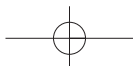
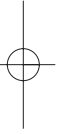
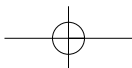
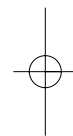
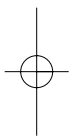
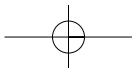




Part 1

Current issues in behavioral ecology of insect parasitoids





1

Optimal foraging behavior and efficient biological control methods

Nick J. Mills and Éric Wajnberg

Abstract

Insect parasitoids have been used for the biological control of insect pests through classical importations for the control of invasive phytophagous species, through seasonal or inundative releases for short-term suppression of indigenous or invasive pests, and through conservation of parasitoid activity by the provisioning of resource subsidies and alteration of management practises. In all cases, success in the suppression of a pest is dependent upon the behavioral decisions made by the parasitoid in searching for and parasitizing hosts. For example, in the case of classical biological control, patch choice decisions that maximize parasitoid fitness will tend to increase its regional impact, leading to greater suppression of the pest and success in biological control. In contrast, for augmentative biological control, the goal is to provide local pest suppression and behavior that maximizes fitness might, for example, lead parasitoids to abandon local patches of their hosts before the pest has been suppressed to the desired level. Thus, the behavioral ecology of insect parasitoids is central to the successful implementation of biological control programs.

We explore how optimal foraging effects the suppression of global pest densities in a metapopulation context and to what extent the physiological condition and behavioral decisions of foraging parasitoids are likely to influence establishment and impact in classical biological control. In the case of inundative biological control, we discuss the trade-off between optimal foraging behavior and the level of pest suppression at a local scale and consider the use of chemical attractants and arrestants to increase parasitoid activity and patch time allocation. We also discuss the influence of host size and quality, and sex ratio (*Wolbachia* infection) on parasitoid mass rearing. Finally, the influence of nectar subsidies on parasitoid foraging behavior and host suppression is considered in the context of developing more efficient methods for conservation biological control.

1.1 Introduction

Biological control represents the action of living natural enemies in suppressing the abundance or activity of pests. As a naturally occurring ecosystem service, globally, biological control has been loosely valued at \$400 billion per year (Costanza et al. 1997); while a more conservative estimate of \$4.5 billion per year has been attributed to the services provided by indigenous predators and parasitoids of native agricultural pests in the USA (Losey & Vaughan 2006). Although natural enemies include predators (that must consume many prey individuals to complete their development), pathogens (bacteria, fungi, and viruses), parasites (soil-inhabiting entomopathogenic nematodes), and antagonists (competitors) in addition to parasitoids, the latter are the most important group in the context of biological control of insect pests.

There are three broad categories that describe how parasitoids can be used in biological control: importation, augmentation, and conservation. Importation or classical biological control makes use of host-specific parasitoids imported from the region of origin of invasive pests and has received the greatest amount of attention (Mills 2000, Hoddle 2004). The introduction of exotic parasitoids for the control of invasive pests continues to fascinate ecologists, fuel theoretical models of host–parasitoid interactions, and yet defy a simple and unified mechanistic explanation. Since the initial success of the introduction of the vedalia beetle (*Rodolia cardinalis*) from Australia for the control of cottony cushion scale (*Icerya purchasi*) in California in 1886 (Caltagirone & Doust 1989), biological control practitioners have continued to implement biological control as an effective strategy for the management of invasive insect pests, while ecologists have struggled to find a consistent explanation for the success or failure of these programmes (Murdoch et al. 2003).

