daily access to excess hosts to shift the fecundity schedule to a later reproductive age, fecundity was therefore not limited by longevity (Fig. 8.7a-c). *Venturia* is capable of handling hosts

very quickly, with the entire sequence from host encounter to a resumption of searching frequently taking 20 seconds or less (Sait *et al.*, 1995). Limiting host exposure of parasitoids still further (15 minutes daily) may establish the lower fecundity threshold where the shift in reproductivity to a later age in *Venturia* would be unable to compensate for a reduction in early reproduction, with reproductive success therefore constrained by longevity.

Previous studies have shown that parasitoids adjust their fecundity schedules in response to temporal variations in host availability or density. *Trichogramma minutum* provided with excess host (*Anagasta kuehniella*) produced significantly more progeny over the first 2 days of adult life than wasps with restricted host access, although over the remainder of reproductive life daily oviposition totals were fairly uniform in both treatments (Bai & Smith, 1993). Kopelman & Chabora (1992) also found that females of the pro-ovigenic wasp *Leptopilina boulardi* provided continually with hosts exhibited an early peak and subsequent rapid decline in progeny production, followed by a protracted period of post-reproductive survival, whereas wasps with more limited host access extended their reproductive periods to a later period in adult life. Work on other parasitoid species has similarly showed an adjustment of reproduction in response to temporal host limitations (e.g. Mackauer, 1982; Drost & Carde, 1992).

Superparasitism may have influenced L5 larval mortality when parasitoids were provided constantly with hosts, because the total cumulative moth and wasp mortality was significantly higher in this treatment than when host access was more limiting. In the 0.5 h and 2 h host access treatments, 65% of wasps and moths emerged, but this decreased to 60% in wasps with constant host access. Although the length of patch residence for hosts was considerably longer in the constant access treatment, mortality was not significantly higher in the control patches where wasps had no access to these hosts. In Chapter four, I showed that, in L5 (but not L3) hosts, host and parasitoid mortality increases with egg number per host, so that superparasitism potentially represents a considerable constraint upon the reproductive success of parasitoids in situations where the parasitoid-host ratio is high or when most of the L5 hosts are already parasitized.

The results also demonstrate that, given the opportunity, *Venturia* exploits available hosts as much as possible during the first few days of adult life. This contradicts the results of Ahmad's (1936) study, where *Venturia*, provided with 200 hosts (*A. kuehniella*) daily and constant food, appeared to withhold eggs and lay

them in a more evenly distributed pattern through most of its adult life. Another difference between the two studies concerns the cumulative lifetime reproductive success of *Venturia* when provided with excess hosts and food. In this study, several constantly-fed wasps produced in excess of 400 progeny during their lifetimes, including individuals from all 3 host availability treatments, whereas the maximum number of progeny produced by a parasitoid in Ahmad's study was 75, and this individual had been starved throughout its life. Given that hosts (and parasitoids, as shown in the controls) suffered over 30% mortality during the experiment, and accounting for superparasitism (which was not determined), it is not unreasonable to expect that some wasps could easily produce 600, or even 700 progeny under optimal conditions. Therefore, it is hard to understand why long-lived parasitoids in the study by Ahmad (1936) did not have higher realized fecundities. In both studies different hosts were used; *Anagasta* may have possessed a considerably greater encapsulation ability than *Plodia*, although, in Chapter 6, it was shown that the encapsulation rate of *Venturia* by L5 *Anagasta* was less than 20%. However, it is possible that Ahmad's failure to isolate host-containing patches for 24 hours prior to presentation to parasitoids was a more important factor. Waage (1978) showed that host searching and probing behaviour of *Venturia* are profoundly affected by secretions (kairomones) released by hosts during feeding and in frass, in addition to alarm pheromones produced by larvae (Corbet, 1971). The copious production of silk also attracts parasitoids (Vinson, 1985). The importance of allowing host larvae the time to "contaminate" a patch with kairomones could therefore significantly influence the searching and probing intensity of the parasitoid.

This study has therefore revealed that *Venturia* has a higher reproductive capability than has previously been suggested, based on actual measured reproductive success (Ahmad, 1936) or dissections of the oviducts when egg storage capacity has been attained (Trudeau & Gordon, 1990; Chapter 2). The latter method of estimating parasitoid fecundity using ovary and oviduct dissections is frequently seen in the literature and egg load is often found to be positively correlated with adult wasp size (e.g. Price, 1984; Waage & Ming, 1984; Hopper, 1986; Walter, 1988; Volkl & Mackauer, 1990; Rosenheim & Rosen, 1992). For synovigenic species, including *Venturia*, dissections of the reproductive tracts may reflect only short-term egg production, not fecundity, because these parasitoids can potentially mature several times as many eggs during their lifetimes as can be stored in their oviducts or ovaries at a given time in their life (Chapter 2).

One of the most important aims of current parasitoid research is to understand the relationship between the size of a female wasp and her fitness (Godfray, 1994). Besides the somewhat crude measurements of fitness based on ovary dissections, estimates of this relationship have occasionally used fecundity and longevity as measures of fitness (Visser, 1994). In *Venturia*, both fecundity and longevity covaried with adult wasp size, supporting the results of several studies (e.g. van den Assem *et al.*, 1989; Hardy *et al.*, 1992; Figs. 8.1, 8.2 & 8.6) where large parasitoids produced more progeny and lived longer than smaller conspecifics. However, as Visser (1994) points out, size may affect other components of fitness, such as searching and dispersal efficiency, which may be revealed more under natural conditions than in the laboratory. Where hosts are spatially separated, it is likely that metabolic costs for these activities increase, perhaps benefitting larger individuals which have greater storage sites than smaller individuals. This could allow the relationship between size and fitness to be revealed in species where it has not yet been found to occur (e.g. *Spalangia cameroni*; King, 1988). However, Visser (1994), comparing the size-fitness relationship for the braconid parasitoid *Aphaereta minuta* under natural and laboratory conditions, found that fitness increased much more rapidly with increasing female size in the laboratory than in the field. He argued that realistic data on longevity cannot be obtained in the laboratory, because in the field parasitoid mortality will also be influenced by predation and variable weather conditions, which are absent in empirical investigations. Undoubtedly, the dearth of comparative studies evaluating the size-fitness relationship under both natural and empirical conditions hinders our understanding of the importance of size on parasitoid fitness.

Optimality models by Mangel (1987a,b, 1989) and Charnov & Stephens (1988) predict that changes in the internal state of parasitoids (for example, their current egg complement, and nutritional reserves) should affect the oviposition behaviour of parasitoids in response to dynamic changes in these characteristics. The models broadly predict that parasitoids should attack a wider range of host types (incorporating lower quality hosts into their diet) or increase their searching rate for hosts when the risk of mortality is high, for example when food is scarce or environmental conditions are otherwise unfavourable. It is therefore assumed that starved *Venturia* should have produced more progeny over the first two days of adult life than well-fed wasps, because for starved wasps the risk of mortality was much greater than for well-fed wasps. This was clearly not the case, and can probably be explained by closely examining the reproductive biology of *Venturia* in response to host availability. Wasps emerge with up to 50 or so ovulated eggs ready to oviposit

(Chapter 2). Given that some parasitoids produced 60-70 progeny on the first day of adult life (ignoring mortality and superparasitism), it is conceivable that virtually their entire "ready supply" of ovulated eggs was used up over the first 24 hours (perhaps even sooner), and the parasitoids were then constrained by the rate at which further eggs were ovulated, passing from the ovaries into the oviducts. Trudeau & Gordon (1990) monitored the egg maturation rate of *Venturia* at 25°C, and found that wasps matured 1.8 eggs per hour on average (or about 40-45 per day). These wasps were, however, deprived of hosts and it has been suggested in hydropic parasitoids that egg maturation slows as the oviducts accumulate eggs (Flanders, 1942). Wasps constantly provided with excess hosts appeared to oviposit at their physiological limit, whether food was available or not. Consequently, after several hours of intensive foraging on the first day of adult life the oviducts of *Venturia* were probably depleted of eggs and the parasitoid rested until further eggs had accumulated in their oviducts. From this point until death, the reproductivity of parasitoids was effectively constrained by the rate of ovulation, and they were thus unable to adjust their rate of oviposition in response to their physiological state (hunger).

Beling (1932), observing the behaviour of wasps in flour mills, found that many newly-emerged parasitoids exhibit positive phototaxis, leaving the host environment soon after eclosion. This could be a response to hunger, because she also captured a number of wasps returning to the mills with droplets of nectar in their mandibles. It would be desirable, then to begin an experimental programme to accommodate periods of host deprivation and to monitor the reproductive success of *Venturia* in response to variable environmental conditions. Wasps with effectively "no choice" that are constrained in small plastic containers may behave entirely different from conspecifics under natural conditions, where the freedom to disperse is obviously available. Several parasitoid species have been found to ignore suitable hosts for several days after emergence (Vinson, 1985). For example, *Opius fletcheri* (Braconidae) females do not respond to the host habitat for at least 3 days after eclosion (Nishida, 1956). This ensures dispersal from the point of origin. The ichneumonid *Pimpla ruficollis* is repelled by the odour of pine oil at emergence but the oil serves an attractant for the parasitoid several weeks later when her ovaries have matured (Thorpe & Caudle, 1938). Although *Venturia* will oviposit soon after emergence, the rapid egg depletion which will have occurred in the constant and medium host access treatments suggests that access to abundant, readily available final instar hosts, even for relatively short periods, is a laboratory artefact. Under natural conditions the parasitoid must be able to cope when host availability varies

both temporally and spatially, hence the limited host access treatment better reflects these conditions.

Wasps constantly provided with food but no hosts (= controls) lived slightly, though not significantly, longer than wasps provided with hosts, while within the other treatments there was virtually no difference in the longevity of wasps provided with or without hosts. A negative correlation between reproduction and survival is predicted by models (e.g. Reznick, 1985, Bell & Koufopanou, 1986) although evidence supporting this from other parasitoid species is mixed. Hohmann *et al.* (1989) and Orr & Boethel (1990), for example, reported a positive relationship between these two life-history parameters in the parasitoids *Trichogramma platneri* and *Telenomus* spp. respectively, but Bai & Smith (1993) found that *Trichogramma minitum* producing the greatest number of progeny lived much longer than conspecifics that were deprived of hosts throughout their lives. Similarly, studies with other insects have shown mixed results, with reproduction negatively affecting the survival of the rosehip fly, *Rhagoletis basiola* (Roitberg, 1989) but having no discernible effect upon survival of the seed beetle, *Callosobruchus maculatus* (Moller *et al.*, 1989).