When parasitoids of invasive or indigenous pests are unable to persist year round or to increase in numbers quickly enough to suppress pest damage, augmentative biological control, involving the periodic release of insectary-produced parasitoids, can be effective. Augmentation has been used most effectively in protected or semi-protected environments such as glasshouses and cattle or poultry houses (Daane et al. 2002, Heinz et al. 2004), with rather less success under open field conditions (Collier & Van Steenwyk 2004). Augmentative biological control can be approached through inoculation or inundation. Inoculation of small numbers of parasitoids can be used to improve colonization at critical periods for season-long pest suppression, as practised under certain conditions for the control of greenhouse whitefly (*Trialeurodes vaporariorum*) on tomato by *Encarsia formosa* (Hoddle et al. 1998). Alternatively, inundation of large numbers of parasitoids can be used for immediate suppression, but often without a lasting impact, as used for control of house flies (*Musca domestica*) by *Spalangia cameroni* (Skovgard & Nachman 2004). In contrast, conservation biological control focuses on the enhancement of both introduced and indigenous parasitoid populations through provisioning of limiting resources or alteration of crop production practices. Parasitoids are often limited by the availability of essential resources such as nectar or overwintering sites and are excluded from crops by use of incompatible pesticides. Thus, success in conservation biological control can result, for example, from perimeter planting of annual buckwheat as a nectar subsidy for the aphid parasitoid *Aphidius rhopalosiphi* (Tylianakis et al. 2004) or from removal of incompatible insecticides as demonstrated in the effective suppression of the brown planthopper in rice in Indonesia (Kenmore 1996).

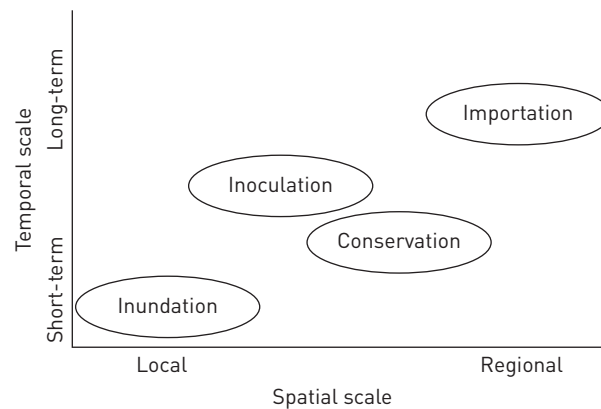


Fig. 1.1 A schematic representation of the four main approaches to applied biological control to reflect the differential spatial and temporal scales of the processes involved.

For each of these categories, success in the suppression of an insect pest is dependent upon the behavioral decisions made by parasitoids in both searching for and parasitizing hosts. Thus, the behavioral ecology of insect parasitoids is central to the successful implementation of biological control programs. However, linkages between variation in parasitoid behavior and its consequences for population dynamics remain few and have proved to be an elusive and difficult goal (Ives 1995, Vet 2001). In the context of parasitoid foraging behavior, there are important distinctions between the different approaches to applied biological control based on both the spatial and temporal scale of the processes involved (Fig. 1.1). The aim of importation differs from all other categories of biological control in that success requires regional suppression of a pest population, extending in some cases to a substantial part of whole continents, as in the successful control of the cassava mealybug through importation of *Anagyrus lopezi* (Neuenschwander 2003). In addition, as relatively small numbers of parasitoids are introduced into spatially and numerically extensive populations of the pest, success in importation biological control takes longer to achieve and may span several years. Bellows (2001) estimated that the average time taken to achieve suppression of an invasive pest through importation of parasitoids is six to 13 generations, but complete suppression on a large regional scale can take up to 12 years as in the case of the cassava mealybug (Neuenschwander 2003). In contrast, inundation, as an approach to biological control, is used for immediate impact, within a single generation of a pest and tends to be confined to a very local scale such as an individual field or orchard. Although the implementation of inundation can extend to large areas, such as releases of *Trichogramma brassicae* in 2002 on 77,000 hectares for suppression of European corn borer in France (Wajnberg & Hassan 1994), the process itself still operates at a very local scale. Intermediate between importation and inundation, both in terms of spatial and temporal scale, are inoculation and conservation. In both cases, the aim is generally to provide season-long control and the hope is that the impact of the intervention might extend on a spatial scale beyond the points of implementation. Inoculation is based on the notion that released parasitoids will continue to affect the pest population over several generations, as in the early season releases of *E. formosa* for control of greenhouse whitefly

(Hoddle et al. 1998) and so can be considered to operate at a slightly greater temporal scale. In contrast, conservation, through enhancement of the suitability of the environment for parasitoids, might be considered to operate on a slightly broader spatial scale as in the provision of nectar subsidies, where parasitoids able to use such subsidies have greater mobility and can be found more distantly from the source (Heimpel & Jervis 2005).