Models of resource acquisition and allocation by van Noordwijk *et al.* (1986) and de Jong & van Noordwijk (1992) suggest that positive or negative correlations between life-history traits depend largely upon variations in the fraction of resources that are allocated for various functions. When conditions are favourable, negative correlations between reproduction and survival become less clear, or may disappear entirely because the organism is able to obtain sufficient resources from the environment to compensate (or offset) the concomitant drain from reproduction (Bell & Koufopanou, 1986; Chapter 9). Studies on other arthropods exposed to stressful conditions including resource variability showed a negative relationship between reproduction and survival, which disappeared when the organisms were reared under favourable conditions (e.g. Calow, 1973; Browne, 1982). However, in the limited food and starvation treatments, *Venturia* exposed to hosts lived as long as controls reared under the same nutritional regime. This could be due to the relatively short life-spans of the parasitoids reared under these conditions, where the stresses are so severe that even wasps deprived of hosts deplete their energy reserves in a very short time, so that the effects of foraging are not clear. An experimental programme, subjecting the wasps to slightly less nutritional stress (thereby increasing their longevity) may reveal trade-offs between reproduction and survival that were absent in the extreme feeding treatments tested in this study.

In studies where the relationship between reproduction and survival is neutral or positive (e.g. this study; Bai & Smith, 1993) it is necessary to examine other factors that may limit the life-expectancy of wasps deprived of hosts. In hydropic parasitoids the eggs are comparatively small and may be stored pending their deposition in the paired oviducts and in the basal portion of the ovaries (Flanders, 1942). Many parasitoids have the capacity to store hundreds of eggs in their oviducts (Flanders, 1950) but the metabolic costs of egg storage are poorly understood. Wasps which have a constant access to hosts carry proportionally lighter egg complements that might reduce the costs of foraging. On the other hand, many parasitoid species possess the capacity to resorb some or all of their egg proteins under conditions of host deprivation, an adaptive mechanism that allows the parasitoids to reallocate germinal tissue for maintenance (Jervis & Kidd, 1986). In these species, the oviducts may be reduced or even absent altogether. However, the premature death of several encyrtid parasitoids deprived of hosts has been attributed to perforation of the resorbed egg exochorion into the body cavity. Flanders (1942) found that, in *Encyrtus fuliginosus*, the complete exochorion of each disintegrated egg extruded into the body through the walls of the tunica propria, the membrane-like wall surrounding each ovariole. In line with these findings, ovipositing females of *E. fuliginosus* lived three times as long as wasps that were not permitted to oviposit (Flanders, 1942). In several anhydropic species, all eggs must be deposited soon after ovulation because precocious embryonic development may be completed while the eggs are still in the oviducts. Chewyreuv (1912) reported several cases where the premature death of female parasitoids was caused by perforation of the oviduct wall by 1st-instar larvae. Therefore, physiological factors may influence the longevity of parasitoids, and could account for deviations from the expected correlation between reproduction and survival.

Most existing experimental designs investigating lifetime reproductive success in parasitoids have continually exposed female wasps to high density patches (with food) for 24 hour periods. If it is true that suitable hosts and food sources for most parasitoids are patchily distributed (Price, 1980), then experiments should be designed limiting, or interrupting host and food access for parasitoids that more closely approximate the patchy and ephemeral nature of these two resources (Kopelman & Chabora, 1992). Laboratory-based life-history studies should include cohorts where host and food availability are restricted, particularly in the case of pro-ovigenic species, which may deplete their egg complements rapidly (Kopelman & Chabora, 1992) or, at the other end of the spectrum, pupal parasitoids and those attacking highly dispersed, scarce or concealed hosts (Jervis & Kidd, 1986). For

anhydropic host-feeding parasitoids, the relationship between host availability, host-feeding activity, longevity and lifetime reproductive success offers considerable promise in our understanding of trade-offs between life-history characters.

These experiments have demonstrated that there is a correlation between early and late reproduction in *Venturia*. The parasitoid clearly adjusted its fecundity schedule in response to temporal variations in host access, and there were correlations between adult wasp size and both longevity and fecundity, supporting the predictions of models (e.g. Charnov, 1982; Charnov & Skinner, 1985). However, *Venturia* was unable to adjust its fecundity schedule in accordance with food availability, and the predicted correlation between fecundity and survival was not supported by the data. Further studies are still required on a wider range of parasitoid species, especially under natural conditions, to determine the applicability of the trade-off hypothesis in parasitoids.

9. General discussion

9.1 The nutritional ecology of *Venturia canescens*: a summary

This study has detailed an investigation on the influence of several diverse host-related and environmental constraints on various aspects of the host selection behaviour, larval development and reproductive success of *Venturia*. In each of the preceding chapters, detailed discussions were presented relevant to each experiment, so that in this chapter I will restrict myself to presenting a synthesis of my findings.

Chapters three to six explored the effects of some physiological constraints on the growth and development of *Venturia*. For koinobiont parasitoids, host suitability is difficult to measure objectively, because it refers to a diverse set of attributes characteristic of hosts that may vary in size, age or physiological condition at, and during, parasitism. Host stage, species, nutritional status, the presence of conspecific eggs or larvae and pathogenic infection are just some of many factors that potentially influence host suitability. However, few studies have detailed the influence of different constraints on the development of a single parasitoid species, therefore ignoring a number of potentially complex factors that may incur stage-specific effects upon suitability and parasitoid fitness. Host suitability for the development of immature *Venturia* is not a fixed property of host instar or species at parasitism, but varies in accordance with the type of constraint, resulting in a series of different trade-offs between life-history characters (9.2.1-9.2.4).

Far from being passive participants in the host selection process, many hosts actively resist parasitism, employing a number of behavioural, morphological and physiological defences to do so (Gross, 1993). Host suitability commonly refers to a stage or size of the host most physiologically compatible with larval parasitoid development (e.g. Vinson & Iwantsch, 1980a); however, a number of studies have shown that the acceptance of smaller, presumably less suitable hosts may be due to behavioural interactions between hosts and parasitoids that prevent the parasitism of larger hosts (Campbell & Duffey, 1979; Allen, 1990; Gerling *et al.*, 1990; Kouame & Mackauer, 1991). Therefore, host defensive behaviour potentially represents a second constraint upon parasitoid performance, but may be overcome through a separate set of trade-offs that occur during the host-selection process. A reproductive strategy that incorporates the acceptance of less well-defended hosts that are less suitable nutritionally or physiologically may still improve parasitoid fitness in the long run, bearing in mind the costs incurred in unsuccessful attacks on larger hosts of higher nutritional quality. Host species and behaviour limit the expression of host

acceptance by *Venturia*, although this constraint may benefit, rather than hinder, the performance of the parasitoid (9.3.1).

The lifetime reproductive success of organisms is often assumed to be the most accurate measure of fitness simply because actual (rather than potential) fecundity is measured. The lifetime reproductive success of parasitoids has frequently been measured by exposing wasps to excess numbers of hosts and constant food, where the only constraint upon parasitoid fitness is the number of eggs that can be matured and mobilized for oviposition at a given time (in synovigenic species). In nature, parasitoids may emerge into host-depleted environments, where the population has shifted spatially or has become locally extinct. Furthermore, sources of nutrition for adult parasitoids, including plant exudates, may be located a considerable distance from hosts (Jervis *et al.*, 1993). Trade-offs between life-history characters for adult parasitoids are the result of constraints on the rate at which resources can be obtained and allocated to physiological functions, and may result in a negative correlation between fitness components. Trade-offs are usually expressed as a negative correlation between early and late reproduction (Charlesworth, 1980; Lessells, 1992) or between reproduction and survival (Roitberg, 1989). In this study on the lifetime reproductive success of *Venturia* when provided with hosts and food for variable periods of time, a number of constraints on parasitoid fitness were identified. However, the experiment raised a number of questions about the nature of trade-offs in parasitoids (9.3.2).

9.2 Host suitability constraints on the immature parasitoid

Although there is a wealth of data on the effects of host size and suitability on parasitoid size, development time, longevity, fecundity and oviposition decisions (offspring sex) (Godfray, 1994), these studies have largely concentrated on the end results, thus ignoring interactions between the immature parasitoid and host during the interaction. In Chapter 3, the growth trajectory of *Venturia* developing in 4 instars of *Plodia* was monitored from early-1st instar through to the eclosion of the adult. The trajectory of larval growth provides a direct measure of host suitability because it reflects the nutritional relationship between the parasitoid and host during the entire course of parasitism (Mackauer & Sequeira, 1993). Subsequent chapters detailed the dynamics of parasitoid development under constraints imposed by superparasitism, nutritional status and host species. The data generated provides a more comprehensive picture of host suitability, and should serve two purposes: (i) to identify, in various parasitoid species, the most important developmental

characteristics that influence fitness; (ii) to determine the dynamic relationship between the different constraints and host suitability. These points will be discussed separately.

9.2.1 Patterns of host utilization by parasitoids

Host suitability constraints on larval parasitoid growth and development influence three main aspects of parasitoid fitness: survival (to eclosion), size and development time. Survival is obviously of major importance to the parasitoid, while some empirical evidence clearly shows that the size of the adult has a major influence on the lifetime reproductive success of parasitoids (see King, (1987) and Visser, (1994) for reviews). The importance of development time on fitness is much less clear, and as Godfray (1994) points out, probably applies under a very limited set of conditions. For example, if the population sizes of hosts and parasitoids are constant, a female parasitoid's fitness should not be affected when her progeny emerge, irrespective of their development time, assuming that mortality is independent of time-to-adult. However, when the population is growing, as early in the spring, fast development would be favoured, because the sooner that parasitoids can complete development, the sooner they themselves can reproduce. Fisher (1930) and Lewontin (1965) have stressed the evolutionary importance of early reproduction in growing populations with overlapping generations. Moreover, development time may affect the ability of emerging parasitoids to locate suitable hosts (due to fluctuations in the availability of hosts over the course of a season) so that females emerging at different times may experience better or worse conditions for reproduction (Godfray, 1994). Mate-finding ability may also vary with development time (Godfray, 1994) while extended development time may increase parasitoid mortality during the "window of interaction" with the host, because parasitoid mortality is proportional to host mortality during the interaction, hence rapid development would be selected for (Slansky, 1986; Blackburn, 1991). However, as Godfray (1994) points out, there are very little data available on the relationship between development time and fitness in parasitoids.