In this chapter, we explore how the distinct spatial and temporal scales of the four main approaches to applied biological control are influenced by different aspects of parasitoid foraging behavior. In considering each of the approaches, we begin with a brief discussion of the pertinent foraging decisions and subsequently consider practical applications and future opportunities. First, we consider optimal patch choice and the extent to which it might affect the success of importation biological control. In the context of augmentative biological control, we discuss the trade-off between optimal foraging behavior and level of pest suppression at a local scale and consider the use of infochemicals to increase patch residence time (see also Chapter 5 by Hilker and McNeill). We also discuss the influence of host size and quality, and sex ratio (*Wolbachia* infection) (see also Chapter 12 by Ode and Hardy) on the efficiency of parasitoid mass rearing. Finally, we focus on foraging decisions that affect current versus future reproduction in the context of nectar subsidies as a component of conservation biological control.

1.2 Importation biological control

For importation biological control, host-specific parasitoids are imported from the region of origin of an exotic invasive pest. The goal of this approach is for the introduced parasitoid to become established throughout the region colonized by the invasive pest and to provide long-term suppression at low pest densities. The introduction of *Aphytis paramaculicornis* and *Coccophagoides utilis* into California in the 1950s to control olive scale (*Parlatoria oleae*) provides a stellar example with olive scale remaining a scarce insect in California some 50 years after the initial parasitoid introductions (Huffaker et al. 1986, Rochat & Gutierrez 2001). While there has been a series of dramatic successes against invasive insect pests in many different regions of the world, there remains an even greater list of failures in which the introduced parasitoids either did not become established in the target region or, if they did so, there was no notable impact on the abundance of the target pest. Using the historical record of classical biological control introductions worldwide, only 38% of 1450 unique pest-introduced parasitoid combinations have resulted in establishment and 44% of 551 established parasitoids have provided partial to complete control of the pest, corresponding to a 17% overall rate of success (Mills 1994, 2000).

An important question that arises from the historical record is to what extent the overall rate of success in classical biological control can be improved. In this context, as noted by Mills (2000), it is important to distinguish between establishment, i.e. the colonization of a new environment by an introduced parasitoid and impact, and the reduction of pest population abundance by the action of an established parasitoid. From studies of invasive species, it is apparent that there are no widely applicable characteristics of successful invaders (Mack et al. 2000, Sakai et al. 2001), with establishment being determined by the ability of a small founder population to survive and reproduce in a novel environment. Thus, the establishment phase of importation biological control seems less likely to be influenced

by foraging decisions than by more general population processes, such as Allee effects, genetic bottlenecks, and demographic stochasticity, and by the favorability of the environment, as determined by species richness, disturbance, and environmental stochasticity. Nonetheless, Mills (2000) suggested that the success of parasitoid establishment could be enhanced through manipulation of the holding conditions to maximize the fitness of parasitoids destined for field release.

In contrast, pest suppression results from the impact of an exotic parasitoid that does become established in a favorable environment and this process typically occurs over a period of 6 to 13 generations (Bellows 2001) and extends over a broad geographic scale (Fig. 1.1). Taking this into account, it is not unreasonable to assume that larger-scale processes will dominate smaller-scale processes and there is some supporting evidence for this assumption from field studies of parasitoids (Thies et al. 2003, Cronin 2004). In addition, there is growing evidence that parasitoids can assess variation in host densities among patches from a distance using volatile infochemical signals (Geervliet et al. 1998, Vet 2001). Thus, patch choice decisions by parasitoids that determine the distribution of parasitoid foraging effort among host patches are more likely to influence the impact of classical biological control than foraging decisions made within host patches.

1.2.1 Behavioral context – optimal patch choice

Phytophagous hosts occur in discrete patches in the environment (Godfray 1994, Wajnberg 2006) and parasitoids seldom exist as isolated individuals within host patches and almost certainly interact with conspecific individuals (see also Chapter 9 by Haccou and van Alphen), if not with competing species or enemies, requiring them to make decisions with regard to patch choice. The optimal strategy for patch choice for a population of foragers is frequently represented by the ideal free distribution (IFD) in which individual foragers are distributed among patches such that each has an equal rate of gain from the patches that they occupy (Fretwell & Lucas 1970, Kacelnik et al. 1992, Tregenza 1995). This simple representation of patch choice includes the simplifying assumptions of instant movement among patches at no cost, equal competitive ability of foragers, and perfect knowledge of the variation in resources among patches. Although experimental evidence suggests that few foragers exactly match the simple model of an IFD (Tregenza 1995), it has nonetheless become one of the most widely applied theoretical concepts in behavioral ecology.

An IFD can be generated by both exploitative and interference competition between animals foraging among patches in which resources are depletable and thus, decline in suitability over time (Tregenza 1995, Sutherland 1996). Foragers will tend to favor patches with the highest resource densities for ease of resource acquisition, but at the same time will experience interference competition that will tend to reduce the rate of gain of resources. Thus, one particularly interesting interpretation of the IFD is that it represents the point at which acquisition and interference balance out to generate an equal rate of gain among patches (Sutherland 1983, 1996). In this way, the IFD can be defined by the interference coefficient m of Hassell and Varley (1969), such that when $m = 1$ (exact matching), foragers match the distribution of resources and the impact on the resource population is spatially density independent. However, when $m < 1$, foragers aggregate in patches of higher resource density, such that when $m = 0$, all individuals forage in the patch with the highest resource density and this generates a spatially density-dependent pattern of mortality among patches.

Walde and Murdoch (1988) assembled a set of 75 previous studies of spatial patterns of parasitism in the field. Although parasitism does not necessarily represent the distribution of adult parasitoids, being confounded by per capita rates of attack within patches, it provides a preliminary picture of the possible patterns of mortality that result from parasitoids foraging among host patches. From the 75 studies, 49% showed density independence, 23% showed positive density dependence, and 28% inverse density dependence. This evidence suggests that, while an IFD with $m = 1$ is consistent with approximately half of the studies, both higher and lower levels of interference would be necessary to account for the full range of spatial density dependence observed from patterns of parasitism among patches. Aside from this broad approach, only two studies have more specifically addressed IFD for parasitoids, a laboratory study with *Venturia canescens* (Tregenza et al. 1996) and a greenhouse study of the foraging behavior of *Lysiphlebus testaceipes* (Fauvergue et al. 2006), although several studies have monitored aggregation by parasitoids in the field (Waage 1983, Wang et al. 2004, Legaspi & Legaspi 2005). In each case, in common with more extensive tests using vertebrates, these studies show a greater level of foraging by parasitoids at lower density host patches, or under-matching, than expected.

A number of theoretical studies have examined the consequences of relaxing the basic assumptions of an IFD to include factors such as learning ability, travel costs, unequal competitive ability, and speed of patch quality assessment that might account for deviations from exact matching (Bernstein et al. 1988, 1991, Tregenza 1995). Each of these factors can influence the distribution of foragers among patches, indicating that simple individual behaviors can lead to complex distributions of competitors. More recently, Jackson et al. (2004a) suggested that under-matching of foragers to resources can readily be resolved by incorporating simple random movements into an individual-based model of the IFD. Of course, one of the other factors that could influence the distribution of foragers among patches is the risk of predation and observations of foraging under field conditions, highlighting the importance of predation for adult parasitoids (Rosenheim 1998). In this regard, it is interesting to note that Jackson et al. (2004b) developed a model in which foragers minimize the risk of predation per unit of resource gain. This model leads to perfect matching of foragers and resources when there is perfect knowledge at both trophic levels, but results in under-matching if the level of knowledge or movement of the resource population is greater than that of the forager population.

Although the spatial ecology of host–parasitoid interactions has received increasing attention in recent years (Hassell 2000, Murdoch et al. 2003, Cronin & Reeve 2005), reflecting a more general awareness of the importance of spatial processes in population and community ecology, the link between patch choice and population dynamics has yet to be explored in detail. For simplicity, many host–parasitoid models that incorporate spatial heterogeneity are based on just two host patches, but spatial structure and the population consequences of patch choice decisions by parasitoids can be more explicitly developed through lattice models (Rohani & Miramontes 1995, Kean & Barlow 2000, Childs et al. 2004). Despite the proliferation of spatial host–parasitoid models, the prime focus of these studies has been on mechanisms for the persistence of metapopulations that are locally unstable (Bernstein et al. 1999, Briggs & Hoopes 2004). In the context of classical biological control, although metapopulation persistence is one of the two characteristics of success, it is the degree of suppression of host abundance that is of greater importance.