Parasitoids depend entirely upon host-derived nutrients for larval development and growth, hence natural selection should favour mechanisms that maximize the efficient utilization of these resources. Metabolic processes that mediate patterns of growth and development in organisms, and ultimately determine their fitness, are generally dependent upon the size of the reproductive adult (Peters, 1983; Schmidt Nielsen, 1984). Research has shown that body size usually correlates with life-

history and demographic parameters in parasitoids (King, 1987), suggesting that body size is the main target of selection. However, due to host-size (suitability) constraints, adult size and rate of development in parasitoids may have different, perhaps even opposite, effects on fitness (Roff, 1981; Mackauer & Sequeira, 1993). As a result, the developmental strategy adopted by a particular species of parasitoid for these characteristics may vary in accordance with the nature of the constraint, being determined by fitness trade-offs between adult size and development time that optimize fitness. Trade-offs are assumed to be the result of constraints on the rate at which resources can be acquired and allocated to vital functions (Reznick, 1985; Lessells, 1991) which results in a negative correlation between fitness-related components. Sibly & Calow (1986) argued that natural selection, in response to host size constraints, acts either by pushing phenotypes and their underlying physiologies to their limit, or optimizes phenotypes by trading off individual characters to maximize fitness. Consequently, if a parasitoid "decides" to grow larger, development time may be extended; on the other hand, if it matures earlier, size may be compromised. Both of these parameters depend upon the adaptive variability in the growth rate. When a parasitoid is developing at its physiological maximum, an increase in body size will only be achieved if development time is prolonged, unless the parasitoid can increase its growth rate during larval development. Thus, the allocation of limited (host) resources to competing fitness functions may result in trade-offs between life-history characters that determine an "optimal life-history set" and thus shape the evolution of a species life-history strategy.

9.2.2 The development of models: (a) host suitability and sex ratio

When a parasitoid female encounters a host, one of the decisions she faces is what sex to allocate (assuming, of course, that the species does not reproduce by thelytoky). Considerable research in the parasitic Hymenoptera has concentrated on sex ratio decisions, because, in most species, males develop from haploid (unfertilized) eggs and females from diploid (fertilized) eggs. Consequently, the sex determining mechanism is under direct maternal control, and it has been known for well over a century that many female parasitoids facultatively alter the sex of the egg in response to environmental conditions and certain attributes of the host (Godfray, 1994). This subject has received much theoretical and experimental attention (see King, (1989) and Godfray (1994) for reviews) and provides evidence that optimal resource allocation to adult body size is the most important component of fitness in hymenopteran parasitoids.

Sex-ratio manipulation is closely associated with host suitability, because parasitoids develop on limited resources and in both idiobionts and koinobionts, the size of the emerging adult wasp is often influenced by the size of the host at parasitism (Arthur & Wylie, 1959; Cloutier *et al.*, 1991; King, 1987). Charnov (1981) argued that differences in host suitability as affected by host size explain why female parasitoids frequently lay male eggs in small hosts of lower nutritional quality, and female eggs in larger hosts (Clausen, 1962; Sandlan, 1979a). His model, the size advantage hypothesis, argues that sex-ratio is adjusted because large females emerging from bigger hosts are correspondingly fitter than large males. Female size is assumed to have a major effect on fitness because large females are able to mature more eggs, locate hosts more efficiently, and live longer than small females, whereas the ability of the male to inseminate the female is less dependent on size (Godfray, 1994). Large males also benefit from increased adult size, but the advantage of being large is more pronounced in female than male parasitoids. Several studies comparing intraspecific fitness in male and female parasitoids (e.g. Jones, 1982; van den Assem, 1989; Heinz, 1991) appear to support Charnov's size advantage hypothesis. The results of these investigations reinforce King's argument that, in many parasitoids, size is of greater relative importance for fitness than development time. In idiobionts, parasitoid development often proceeds more slowly in large than in small hosts, probably for the simple reason that large hosts take longer to consume (Arthur & Wylie, 1959; Carpenter *et al.*, 1994). Therefore, the benefit of large size overrides the gains from the reduced development time observed in smaller hosts.

Charnov's size-advantage hypothesis provides a useful tool in our understanding of host suitability and its influence on parasitoid oviposition decisions and other aspects of the host selection process. Unfortunately, as discussed earlier, the models and existing data sets are largely based on the the beginning (oviposition) and end results of the interaction, thus ignoring the physiological and nutritional integration between host and parasitoid that is characteristic of each association (Thompson, 1985). Differences in host exploitation and development strategies by parasitoid wasps are specific adaptations to available host biomass, growth potential and survivorship. Parasitoid development is constrained by host suitability, which may vary between and within associations in response to factors that affect the condition of the host during parasitism.

9.2.3 The development of models: (b) life-history strategies of koinobionts and idiobionts

A series of recent papers by Sequeira & Mackauer (1992a,b, 1993) addresses the question of adaptive patterns of growth and development in parasitoid wasps by targeting the development trajectories of the host and parasitoid from start to finish. Although their studies were confined to aphidiid koinobiont parasitoids, these studies set a framework for the field. Examining empirical data, Mackauer & Sequeira put forward three development strategies for koinobiont and idiobiont parasitoids in response to host quality constraints, and described these strategies using a series of graphical models.

In the first model, the host represents a closed resource environment and parasitoid growth and development is constrained entirely by host suitability. The host contains finite resources that are determined at parasitism, and host suitability is not highly variable during the interaction (although it may vary between hosts of different ages or species). The parasitoid's development strategy is aimed at maximizing adult biomass (assumed to be the major component of fitness) per unit of host resources; the larval parasitoid growth trajectory reflects nutrition-related constraints imposed by the host and environmental conditions, and is relatively inflexible. Adult parasitoid size is assumed to be positively correlated with host size, reflecting host suitability, because larger wasps are presumably more fecund and longer-lived than small wasps emerging from smaller hosts, although they may require more time to complete development. This model describes the predicted development pattern for solitary idiobiont parasitoids.

The second model assumes the host represents an open resource environment (where additional resources may be added during parasitism) and parasitoid growth and development are constrained entirely by host suitability. Therefore, both suitability and resource availability may vary over time with host age at parasitism. Host feeding and growth may continue during the initial stages of parasitism, although at modified rates. In hosts of lower nutritional suitability (e.g. early instars), parasitoid development may be slowed or arrested, during which time host growth continues. The parasitoid development strategy is to maximize biomass per unit of host resources (as in Model 1). Any fitness losses incurred by delayed growth in smaller hosts are balanced against gains from increased adult size, which is assumed to be of greater importance for fitness. This development strategy requires the host to

attain a minimum or critical size for the successful completion of parasitoid development to the adult stage.

Model three also assumes that the host represents an open resource environment, and that parasitoid growth and development are constrained by time and resource limitations. The dynamics of host suitability are the same as in Model 2, but this model assumes a developmental strategy that optimizes a number of characters that jointly determine fitness, such as adult size and development time. Time constraints may result in a fixed period of host survival after parasitism, or a marked reduction in parasitoid survival in older hosts. In small, or otherwise less suitable hosts, resource limitation may result in delayed parasitoid development during initial stages, or early death in older larvae. The growth trajectory of the parasitoid is variable and reflects constraints imposed by host age, size or stage on the amount of available resources. Parasitoids adopting this strategy display varying degrees of phenotypic plasticity, compensating for early developmental arrest by increasing the growth rate during later stages, thereby balancing any fitness gains (from increased adult biomass) against losses (from increased development time). Models two and three conform to the development pattern of solitary koinobionts.

For idiobionts, host biomass at parasitism represents the main constraint on parasitoid biomass and development time. Idiobionts typically continue to feed and grow until all host tissues are consumed (Mackauer & Sequeira, 1993), but in some species the host may be so large that the parasitoids are unable to dispose of all host biomass (Salt, 1941; Wylie, 1965; Gunasena *et al.*, 1989). Many egg and pupal parasitoids habitually arrest host development at oviposition, through the injection of secretions from the poison gland of the female wasp (Laughton, 1965; Vinson & Iwantsch, 1980b; Strand, 1986). This ensures that host suitability remains fairly constant during the course of parasitism, because in non-paralyzed hosts, suitability may decrease with host age due to developmental changes within the host. Sandlan (1982) and Carpenter *et al.* (1994) found that the development times of the pupal ichneumonid parasitoids, *Pimpla turionellae* and *Ichneumon promissorius* respectively, increased with the age of the host pupae at the time of oviposition. Although the amount of nutrients available to egg and pupal parasitoids are relatively constant after parasitism, weight loss occurs as the host uses more energy for itself and it may be metabolically more expensive to convert developing embryonic or adult tissue into a form usable by the parasitoid, accounting for the increase in development time (Anderson, 1972). Strand (1986) suggests that, in egg parasitoids, selection favours a reduction in development time through a compensatory increase in the

growth rate to offset the deleterious effects of host embryogenesis. He argued that egg parasitoids, for example *Trichogramma* species, are largely polyphagous because of the uniformity of eggs as a food resource, particularly since the cellular defences of eggs are reduced or even absent altogether. If this hypothesis is correct, the growth rate of generalist egg parasitoids should be relatively constant (Mackauer & Sequeira, 1993) although few detailed studies have closely examined the growth and development of egg parasitoids under host size-related constraints (but see Marston & Ertle, 1973; Bigler *et al.*, 1987).

Because host growth does not occur after parasitism, idiobionts are able to determine the suitability of the host before oviposition. Several studies have shown that female wasps assess host suitability by mounting hosts (Edwards, 1954; Rotheray *et al.*, 1984), measuring the surface of the host with antennae (Schmidt & Smith, 1985) or after ovipositor insertion (Price, 1970; Smilowitz & Iwantsch, 1975). Less suitable hosts may well be rejected, or the wasp will adjust sex ratio, with haploid (male) eggs being laid on smaller hosts (Sandlan, 1979a; King, 1987). During early development, idiobiont parasitoids are not protected against host immunology, although many ichneumonid and braconid koinobiont parasitoids carry particles, characterized as viruses, in the calyx region of the ovaries (Stoltz & Vinson, 1979; Fedderson *et al.*, 1986). These particles invade host cells and tissues, and alter host development in a number of ways, including suppression of the host's immune response towards the egg (Edson *et al.*, 1981). First instar idiobiont larvae frequently overcome host defences by rapacious feeding soon after eclosion from the parasitoid egg, because there is no need to arrest development (Salt, 1968). This accounts for the rather inflexible developmental pattern of most idiobionts, described by Mackauer & Sequeira (1993). Blackburn (1991), examining published data, compared development times of idiobiont and koinobiont parasitoids, and noted that the pupal periods and pre-adult lifespans of idiobionts are shorter than in koinobionts, suggesting that these two groups have probably evolved under different constraints with regard to resource usage and allocation. Idiobiont growth and development is restricted to a single stage, where suitability is primarily determined before parasitism; the development of koinobionts, on the other hand, frequently spans several host instars, where suitability is largely a property of the host after parasitism.