The only metapopulation model to have addressed host suppression is that of Rohani and Miramontes (1995), in which parasitoids respond to the distribution of host densities

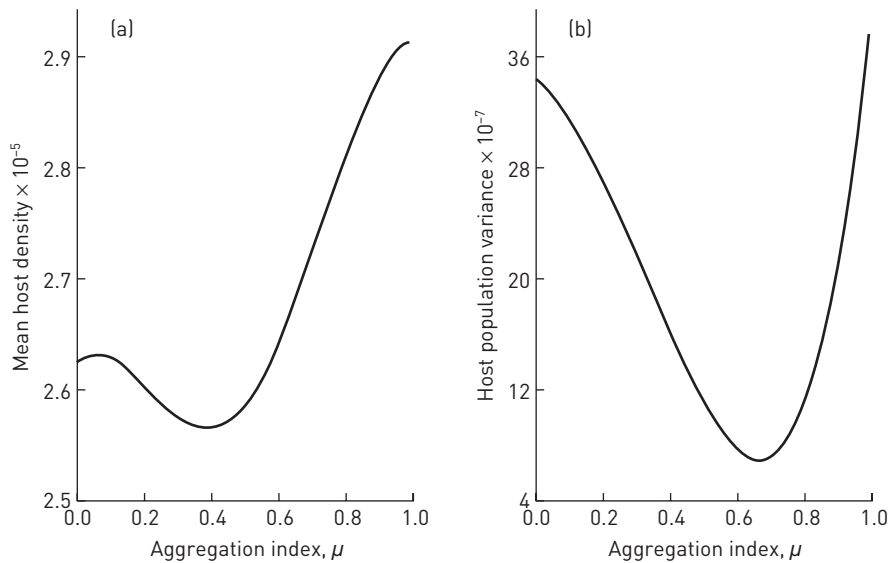


Fig. 1.2 The influence of parasitoid aggregation on (a) the global mean host density and (b) the variance in patch densities for a lattice metapopulation model of a Nicholson–Bailey parasitoid [adapted from Rohani & Miramontes 1995]. An aggregation index of 1 represents exact matching, while an index of less than 1 reflects under matching or the inefficiency of the parasitoid in responding to the distribution of hosts among patches.

among neighborhood patches as defined by an aggregation parameter μ (Hassell & May 1973), such that $\mu = 1$ represents exact matching and $\mu < 1$ represents under-matching. It is important to note that there are two aspects of host suppression in a spatially structured environment, one being the mean host density among patches and the other being the variance in host densities among patches. The Rohani and Miramontes (1995) model indicates that the lowest mean host metapopulation densities are achieved at a relatively low aggregation index ($\mu = 0.4$) representing a high level of under-matching by the parasitoid (Fig. 1.2a). This suggests that parasitoids that are less than perfect in their distribution of foraging effort in relation to host densities among patches could still play an important role in biological control. On the other hand, it may be more valuable in the context of classical biological control to ensure that no host patches experience damaging host densities, in which case variance in host densities may be more important than the overall mean. The Rohani and Miramontes (1995) model indicates that the lowest variance in host metapopulation density can only be achieved at a higher aggregation index ($\mu = 0.7$), suggesting that more optimal parasitoid behavior (Fig. 1.2b) may be needed to prevent damaging host densities in all patches, albeit at the expense of a greater mean host metapopulation density. To what extent these results would change through incorporation of host density dependence within patches, a saturating functional response, or density-dependent dispersal into the model remains to be explored, but this study does provide an initial indication that parasitoid inefficiencies in responding to the patchiness of hosts may not be incompatible with biological control and the success of host suppression.