The second model of Mackauer & Sequeira (1993), describing koinobiont development, explains a strategy that favours the evolution of a minimum or critical body size for the completion of development to the adult stage and conforms to the

development pattern of several solitary parasitoids attacking larvae of Lepidoptera, including *Hyposoter exiguae* (Smilowitz & Iwantsch, 1973; Beckage & Templeton, 1985), *Campoletis sonorensis* (Vinson, 1972; Gunasena *et al.*, 1989) and *Microplitis* species (Jones & Lewis, 1971; Tanaka *et al.*, 1984; Strand *et al.*, 1988). The growth and development of *Venturia* also conforms to this model. In well-nourished *Plodia* larvae, the development of *Venturia* is clearly affected by the instar parasitized, although the differences are only recognizable between L2 and L3-L5 hosts. Parasitoids from L2 hosts are smaller, take longer to complete development and suffer higher mortality than parasitoids from instars three to five. In smaller hosts (L2/L3) of presumably lower quality, the growth of *Venturia* is characterized by developmental arrest during the first instar, with accelerated growth occurring soon after the final moult of the host to the final (L5) instar. The parasitoid always allows the host to spin a pre-pupal cocoon before it is destroyed. *Venturia* also regulates two major aspects of host development during the course of parasitism. Hosts parasitized as L2-L4 instars were prevented from pupating, allowing additional resources to be made available for the parasitoid. This may also have benefitted the parasitoid by reducing larval mortality, which was higher in late L5 hosts that pupated soon after being parasitized. Perhaps more significantly, the trajectory of host growth is reduced after parasitism in L2 and L3 hosts, showing that *Venturia* adjusts the commencement of destructive feeding in accordance with host conditions (Fig. 3.4, Chapter 3). This may be a compensatory mechanism that balances any potential fitness losses incurred by reduced adult biomass against fitness gains from reduced development time.

Increasing the larval development time of parasitized L3 *Plodia*, through starvation, correspondingly extended the development of *Venturia* (Chapter 5), supporting the prediction of the second model. *Venturia* remain as first instars as long as *Plodia* larvae do not enter their final larval moult, demonstrating that the critical host size for parasitoid maturation in *Plodia* occurs during the host's final larval instar. This strategy, however, varies between host species with different growth potential (see below) and is evidence that natural selection favours an increase in adult biomass irrespective of time-to-adult, at least in some parasitoid species (Mackauer & Sequeira, 1993). Parasitoids which emerged from hosts starved early in the final host instar were themselves tiny runts, eclosing with very low egg complements (Chapter 2, Fig. 2.1).

The growth and development of *Venturia*, like several other ichneumonids, varies between different host species (Chapter 6), suggesting that the parasitoid alters its developmental programme in accordance with its own physiological requirements.

Irrespective of instar at parasitism, *Plodia* parasitized by *Venturia* always attained the size of healthy, mid-5th instars (Chapter 3, Fig. 4.4) whereas the growth of L4 *Corcyra* was arrested soon after parasitism (Chapter 6, Table 6.1). *Venturia* requires a critical host biomass to mature to the next stage, and this occurs earlier in a large host of the parasitoid, *Corcyra*, compared to *Plodia*, which is considerably smaller at all corresponding stages of its life history (Chapter 2, Tables. 2.3 & 2.4). The stage at which host growth is arrested is different, presumably due to the size differences between the two hosts, and is probably mediated by virus-like particles and other parasitoid-derived products at oviposition (Fedderson *et al.*, 1986; Vinson, 1990) and selective tissue feeding or secretions from the parasitoid larvae, such as juvenile hormone titres (Iwantsch & Smilowitz, 1975). The interactions between the solitary parasitoid, *Hyposoter exiguae*, and its various host species are also characterized by host developmental arrest, which varies with the species of host (Smilowitz & Iwantsch, 1973; Thompson, 1982; Campbell & Duffey, 1979; Beckage & Templeton, 1985; Table 9.1).

Lawrence (1986, 1990) considers host regulation (Vinson & Iwantsch, 1980b; Vinson & Barbosa, 1987) and flexibility in the larval development of the parasitoid (Corbet, 1968; Jones, 1985; Chapter 3) as alternate development strategies, stressing proximate mechanisms of parasitoid survival as a consequence of physiological and biochemical interactions between hosts and parasitoids. She goes on to propose a distinction between "conforming" parasitoids, which adjust their development in response to host conditions (e.g. nutritional quality), and "regulating" parasitoids, which alter certain aspects of host behaviour development and physiology in ways that improve parasitoid fitness (Slansky, 1986). Clearly, many koinobionts exhibiting growth and developmental characteristics of Mackauer & Sequeira's second model possess adaptations of both conformers and regulators (*Venturia* is a good example). In other host-parasitoid associations, any parasitoid-mediated alterations in certain host characteristics may be more subtle (Vinson & Iwantsch, 1980b; see below).

By comparison, koinobiont parasitoids exhibiting developmental characteristics of the third model do not display such high degrees of phenotypic plasticity or host regulation in response to host-mediated resource constraints at oviposition. Thus far, Mackauer & Sequeira (1993) have singled out only one taxonomic group of parasitoids (the Aphidiidae) which fit this development pattern (e.g. Sequeira & Mackauer, 1992a,b, 1993). This strategy appears to be based on a limited series of trade-offs that result in the optimization of both adult biomass and development time.

Resource availability for aphidiid wasps is limited to a fixed period before host death, thus the survival of parasitized aphids is independent of host age at parasitism (Liu & Hughes, 1984). For several aphidiids, host size has been found to correlate with resources to the progeny, even though they are koinobionts (King, 1989). In *Ephedrus californicus*, parasitism has a consistent effect upon host growth and development, such that the host represents a food supply that is largely pre-determined at parasitism (Cloutier *et al.*, 1991). Large differences between host size at oviposition were carried on, through destructive feeding to adult parasitoid eclosion, thus host size was a reasonably good indicator of resource availability to the progeny. The egg-to-pupal development times in *Ephedrus* were longer in L2 than in L1 and L4 hosts, demonstrating that the parasitoid does not adjust its growth trajectory in accordance with host conditions (Sequeira & Mackauer, 1993).

The growth and development trajectories of parasitoids are clearly influenced by more than a host's nutritional suitability, even if this represents the major constraint on parasitoid fitness. For example, any variability in the trajectory of larval growth could have beneficial or deleterious effects upon parasitoid survival, including the influence of host immunology and behaviour. Developmental arrest is characteristic of many koinobiont parasitoids that attack holometabolous hosts (Corbet, 1968; Allen & Keller, 1991). These parasitoids, including *Venturia*, require the host to attain a critical size or stage for successful development to the adult (model 2, see above) and frequently allow the host to spin a cocoon before it is destroyed (Jones & Lewis, 1971; Gauld & Bolton, 1988). Any costs incurred from increased development time in early or less suitable host stages are balanced against increased adult parasitoid size at eclosion, and a potential reduction in mortality due to the cryptic location of the cocoon by the host (Gauld, 1988). On the other hand, aphidiid parasitoids attack hosts which show little ecological variability throughout their life-history (but see Brodeur & McNeil, 1989). Consequently, the benefits of developmental delay from early host stages may be offset by a reduction in survival due the effects of various selective agents on the host (e.g. predators, other parasitoids etc.). Development trajectories of idiobiont and koinobiont parasitoids are expected to differ markedly as well, because a life-history strategy that incorporates flexibility in larval growth, while adaptive for some koinobionts in responding to hosts of variable suitability, would be of little use for idiobionts.

The three models of Mackauer & Sequeira (1993) are based on a very limited data set, primarily obtained from solitary koinobionts. The authors themselves stress that the existing data are fragmentary, thus the models should be seen as preliminary.

Further experiments are needed to test the underlying assumptions of the models. For example, the authors imply that there is a positive relationship between larval development rate and parasitoid fitness, which may not be true in all cases. Time-to destructive feeding provides a fairly accurate picture of resource availability, but survival in later host stages may be reduced because of the host's stronger physiological defences (Slansky, 1986; Chapter 6). Another potentially interesting area is to compare the growth trajectories of male and female parasitoids. Gunasena *et al.* (1989) reported that hosts (*Heliothis virescens*) containing female larvae of the ichneumonid koinobiont *Campoletis sonorensis* attained a higher final maximal weight than male parasitoids. Therefore, it appears that, at least in some koinobionts, there is a dynamic relationship between parasitoid sex and host growth after parasitism, further implying that a larval female parasitoid may regulate host development more effectively than a conspecific larval male. Little is also known about the growth trajectories of gregarious parasitoids, although in endoparasitic species this may be exceedingly difficult to measure for the simple reason of clutch size variability. The influence of host nutritional stress, as affected by starvation or crowding, and superparasitism may also shed considerable light on the evolution of life-history strategies in parasitoids. There is unquestionably considerable scope for the investigation of larval development patterns in parasitoids, monitoring their growth trajectories under different host quality constraints.

9.2.4 Host suitability under different constraints

One of the main problems in assessing host suitability for koinobiont parasitoids concerns the nature of the constraint under investigation. For idiobionts, host suitability is easier to measure because it is primarily determined by the history of the host before parasitism (Vinson & Iwantsch, 1980a). Consequently, for idiobionts, the only important constraints are available host biomass, age-related variations in nutritional quality, and extrinsic factors such as temperature which may influence development rate (Atkinson, 1994). Koinobiont development is dependent upon varying degrees of host growth after parasitism, which in turn are governed by an enormous number of factors. Therefore, host size or stage at parasitism are not the only factors which determine its suitability; others are the host's feeding rate and capacity for growth during the interaction with the parasitoid (Mackauer, 1986).

The models of Sequeira & Mackauer (1993) and virtually all existing data sets (Tables 9.1 & 9.2) have measured suitability for koinobionts under at most one or two host quality constraints, for example host stage or size at oviposition. In these

studies, parasitized hosts have been reared with unlimited food, thereby optimizing the nutritional conditions for parasitoid growth and development. When parasitized L2-L5 *Plodia* were provided with excess food, the difference in parasitoid mortality, development time and adult size in instars three to five was not significant (wasps from L2 hosts suffered higher mortality, took longer to complete development and were much smaller under these conditions). Thus, it could be argued that host suitability for *Venturia* is fairly uniform over most instars of *Plodia*. However, a dynamic reduction in host suitability between different host stages was only shown when additional constraints were incorporated into the experimental programme. The expression of trade-offs on life history characters may only be observed when parasitoids are subjected to further stresses on their development, for example in response to host starvation and superparasitism. When nutritional conditions were optimal (Chapter 3), negative correlations between host instar and parasitoid fitness components became less clear, and were difficult to determine in mid to late instars of *Plodia*.

Venturia was able to develop at its physiological limit in well-fed L3-L5 hosts because the hosts had an over-abundance of food and correspondingly developed very rapidly. The addition of extra constraints, in the nature of superparasitism (Chapter 4) and host starvation (Chapter 5) reduced the suitability of some host instars more than others, demonstrating that host suitability is not a static property of the host, but varies in response to the type of constraint imposed on the parasitoid. In superparasitized hosts, the progeny of *Venturia* from L5 *Plodia* suffered higher mortality, took longer to develop and were much smaller than wasps from L3 hosts containing the same number of parasitoid eggs (2 or 4); however, when hosts were starved, parasitoid development was affected more adversely in L3 than in L5 hosts, probably for the simple reason that L3 hosts must continue feeding for the successful development of *Venturia* while L5 hosts do not. Therefore, studies interpreting host suitability for koinobionts on the basis of a single constraint (usually host size or stage at oviposition) have ignored a number of important aspects which potentially influence suitability. Surprisingly, a comprehensive picture of host suitability is available for very few parasitoid species (Tables 9.1 & 9.2).

The development of *Hyposoter exiguae* (Ichneumonidae) has been compared in different host stages from several host species (e.g. Puttler, 1961; Smilowitz & Iwantsch, 1973; Campbell & Duffey, 1979; Beckage & Templeton, 1985; Table 9.1) and in third-instar hosts infected with nuclear polyhedrosis virus (Beegle & Oatman, 1975). The development of *Hyposoter* is characterized by host developmental arrest,

which varies with the species and stage of the host attacked. The biology of *Campoletis sonorensis* (Ichneumonidae) has also been well studied for many years, and a considerable amount of information is known about the host range of the parasitoid (e.g. Lindgren *et al.*, 1970). More recently, studies have revealed that *Hyposoter* and *Campoletis* both prefer early host instars (Smilowitz & Iwantsch, 1975; Gunasena *et al.*, 1989) even though later instars produce larger, presumably more fecund parasitoids. However, later instars of their hosts are more aggressive and possess stronger physiological defences than earlier instars, so that the greater success in parasitizing early instars may demonstrate an evolutionary compromise increasing the fitness of the parasitoid. In the field, early instars are more numerous, and perhaps more accessible for parasitism, although the larger, longer-lived wasps from later host stages may be able to compensate for their fewer numbers (Campbell & Duffey, 1979).

The tables also show that host preference and suitability are largely dependent on the growth potential of unparasitized hosts. The various hosts of *Hyposoter* and *Campoletis* grow considerably larger than hosts attacked by *Venturia*, even though the adult parasitoids are fairly similar in size. Therefore, whereas the successful development of *Venturia* is dependent upon its preferred hosts (*Plodia*, *Anagasta* spp.) attaining the mass of healthy fifth instars (the "critical" size), hosts attacked by *Hyposoter*, *Campoletis* and *Microplitis* spp. grow as large as L5 *Plodia* during their third (or even second) instar. This may explain why any parasitoid-induced changes in host growth and development (=regulation) by *Venturia* are more subtle than for these other parasitoids, which must arrest host growth at a much earlier stage in order to ensure their suitability. It would be interesting to investigate the development of *Venturia* in early instars of an extremely large host (e.g. *Galleria mellonella*) to determine if the parasitoid possesses the same regulatory capabilities as several other braconid and ichneumonid koinobionts.

A comparison of host suitability for idiobiont parasitoids (Tables 9.1 & 9.2) also reveals that, while suitability is generally positively correlated with host size at oviposition, older hosts are often of lower nutritional quality (see earlier in discussion). In gregarious parasitoids, suitability is even more difficult to determine than with solitary parasitoids for the simple reason that clutch size incorporates another element of complexity. For example, low numbers of parasitoids developing in large hosts suffer higher mortality from encapsulation (Kitano, 1986) which Godfray (1994) has suggested may result in the evolution of a minimum clutch size in some parasitoids. In large hosts, some gregarious parasitoids may also be unable

to consume and dispose of all host tissues prior to egression (Wylie, 1965) or are forced to overeat, and emerged deformed (Strand & Vinson, 1985). On the other hand, hosts that are heavily parasitized may be devoured before the parasitoids reach maturity (Wylie, 1967) or lead hosts to prematurely split open, leading to the death of the entire brood (Jackson, 1958). Gregarious koinobiont endoparasitoids frequently regulate the developmental programmes of their hosts through the injection of secretions from the reproductive tracts, including polydnaviruses, at oviposition (Dushay & Beckage, 1993). This could expand the suitable range of host instars available to the parasitoid, or allow the female wasp to increase her clutch size in response to extra host-feeding and growth mediated by the parasitoid (Slansky, 1978).

9.2.5 Life-history strategies and host range

Askew & Shaw (1986), comparing idiobiont and idiobiont strategies as a correlate of host range, found that idiobionts tend to be highly polyphagous, attacking hosts across a range of families within (and even between) orders, while koinobionts are more specialized because of their greater dependence on host physiology and development. Moreover, idiobionts are often highly synovigenic, produce small numbers of anhydropic eggs, and develop in concealed hosts. By contrast, koinobionts usually produce hydropic eggs, attack free-moving hosts and are typically endoparasitic (Gauld & Bolton, 1988).

Examining the acceptance and suitability of different hosts, Salt (1975) found that *Venturia* will readily attack alien hosts if deprived of a more suitable choice. Furthermore, although some hosts were extremely unsuitable for *Venturia*'s development, this did not prevent the wasps ovipositing in them. Analysis of the relationship between *Venturia* and *Plodia* (Chapter 3) revealed that the parasitoid is tolerant of differences in suitability between different host instars (L2 and L3-L5) and readily oviposited in L2 hosts. *Venturia* will not even hesitate to attack tiny first instars, which are mutilated by the insertion and removal of the parasitoid ovipositor (personal observations).

The production of offspring by parasitoids is determined by a correlation between host selection and host suitability (Mackauer, 1973). Fecundity is maximized if the female parasitoid is able to locate sufficient hosts of the highest quality, allowing her to reject less suitable host types. However, many koinobionts are endoparasitoids, and thus are often restricted in the number of host species from

which they can successfully develop due to the taxonomic specificity characteristic of host immunology (Askew & Shaw, 1986). Although *Venturia* is a polyphagous parasitoid, and can develop to adult from at least 14 host species (Salt, 1975), all of these are closely related pyralid moths. Salt (1938), suggested that host selection may play a greater role in determining a parasitoid's host range than suitability, however several studies have shown that female wasps frequently oviposit into less suitable (Hafez, 1961) or even unsuitable (Temerak, 1984) hosts. Some of these anomolies may be stress-induced laboratory artefacts (as Salt (1975) found with *Venturia*) or failures in the sensory system of the parasitoid (Mackauer, 1973). These factors, however, do not satisfactorily explain the absence of discrimination by many parasitoids between differently suitable instars of the same host species.

In the parasitic Hymenoptera, a functional division can be made between the adult parasitoid and immature stages. Adult wasps are adapted for efficient host selection (Vinson, 1985) whereas immature parasitoids are adapted for host exploitation (Slansky, 1986). Lawrence (1990) argued that koinobiont parasitoids are able to develop in a wider range of species and instars because of two proximate mechanisms that influence their growth (and survival). Flexibility in larval development and host regulation reduce selection pressures for a fixed maternal response at oviposition time (Cloutier *et al.*, 1991), allowing the female parasitoid to select a wider range of instars and species. Flexibility in host stage and species selection may also relax selection pressures on a parasitoid brought about by geographic differences in the encapsulation ability of certain hosts (Doutt, 1959; Blumberg & Luck, 1990). Moreover, flexibility in host selection provides an additional benefit in allowing new species, strains or stages to become suitable as hosts, thereby allowing a secondary extension of host range.

Hopper & King (1984), examining interactions between the braconid wasp *Microplitis croceipes* and its host *Heliothis* (= *Helicoverpa*) *zea* and *Heliothis virescens*, found that wasps preferred third instars most, correlating with development time which was most rapid from this instar. Parasitoids were reticent to attack and oviposit in fifth instar hosts, presumably due to aggressive host behaviour and the reduced physiological suitability of very large larvae (Jones & Lewis, 1971). Hopper & King (1984) suggest that the correlation between preference and development time in *Microplitis* may have arisen because the parasitoid has only recently specialized on these two hosts, and may still be adapting to the different instars. However, the authors stress that further investigations need to be carried out on other fitness-related components (fecundity, longevity) and on the mechanisms of

heritability of preference before such conclusions can be made on observed correlations.

9.3 Constraints on the adult parasitoid

9.3.1 Host behaviour

Once a suitable host is located, the female parasitoid is confronted with a sequence of decisions leading to acceptance of rejection of the host. It is frequently assumed that any decisions made by the female after host contact (whether to use the host for food or oviposition, what clutch to lay, should the host be ignored) are completely under the control of the parasitoid. When host suitability varies, optimal foraging models imply that parasitoid wasps should select hosts in ways that increase their individual fitness (Charnov & Skinner, 1985; Waage & Godfray, 1985; Charnov & Stephens, 1988; Mangel, 1989a,b). Implicit in this assumption is that wasps are able to assess any qualitative differences between hosts through antennation or ovipositor insertion. The models incorporate various parameters into their predictions, including host quality and handling time, although they frequently assume that handling time is a constraint imposed by certain physiological characteristics of the parasitoid, such as the size of the the egg and its effect on oviposition time, rather than the hosts active resistance to parasitism (van Alphen & Visser, 1990). The models also imply that host quality is correlated with host size at oviposition, because large hosts contain more resources than small hosts (9.2). Therefore, observed host preferences by parasitoids should reflect differences in host size, rather than any variable costs to the parasitoid when handling hosts that differ in size.