1.2.2 Optimal foraging and importation biological control

The aim of importation biological control is the long-term suppression of pest populations through the introduction of exotic specialist parasitoids from the region of origin of an invasive species. As noted above, the two phases of an introduction are establishment and impact and little attention has been paid to improving the success of establishment. In this respect, it is interesting to note, from the biological control record, that 63% of the phytophagous insects introduced for the control of weeds become established (Syrett et al. 2000) in comparison to 36% of the insect parasitoids introduced against insect pests (Mills 2000). This suggests that there could be opportunities for improving establishment rates of parasitoids and one that has been explored to a limited extent is the influence of holding conditions on the subsequent reproductive capacity and behavioral characteristics of parasitoids that are being processed for field release (Hougardy et al. 2005, Hougardy & Mills 2006, 2007).

In any introduction program it is necessary to hold adult parasitoids for a period of time in rearing cages to accumulate sufficient emergence to justify effective field releases. During this holding period, which can typically last several days and can sometimes represent up to 25% of the adult life span, parasitoids are mated and given sugar-rich food and will experience either host deprivation if hosts are withheld or egg depletion if hosts are provided. In the absence of hosts, parasitoids might be expected to accumulate mature eggs, which could increase their motivation for foraging once released, but could also experience egg resorption and become temporarily unable to oviposit. The absence of hosts might also reduce egg maturation rates and prevent the acquisition of host-associated cues for host finding. In contrast, in the presence of hosts, although parasitoids would learn to find hosts, the expenditure of eggs would necessarily lead to a reduction in future reproduction and may also reduce the motivation for host finding.

In conjunction with parasitoid introductions for classical biological control of the codling moth in California (Mills 2005), we considered the effects of both host deprivation and egg expenditure on the reproductive capacity and behavior of a cocoon (prepupal) parasitoid, *Mastrus ridibundus* (Hymenoptera, Ichneumonidae). When deprived of hosts, *M. ridibundus* maintained a maximal egg load for up to 7 days and showed a peak of oviposition on the first day that hosts became available, although daily rates of host attack fell to a lower level subsequently, with a relatively low lifetime fecundity that was independent of the duration of deprivation (Hougardy et al. 2005).

In contrast, although egg expenditure led to declining egg loads, daily attack rates, and lifetime fecundity with increasing duration of holding, only egg load was lower than the comparable values for host-deprived parasitoids. When parasitoids that had experienced 1–9 days of host deprivation or egg expenditure were released into a field cage to estimate the success of patch and host finding, those that had experienced host deprivation showed no reduction in foraging success even after 9 days in the absence of hosts, whereas those that had experienced egg expenditure showed a progressive decline in both patch and host finding (Hougardy & Mills 2007). In addition, using mark-release-recapture experiments with immunological markers in the field, *M. ridibundus* females showed a dispersal rate of 81.5 m²/h after experiencing four or more days of host deprivation, as compared to a rate of 2.1 m²/h for those that experienced either a lower level of host deprivation or all levels of egg expenditure (Hougardy & Mills 2006). Thus, pre-release conditions can have

a marked influence on post-release performance, both in terms of reproductive potential and foraging behavior and deserves closer attention in the future. For *M. ridibundus*, if large numbers of parasitoids are available and the aim is to establish the parasitoid over a broad area as quickly as possible, then depriving parasitoids of hosts for 4 days before release would enhance their dispersal through the release region. A more likely aim, however, would be to establish the parasitoid in a more localized area and, in this case, parasitoids should be exposed to hosts, but should not be held for more than 2 days prior to release to avoid any reduction in foraging ability.