The profitability of attacking a host, however, may depend on other factors besides its nutritional suitability (Taylor, 1988). Several studies have shown that host preference and acceptance by parasitoids does not fit the predictions of these models, based on perceived differences in host suitability at oviposition (e.g. Campbell & Duffey, 1979; Temerak, 1984; Nechols & Kiguchi, 1985; Takagi, 1985; Taylor, 1988). Kouame & Mackauer (1991) found that, although the size of emerging adult *Ephedrus californicus* was smaller in starved hosts, parasitoids completed their development more rapidly and took less time to handle starved than well-fed hosts. *Acyrthosiphon pisum*, the host of *Ephedrus*, has several overlapping generations during the course of a season, allowing parasitoids to reproduce continually. Under these conditions, the authors suggest that development time has a potentially greater

influence than fecundity on fitness, based on their intrinsic rate of increase (Lewontin, 1985). Therefore, an argument can be made that starved aphids are more suitable than non-starved aphids (Kouame & Mackauer, 1991).

The host acceptance behaviour *Venturia* is clearly influenced by host behaviour after contact, supporting the results of several recent studies (see Gross, (1993) for a review). Host behaviour is expressed through host and stage-specific differences escape and defence reactions (Chapter 7). After antennation by *Venturia*, L5 *Plodia* and *Corcyra* exhibited differences in their tactical responses, with some behaviours more successful in avoiding parasitism than others. Each host species possessed an 'option set' consisting of about four or five different behavioural responses to parasitoid touch, including both passive defences ("catalepsis", rapid crawling) and aggressive defences (biting, rearing). *Corcyra* was generally more belligerent than *Plodia*, which usually remained still after parasitoid contact. Rotheray (1981), examining the different behaviours of syrphid fly larvae to the antennal examination by several ichneumonid wasps, found that the relative success or failure of hosts to defend themselves depended largely on the tactics they adopted. Most larvae remained still after contact, while contracting the anterior segments, while more active defences were only utilized if an attack persisted. Host movement was not necessary to elicit oviposition behaviour in the parasitoids, therefore most hosts should have exhibited aggressive defences at an earlier stage in the interaction. Rotheray (1981) suggested that two opposing selection pressures, one from predators which selects for frozen posture, and another from parasitoids selecting for vigorous activity, are responsible for the option sets of tactical responses exhibited by syrphid larvae. Similarly, the success of *Plodia* against parasitism by *Venturia* depended primarily on the tactic it adopted, with frozen posture considerably more successful than rapid crawling or wriggling (Chapter 7, Fig. 7.4).

The implications of host defensive behaviour has been ignored in most existing models of host acceptance (e.g. Charnov & Skinner, 1985; Charnov & Stephens, 1988; Mangel, 1987, 1989a,b). The vigorous defensive action exhibited by some hosts may actively discourage wasps from attacking a given instar or species when an alternative is present, or lead to the evolution of preference for a less suitable host. However, in some instances behavioural interactions between hosts and parasitoids may have fitness-related benefits for the parasitoid. During their fifth (final) larval instar, *Corcyra* are nearing the end of their 'window of suitability' for the development of *Venturia*. Parasitoids suffered high mortality in late L5 *Corcyra*, due mostly to encapsulation, although in very large hosts the parasitoid was occasionally

unable to consume all host tissues and became trapped within the larval integument of the host (see also Salt, 1964). The inability, or reluctance, of *Venturia* to parasitize large *Corcyra* larvae, because of their aggressive behaviour (Chapter 7, Fig. 7.3), prevents egg wastage, especially in situations where hosts of differential suitability occur together. Younger *Corcyra* larvae are much more suitable for parasitoid development, and *Venturia* attacked these larvae with the same vigour as L2-L5 *Plodia* instars (personal observations).

It is clear from many published studies, that behavioural interactions between hosts and their parasitoids influence the range of species and instars attacked, in addition to their suitability. Moreover, as discussed in Chapter 7, host defences select for parasitoid counter defences, including rapid oviposition, temporary host paralysis and holding the host physically still with the tarsi during oviposition (Gross, 1993). Observed patterns of parasitism do not necessarily indicate preference for a given host type in the strictest sense, instead they reflect the outcome of a series of behavioural interactions, shaped by evolution, in which the parasitoid must counter, or otherwise overcome the escape and defensive behaviour of the potential host. Undoubtedly, host behaviour represents a second important constraint on parasitoid fitness.

9.3.2 Resource variability and lifetime reproductive success

An understanding of parasitoid biology is important, because many species are major biological control agents, attacking serious pests of agriculture and forestry (Huffaker *et al.*, 1971). Of particular importance is to determine the abilities of parasitoids to increase in number, and to find and parasitize hosts which influences their population dynamics (Waage & Hassell, 1982; Mackauer, 1983). The response of parasitoids to temporal variations in host availability, or to differences in host density, is considered to be an important pre-requisite for the stability of the host-parasitoid interaction, and thus the success of biological control programmes (Hassell & Waage, 1984). Moreover, if estimates of survival and fecundity rates of parasitoids can be determined under natural conditions, the efficiency of parasitoids as biological control agents can be measured more accurately . Therefore, it is hardly surprising that many workers have studied the lifetime reproductive success of potential biological control agents in the laboratory, where the insects can be monitored closely (Godfray, 1994).

9.3.3 Life-history trade-offs and the influence of constraints

One of the most interesting, yet least studied aspects of parasitoid biology concerns the evolution of life histories, and how they influence the lifetime reproductive success of parasitoids under different constraints. Constraints are based on decision variables, and their relation to a currency, for instance energy reserves (Lessells, 1991). Optimality models typically incorporate two kinds of constraint: the relationship between fitness and the value of a trait, or character, and the relationship between different traits of the same individual that result from variable resource allocation between these traits, or what is commonly referred to as a trade-off (Stearns, 1989). As Lessells (1991) points out, many problems arise when measuring constraints, and their influence on optimality models. Constraints have frequently been measured by comparing different characters, such as longevity and fecundity, and plotting them against each other. The hypothesis of trade-offs between life-history characters implies that the relationship between different characters should be negative. Relationships between measured phenotypic values are commonly called phenotypic correlations, and, in spite of the predicted negative correlation between traits, the opposite is often found to occur (Partridge, 1989). For example, the phenotypic correlation between longevity and fecundity in the egg parasitoid, *Trichogramma minutum*, is positive (Bai & Smith, 1993).

Lessells (1991) stresses that two conditions reduce the accuracy of using phenotypic correlations to measure trade-offs: (i) a lack of non-adaptive variation in allocation, and (ii) adaptive variation in allocation (see also Reznick, (1985), and Stearns, (1989)). In the former, the measurement of trade-off curves requires variation in character values. However, resources may not always be allocated optimally, and, when this occurs within all individuals of a population, there would be no variation ('yardstick') against which trade-offs could accurately be measured. On the other hand, when individuals have access to different amounts of resources vital for various metabolic functions, the optimal allocation may also vary. Natural selection should thus favour a genetically determined allocation rule, specifying how variable resources should be allocated (Stearns, 1989). When food is a limiting resource, it may be allocated for reproduction or longevity (germinal or somatic tissue), but not to both competing fitness functions. However, an increase in food availability will reveal a positive phenotypic correlation, because the organism may choose (or be able to) invest the additional resources to both, as opposed to one of these traits.

Many studies of lifetime reproductive success in parasitoids have failed to establish a negative correlation between fecundity and survival (but see Orr & Boethel, 1990), because a source of adult nutrition (honey, or sugar solution) has been constantly provided and the insects are thus able to replenish energy resources for both longevity and fecundity faster than it is being depleted when foraging (van Noordwijk & de Jong, 1986; Bai & Smith, 1993). Phenotypic correlation curves are therefore not trade-offs because phenotypes are not randomly distributed in regard to environment or resources (Lessells, 1991). However, random allocation can be achieved by manipulating certain features of the environment, such as host density or food availability (Reznick, 1985). Simple experimental manipulation of food access to *Venturia* revealed a trade-off between longevity and fecundity, because the parasitoids were unable to acquire and retain enough metabolic energy when starved or given limited access to food, and thus died before their egg complements were depleted (Chapter 8). In response to variable host availability, a further trade-off was demonstrated between early and late fecundity. Constantly-fed wasps adjusted their fecundity schedule in accordance with temporal host access, such that reproduction was extended to a later period of adult life when hosts were available for the shortest period daily (30 minutes; Chapter 8, Figs. 8.7a-c). Parasitoids constantly exposed to hosts and food often depleted their egg complements before their 10th day of adult life (Fig. 8.7c), showing that, given the opportunity, *Venturia* exploits hosts as much as possible early in life.

Although the predicted correlation between reproduction and survival did not support the trade-off hypothesis (in line with Lessell's (1991) argument, above), I found that there was a correlation between adult wasp size and longevity and fecundity in *Venturia*. However, several other studies have failed to establish a size-longevity/fecundity relationship in parasitic wasps (reviewed by Visser, 1994). The wealth of accumulated knowledge about the biology of *Venturia*, and ease with which it can be cultured in the laboratory, make it possible to understand processes that are presently confounded in large or less well-studied animals. On the other hand, the biology of *Venturia* under natural conditions, like that of many other parasitoids, is virtually unknown, largely due to their small size and vagility, which makes marking and monitoring the movement of individual wasps at best difficult, and at worst impossible (therefore, the benefits of large size for *Venturia* are less clear in the field). Size-related effects on fitness have frequently been measured in the laboratory only through longevity and fecundity, thus ignoring other important factors that may occur in nature. For example, fitness may be influenced by more than just simple physiological costs associated with foraging (e.g. probing) independently on patches.

Hughes *et al.*(1994a), found that parasitoids fight for access to oviposition sites. If large wasps are able to competitively displace smaller wasps when foraging together, then they will benefit in having immediate access to hosts, whereas smaller conspecifics may have to disperse and locate hosts elsewhere. Therefore, body size may confer other advantages to the reproductive success of parasitoids, other than simply through egg complements, or the possession of greater metabolic storage sites (hence influencing longevity). In my experiments, intraspecific interactions were not included because wasps were reared alone. Moreover, the ovipositor lengths of large wasps is proportionately greater than on small wasps, potentially allowing larger wasps to probe deeper into host-containing food medium. This was not a factor in these experiments, because the maximum patch depth was standardized (no deeper than 5mm) allowing all parasitoids, irrespective of size, the same access to hosts. Under natural conditions, parasitoids may also disperse when suitable hosts are in short supply, or after bouts of oviposition (Mackauer, 1982, 1983), a factor that is ignored in most empirical investigations for the simple reason that the insects are confined in containers. This probably reduces any costs associated with dispersal, which may be size-dependent (but see Visser, 1994). On the other hand, smaller wasps may be able to locate, handle and thus parasitize early-instar hosts more effectively than larger wasps (personal observations for experiments in Chapter 3). This is especially important when patches are located containing only early-instar hosts, or where the parasitoid:host ratio is high and competition for host exploitation is high (one of the possible factors for the evolution of koinobiosis). In my experiments, only late L5 hosts were used, thus removing another potentially important constraint.