While there are no options available to manipulate the host patch choice decisions made by parasitoids introduced as classical biological controls, it is nonetheless valuable to know whether the impact of established parasitoids is influenced by their ability to match their foraging effort to the heterogeneity in host densities among patches. We know of no studies that have directly addressed host patch choice by parasitoid species used in classical biological control, but there is some indirect evidence from aggregative distributions of parasitism. For example, Hassell (1980) showed that there is a positive relationship between parasitism by the tachinid *Cyzenis albicans* and winter moth density among trees. Although the success of the biological control programs against the winter moth in Nova Scotia and British Columbia seems likely to involve the indirect influence of predation of winter moth pupae in the soil (Roland 1988), the role of *C. albicans* continues to be disputed (Bonsall & Hassell 1995, Roland 1995). In contrast to the winter moth example, however, there is no evidence of a relationship between parasitism and host density among trees for parasitoids that have proved to be successful in the biological control of diaspid scales: *Aphytis melinus* for California red scale (Reeve & Murdoch 1985, Smith & Maelzer 1986), *A. paramaculicornis* and *C. utilis* for olive scale (Murdoch et al. 1984), and *Aphytis yanonensis* and *Coccobius fulvus* for arrowhead scale (Matsumoto et al. 2004). The lack of response of parasitism to host density could result either from under-matching in the spatial distribution of adult parasitoids or from a reduction in the per capita performance of parasitoids that do effectively orient toward the higher host density patches. However, in the absence of any direct evidence of the distribution of foraging adults for parasitoids that have become established in biological control programs, it remains unclear to what extent host patch choice decisions are likely to support or constrain the impact of introduced parasitoids and if this is an aspect of biological control that deserves closer attention in the future.

1.3 Augmentative biological control

Besides introductions of natural enemies from the region of origin of invasive pests, biological control also includes the periodic release of individuals for immediate or season-long suppression of pests. Augmentative releases of mass-reared parasitoids have resulted in the development of small-scale commercial insectaries in many regions of the world over the last 30 years and it is estimated that more than 125 natural enemy species are commercially available and used on about 16 million ha globally each year (van Lenteren 2000). Inoculative releases are most frequently used early in the season to create a reproducing population of natural enemies in the crop or target environment, with the founder population initiating a series of generations that persist throughout the growing season. The best example of inoculative augmentation for parasitoids is the use of *E. formosa* for control of greenhouse whitefly in Europe (Hoddle et al. 1998). For inoculative releases of *E. formosa*

to be successful, the crop must be able to tolerate a sufficient whitefly population to allow the parasitoid to persist through reproduction. As *E. formosa* is a host feeder, too low a host density will lead to hosts being used more frequently for host feeding than for reproduction, which often leads to extinction. Thus, inoculative releases have worked most effectively in vegetable crops, such as cucumber and tomato, which are able to tolerate some honeydew production, whereas in floral crops, where control requirements are more stringent, inundative releases are necessary, which do not allow for sustained reproduction by *E. formosa*. van Lenteren (2000) estimated that biological control is used on 14,000 of a total 300,000 ha of protected crops globally, with *E. formosa* being the most frequently used natural enemy representing 33% of the monetary sales of natural enemies used in glasshouses.

Inoculative augmentation of parasitoids in biological control is functionally similar to the introduction of parasitoids in classical biological control. The difference is one of temporal and spatial scale (Fig. 1.1) but, in both cases, success is dependent upon a reproducing parasitoid population suppressing the density of a pest population. Thus, in common with classical biological control, spatial processes and patch choice is expected to be among the most important aspects of the foraging behavior of *E. formosa* with regard to seasonal control. In this respect, it is of interest to note that suppression of greenhouse whitefly is less stable in small greenhouses (van Lenteren et al. 1996). This suggests that, in the absence of sufficient spatial scale, a small glasshouse acts more like a local patch in which Nicholson–Bailey dynamics dominate (Nicholson & Bailey 1935) and extensive host feeding and superparasitism by *E. formosa* can accelerate the likelihood of extinction.

Inundative releases of insect parasitoids are used for immediate impact on the pest population, often with no expectation of successful reproduction and carry over to subsequent generations. In this way, the use of parasitoids in inundative augmentation can be likened to the use of a biological insecticide. Thus, inundation is based on maximizing the immediate killing power of the released parasitoids rather than on the dynamics of interacting host–parasitoid populations over a series of generations. The most frequently used parasitoids in inundative release programmes include *Trichogramma* species for control of lepidopteran pests in cereals, cotton, and field vegetables worldwide (Wajnberg & Hassan 1994), *Cotesia flavipes* for sugarcane borer control in South America, *A. melinus* for control of California red scale in citrus in the USA, and *Muscidifurax* and *Spalangia* species for control of filth flies in North America and Europe (van Lenteren 2000). A particularly interesting success story is the development of inundative releases of *A. melinus* in citrus. Mass production of *A. melinus* was initiated by the Fillmore Insectary, USA in 1960 as part of the biological control focus of the 9000 acres of citrus grown by Fillmore Citrus Protective District, a grower cooperative. In 1986, releases of *A. melinus* from the Fillmore Insectary were estimated at 190 million parasitoids (Carpenter 2005). Not only have inundative releases worked well in coastal citrus in southern California, they have also proved effective and commercially viable in the San Joaquin Valley where higher temperatures result in the production of smaller California red scale that are less preferred by *A. melinus* (Moreno & Luck 1992, Luck et al. 1996).