Partridge (1988) stressed that, in nature, there are a number of proximate causes for variation in reproductive success. For example, one of the major drawbacks in using organisms that do not show any parental care for experimentation is that it is virtually impossible to determine pre-adult mortality in the field. Several important factors influencing pre-adult mortality, hence the reproductive success of *Venturia*, are the effects of superparasitism (both due to larval fighting and on host survival), intensive host competition for food, thus leading to cannibalism or host starvation, and encapsulation. Disentangling these processes is difficult, even in the laboratory. Therefore, host mortality may increase disproportionately in heavily exploited patches, because superparasitism is higher (as may have been the case in the constant host access treatments, as shown by the reduction in total insect survival). Furthermore, most adult parasitoid mortality was presumably due to starvation (in the 24.48h and starvation treatments) and old age (in the 24h food

access treatment). In the field, other factors may be equally important contributors to adult mortality, including predation and localized fluctuations in weather conditions.

In spite of the vast array of potential (and inescapable) shortcomings in an investigation of this kind, the manipulation of parasitoid access to food and hosts did shed considerable light on the nature of trade-offs and their effect on the reproductive success of *Venturia*. It is perhaps of equal importance that some of the results support the contention of Stearns (1989) and Lessells (1991), that phenotypic correlations should not be used to measure trade-offs. Further studies are definitely required, where parasitoid reproductive success is measured under a variety of additional constraints, including more widely separated host patches, by integrating different host stages into the design and allowing parasitoids to forage in groups, rather than as individuals.

Table 9.1 Host suitability and preference for a number of solitary idiobiont and koinobiont parasitoids.

Parasitoid species	Family	Koino/ Idiobiont	Host species	Host stages attacked	Host preference/ suitability	Reference
Opius dissitus	Braconidae	Koinobiont	*Liriomyza sativae*	L1-L3	L2/3 more suitable than L1	Pettit & Wietlisbach (1993)
Opius concolor	Braconidae	Koinobiont	*Dacus oleae*	6-9 day old final instars	wasp size unaffected by host age	Avilla & Albajes, (1984)
Leiophron uniformis	Braconidae	Koinobiont	*Lygus hesperus* *Lygus lineolaris*	nymphs	*L. hesperus* more suitable; neither host preferred	DeBolt, (1989)
Biosteres longicaudatus	Braconidae	Koinobont	*Anastrapha suspensa*	4-7 day old larvae	5-6 day old larvae most suitable	Lawrence *et al.*, 1976
Cotesia urabae	Braconidae	Koinobiont	*Uraba lugens*	L1-L3	Faster development in L3; L1-L2 preferred	Allen & Keller, (1991)
Cotesis kazak	Braconidae	Koinobiont	*Heliothis virescens*	L1-L4	L1-L3 preferred; L2-L3 most suitable	Tillman & Powell, (1989)
Cotesia rubecula	Braconidae	Koinobiont	*Pieris rapae*	all instars	small hosts (?)	Nealis, (1986)
Alysia manducator	Braconidae	Koinobiont	*Calliphora vicina*	1-8 day old larvae	2-3 day old larvae most suitable	Reznik *et al.*, (1992).
Diolcogaster facetosa	Braconidae	Koinobiont	*Plathypena scabra*	L1-L5	all instars suitable	Yeargan & Braman, (1986)
Cardiochiles nigriceps	Braconidae	Koinobiont	4 *Heliothis* spp.	L1-L5	*Heliothis virescens* and early instars more suitable	Lewis & Vinson, (1971)

Cardiochiles nigriceps	Braconidae	Koinobiont	*Heliothis virescens*	L3	development time longer, survival lower, as egg numbers per host increase	Vinson & Sroka, (1978)
Microplitis mediator	Braconidae	Koinobiont	*Leucania separata*	L1-L4	L1-L3 equally suitable	Tanaka *et al.*, (1984)
Microplitis croceipes	Braconidae	Koinobiont	*Helicoverpa zea*	L1-L5	survival highest in L1-L4	Lewis, (1970)
Microplitis croceipes	Braconidae	Koinobiont	*Helicoverpa zea*	L1-L5	development. time shortest in L2-L3	Jones & Lewis, (1971)
Microplitis croceipes	Braconidae	Koinobiont	*Helicoverpa zea; Heliothis virescens*	L3	higher survival in *H. zea*, and hosts reared on cotton	Mueller, (1983)
Microplitis croceipes	Braconidae	Koinobiont	*Heliothis virescens*	L1-L5	dvt. time shortest in L2-L3;	Hopper (1986)
Microplitis croceipes	Braconidae	Koinobiont	*Heliothis virescens*	L1-L5	L3 preferred survival highest L2-L4; fastest development,	Tillman & Powell, (1989)
Microplitis croceipes	Braconidae	Koinobiont	*Helicoverpa zea*	L2	L3 longer development, smaller size in super-parasitized hosts	Eller *et al.*, (1990)
Microplitis demolitor	Braconidae	Koinobiont	*Heliothis virescens*	L2-L3	larger wasps L3; dvt.time faster L2	Strand *et al.*, (1988)
Microplitis demolitor	Braconidae	Koinobiont	*Heliothis virescens*	L1-L5	survival highest L1; fastest dvt. L2; L1-L3 preferred	Tillman & Powell, (1989)
Microctonus vittatae	Braconidae	Koinobiont	*Phyllotreta cruciferae*	adult	dvt.time longer in super-parasitized hosts	Wylie, (1983)
Meterorus trachynotus	Braconidae	Koinobiont	*Choristoneura fumiferana*	L2-L6	L6 more suitable than L2-L5	Hebert & Cloutier (1990)
Chelonus curvimaculatus	Braconidae	Koinobiont	*Pectinophora gossypiella; Phthorimaea operculella*	egg-larval	greater longevity, more fecund wasps from *Pectin-ophora*	Legner & Thompson, (1977)
Asobara tabida	Braconidae	Koinobiont	*Drosophila melano-gaster*	L1-L3	older hosts unsuitable; no instar preference	van Alphen & Drijver, (1982)
Bathy-plectes curculionis	Ichneu-monidae	Koinobiont	*Hypera postica*	L1-L4	L1-L3 most suitable; no preference L1-L4	Duodu & Davis (1974)
Diadegma armillata	Ichneu-monidae	Koinobiont	*Yponomeuta spp.*	L1-L5	suitability varied with host species attacked	Dijkerman (1990)

Diadegma trichoptilus	Ichneumonidae	Koinobiont	*Exalastis atomosa*	1-10 day old larvae	2-3 day old larvae most suitable	Sathe & Nikam (1985)
Diadegma chrysostictos	Ichneumonidae	Koinobiont	*Anagasta kuehniella*	medium & large larvae	older larvae more suitable (?)	Horstmann & Shaw, (1984)
Campoletis sonorensis	Ichneumonidae	Koinobiont	*Heliothis virescens*	3-4 day old larvae	parasitoids perish in larvae pre-infected with NPV	Irabagon & Brooks, (1974)
Campoletis sonorensis	Ichneumonidae	Koinobiont	*Heliothis virescens*	L1-L4	largest wasps from L3; L1-L2 preferred	Gunasena *et al.*, (1989); Schmidt, (1974)
Campoletis sonorensis	Ichneumonidae	Koinobiont	23 spp.	1-8 day old larvae	2-4 day old larvae most suitable; 5 spp. preferred	Lindgren *et al.*, (1970)
Campoletis sonorensis	Ichneumonidae	Koinobiont	*Heliothis virescens*	L1-L4 (?)	development time increased in starved L4 hosts	Dover & Vinson, (1990)
Campoletis annulata	Ichneumonidae	Koinobiont	*Agrotis segetum*	L2	parasitoid mortality increases with dosage of granulosis virus	Santiago-Alvarez & Caballero, (1990)
Venturia canescens	Ichneumonidae	Koinobiont	14 spp. pyralid moths	various sizes	4 host spp. most suitable	Salt, (1975)
Hyposoter didymator	Ichneumonidae	Koinobiont	*Heliothis virescens*	L1-L4	L1-L3 most suitable	Tillman & Powell, (1989)
Hyposoter exiguae	Ichneumonidae	Koinobiont	*Peridroma saucia*	L1-L3	develops faster in L2	Puttler, (1961)
Hyposoter exiguae	Ichneumonidae	Koinobiont	*Trichoplusia ni*	L3	very little effect of NPV except wasp survival varied with time of dosage; no preference shown.	Beegle & Oatman, (1975)
Hyposoter exiguae	Ichneumonidae	Koinobiont	*Trichoplusia ni*	L1-L5	larger wasps, L3 and L4; lower mortality L1 L1-L2 preferred	Smilowitz & Iwantsch, (1975)
Hyposoter exiguae	Ichneumonidae	Koinobiont	*Trichoplusia ni*	L2 & L4	larger wasps. L4; faster growth L2	Jowyk & Smilowitz, (1978)
Hyposoter exiguae	Ichneumonidae	Koinobiont	*Helicoverpa zea*	L1-L4	L3-L4, although L1-L2 preferred	Campbell & Duffey, (1979)
Hyposoter exiguae	Ichneumonidae	Koinobont	*Manduca sexta*	L1-L3	L1-L2 more suitable and preferred	Beckage & Templeton, (1985)
Hyposoter exiguae	Ichneumonidae	Koinobiont	*Spodoptera exigua*	late L2	host must exceed 20 mg for parasitoid survival	Bloem & Duffey, (1990)
Trathala flavoorbitalis	Ichneumonidae	Koinobiont	*Leucinoides orbinalis*	L1-L5	L3-L4 most suitable; L1 unsuitable	Sandanayake & Edirisinghe (1992)
Temelucha sp.	Ichneumonidae	Koinobont	*Pthorimea operculella*	1-9 day old larvae	(?)	Oatman & Platner, (1974)

Phaeogenes cynarae	Ichneumonidae	Idiobiont (?)	*Platyptila carduidactyla*	pre-pupae & pupae	pre-pupae (?)	Bragg (1974)
Trychosis cyperia	Ichneumonidae	Idiobiont	*Misumena vatia*	egg masses	larger females only on larger hosts	Morse (1994)
Pleolophus indistinctus	Ichneumonidae	Idiobiont	*Neodiprion swaneii*	pupae	larger pupae (?)	Price, (1970)
Exenterus amicorius	Ichneumonidae	Koinobiont	*Neodiprion swaneii*	pre-spinning eonymphs and pre-pupae	eonymphs preferred	McCleod, (1972)
Ichneumon promissorius	Ichneumonidae	Idiobiont	*Helicoverpa zea*	pupae	development time increases with host age and size	Carpenter *et al.*, (1994)
Pimpla examinator	Ichneumonidae	Idiobiont	3 host spp.	pupae	larger wasps emerge from larger hosts	Jackson, (1937)
Pimpla turionellae	Ichneumonidae	Idiobiont	9 host spp.	pupae	larger wasps on larger hosts; dvt. longer on larger hosts	Arthur & Wylie, (1959)
Pimpla turionellae	Ichneumonidae	Idiobiont	5 host spp.	pre-pupae and pupae	larger pupae produce larger wasps; older pupae less suitable	Sandlan, (1982)
Leptopilina boulardi	Eucoilidae	Koinobiont	*Drosophila melanogaster*	larvae	survival higher, faster development, smaller wasps in starved hosts	Wajnberg *et al.*, (1985)
Leptopilina heterotoma	Eucoilidae	Koinobiont	*Drosophila* spp.	larvae	acceptance varied with suitability	Driessen *et al.*, (1991)
Leptopilina heterotoma	Eucoilidae	Koinobiont	*Drosophila melanogaster*	larvae	higher survival in starved hosts	Bouletreau, (1986)
Aphidius smithii	Aphidiidae	Koinobiont	*Acyrthosiphon pisum*	L1-L4	most rapid growth in L2; younger hosts preferred	Mackauer, (1973)
Aphidius nigripes	Aphidiidae	Koinobiont	*Macrosiphum euphorbia*	L1-L4	L1-L4 equally suitable	Cloutier *et al.*, (1981)
Aphidius sonchi	Aphidiidae	Koinobiont	*Hyperomyzus lactucae*	L1-L3	L3 wasps largest and preferred	Liu & Hughes, (1984); Liu, (1985)
Aphidius ervi	Aphidiidae	Koinobiont	*Acyrthosiphon pisum*	L1-L4	most rapid growth in L2; largest wasps L3	Sequeira & Mackauer, (1992a, b)
Ephedrus californicus	Aphidiidae	Koinobiont	*Acyrthosiphon pisum*	L1-L4	larger wasps L3, L4	Sequeira & Mackauer (1993)
Aphelinus semiflavus	Aphelinidae	Koinobiont (?)	*Therioaphis trifolli*	L1-adult	L1-L2 preferred	Schlinger & Hall, (1959)
Aphelinus abdomenalis	Aphelinidae	Koinobiont (?)	*Myzys ascalonicus*	L1-adult	L3 preferred	Wahab, (1985)
Aphytis lingnanensis	Aphelinidae	Idiobiont	*Aonidiella aurantii*	L2-L3	larger wasps L3	Opp & Luck, (1985)
Aphytis melinus	Aphelinidae	Idiobiont	*Aonidiella aurantii*	L2-L3	L2 preferred	Opp & Luck, (1985)
Aphytis mytilaspidis	Aphelinidae	Idiobiont	scale insects (?)	?	accepts unsuitable hosts if preferred hosts unavailable	Baker, (1976)

Telenomus ashmeidi	Scelionidae	Idiobiont	3 hosts (pentatomid bugs)	eggs	largest wasps from largest hosts	Morrill (1907)
Edovum puttleri	Eulophidae	Idiobiont	2 *Leptinotarsa* spp.	eggs	larger wasps from *L. texana* (larger host)	Corrigan & Lashomb, (1990)
Tetrastichus israeli	Eulophidae	Idiobiont	8 host spp.	eggs	largest, most fecund wasps from largest host spp.	Nadarajan & Jaranyi, (1975)
Chrysocharis laricinellae	Eulophidae	Idiobiont	*Coleophora laricella*	?-L4	early instars unsuitable; L4 preferred	Quednau (1967)
Pnigalio flavipes	Eulophidae	Idiobiont (?)	*Phyllonorycter elmaella*	L1-L5	prefers to oviposit on L4-L5; host-feed on L1-L2	Barrett & Brunner, (1990)
Anagyrus mutans	Mymaridae	Idiobiont	*Cicadella viridus*; *Dicranoptis lameta*	eggs	larger, more fecund wasps from *C. viridis*	Moratorio (1987)
Epidinocarsis lopezi	Encyrtidae	Idiobiont	*Phenacoccus manihoti*	L2-L4	L3-L4 preferred for oviposition; L2 for host-feeding	Neuenschwander & Madojemu (1986)
Metaphycus spp.	Encyrtidae	Idiobiont	*Coccus hesperidium*	all instars	lower survival in later instars	Blumberg & DeBach, (1981)
Antrocephalus hakonensis	Chalcididae	Idiobiont	*Opisina arenosella*	pupae	female-biased sex ratio on larger hosts	Mohandas & Abdurahiman, (1992)
Brachymeria intermedia	Chalcididae	Idiobiont	*Galleria mellonella; Lymantria dispar*	pupae	larger wasps from *L. dispar.*	Rotheray *et al.*, (1984)
Trichogramma evanescens	Trichogrammatidae	Idiobiont	3 host spp.	eggs	larger wasps from largest host	Salt, (1941)
Pachycrepoideus vindemiae	Pteromalidae	Idiobiont	*Drosophila* sp.	pupae	reluctant to hyperparasitize pupae with mature larvae	van Alphen & Thunnissen (1983)
Lixophaga diatraeae	Tachinidae	Koinobiont	*Diatraea saccharalis*	L1-pupae	L4-L5 most suitable & preferred	Miles & King, (1975)
Compsilura concinnata	Tachinidae	Koinobiont	*Lymantria dispar*	L2-L5	more rapid development L5; size unaffected by instar	Weseloh, (1984)
Wintheria fumariferanae	Tachinidae	Koinobiont	*Choristoneura fumiferana*	L5-L6	L6 preferred & more suitable	Hebert & Cloutier, (1990)
Archytas marmoratus	Tachinidae (?)	Koinobiont	*Galleria mellonella*	all instars (?)	larger flies emerge from hosts > 200mg	Gross,. (1994)

Table 9.2 Host suitability and preference for a number of gregarious idiobiont and koinobiont parasitoids.

Parasitoid species	Family	Koinobiont/ Idiobiont	Host species	Host stages attacked	Host preference/ suitability	Reference
Apanteles rufricus	Braconidae	Koinobiont	*Pseudoletia separata*	L2-L4	L2-L4 equally suitable; L2 preferred	Sato *et al.*, (1986)
Apanteles rufricus	Braconidae	Koinobiont	*Leucania separata*	L2-L4	L2 preferred	Tagawa *et al.*, (1982)
Apanteles kariyai	Braconidae	Koinobiont	*Pseudoletia sparata*	L3-L6	fastest dvt. L6; larger hosts preferred	Sato *et al.*, (1986)
Apanteles glomeratus	Braconidae	Koinobiont	*Pieris rapae*	all instars (?)	higher encapsulation of small clutches	Kitano, (1986)
Apanteles glomeratus	Braconidae	Koinobiont	*Pieris rapae*	L1-L4	L3 most suitable	Sato, (1980)
Apanteles glomeratus	Braconidae	Koinobiont	*Pieris rapae*	?	greater encapsulation in hosts with small clutches	Wago & Kitano, (1985)
Apanteles congregatus	Braconidae	Koinobiont	*Manduca sexta*	L4-L6	larger clutches in later instars; fastest development L6	Beckage & Riddiford, (1983)
Apanteles militaris	Braconidae	Koinobiont	*Pseudaletia unipuncta*	L3	larvae killed by NPV	Hotchkin & Kaya, (1983)
Apanteles telengai	Braconidae	Koinobiont	*Agrostis segetum*	L2	wasp mortality increases with dosage of granulosis virus	Santiago-Alvarez & Caballero (1990)
Bracon hebetor	Braconidae	Idiobiont	*Anagasta kuehniella*; *Plodia interpunctella*	L4-L5	larger clutches, *A. kuehniella; P. interpunctella* preferred	Taylor, (1988)
Trichogramma minutum	Trichogram-matidae	Idiobiont	3 host spp.	eggs	more fecund, lived longer reared on *Anagasta kuehniella*	Corrigan & Laing, (1993)
Trichogramma minutum	Trichogram-matidae	Idiobiont	*Trichoplusia ni*; *Sitrotega cerealla*	eggs	larger wasps, more progeny from *Trichoplusia ni*	Marston & Ertle, (1973)
Trichogramma chelonus	Trichogram-matidae	Idiobiont	5 host spp.	eggs	differential suitability	Navajan *et al.*, (1981)
Trichogramma pretiosuma	Trichogram-matidae	Idiobiont	artificial medium	(as left)	overfed wasp larvae emerged as deformed adults	Strand & Vinson, (1985).
Trichogramma pretiosum	Trichogram-matidae	Idiobiont	5 host spp.	eggs	fecundity, longevity varies with host	Bai *et al.*, (1992)
Nasonia vitripennis	Pteromalidae	Idiobiont	*Musca domestica*	pupae	more wasps produced on older hosts	Wylie, (1964)

Nasonia vitripennis	Pteromalidae	Idiobiont	*Musca domestica*; *Phaenica sericata*	pupae	live longer, higher fecundity from *P. sericata*	Smith & Pimentel, (1969)
Spalangia cameroni	Pteromalidae	Idiobiont	*Musca domestica*	pupae	larger wasps, female -biased sex ratio in larger hosts	King, (1988)
Pteromalus puparum	Pteromalidae	Idiobiont	*Papilio xuthus*	pupae	larger wasps live longer, have higher egg loads	Takagi, (1985)
Wintheria manducae	Tachinidae	Koinobiont	*Manduca sexta*	all instars (?)	high mortality in L6 hosts with small clutches	DeLoach & Rabb, (1972)

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