1.3.1 Behavioral context – optimal patch and host use

Patch use decisions and optimal foraging theory have been studied extensively, if somewhat sporadically, since the first appearance of the marginal value theorem (Charnov 1976, Houston & McNamara 1999, Green 2006). The latter predicts how long an individual

forager should stay in a patch in order to maximize its long-term rate of gain or fitness and that the patch becomes successively depleted with time (see also Chapter 8 by van Alphen and Bernstein). The optimal time at which to leave the patch is when the current rate of gain falls to the overall rate for the environment.

Patch use decisions have also been studied experimentally for a variety of parasitoid species with an emphasis on the range of factors that can influence patch time allocation and the informational cues that are used by parasitoids in developing patch-leaving rules (van Alphen et al. 2003, Burger et al. 2006, Wajnberg 2006). While patch residence time for parasitoids is primarily determined by the rate of successful oviposition events (or host encounters) within patches, it is now well known that parasitoids can adapt their strategy of patch use in response to experience and information gained while foraging. Patch residence time in parasitoids has been shown to be influenced by genetic variability (Wajnberg et al. 1999, 2004), seasonality (Roitberg et al. 1992), physiological status (Outreman et al. 2005), adult food (Stapel et al. 1997), experience (Keasar et al. 2001, van Baaren et al. 2005), by the presence of competitors (Bernstein & Driessen 1996, Wajnberg et al. 2004, Goubault et al. 2005) or enemies (E. Hougardy & N. J. Mills, unpublished), and by chemical cues associated with host plant damage (Wang & Keller 2004, Tentelier et al. 2005), hosts (Waage 1979, Shaltiel & Ayal 1998), or enemies (Petersen et al. 2000). The mechanism used by parasitoids for optimal patch use appears to be incremental when hosts are aggregated, such that each oviposition increases the probability of staying, but decremental when hosts are regularly distributed, such that each oviposition decreases the probability of staying. In addition, recent evidence suggests that parasitoids may also have the flexibility to switch between the two mechanisms as circumstances change (Driessen & Bernstein 1999, Outreman et al. 2005, Burger et al. 2006). From a biological control perspective, perhaps the most important influences on patch residence time are chemical cues (kairomones or synomones), which are believed to provide an initial evaluation of patch quality (Shaltiel & Ayal 1998, Tentelier et al. 2005) and competition, which can lead either to increased or to decreased patch residence time (Wajnberg et al. 2004, Goubault et al. 2005).

In addition to patch use decisions, parasitoids must also make choices between host individuals and make decisions about host acceptance, sex allocation, and clutch size. As solitary parasitoids seldom exploit host patches alone, both direct competition with other foraging females and indirect competition through encounters with chemical markers or previously parasitized hosts can influence host acceptance and the tendency to super-parasitize (Visser et al. 1992, Plantegenest et al. 2004). Once a host has been accepted, the optimal strategy of host use, assuming that host quality affects female fitness more than male fitness, is to allocate daughters to higher quality hosts and males to lower quality hosts (Charnov et al. 1981, see also Chapter 12 by Ode and Hardy). For parasitoids, host quality is often equated with size and there is good evidence from solitary species that the primary sex ratio is generally correlated with host size (Godfray 1994). Of course, size is not the only component of host quality, as host plant, host species, host age, and previous parasitism can also influence the primary sex ratio (King 1987, Campan & Benrey 2004, Shuker & West 2004, Ueno 2005, see also Chapter 12 by Ode and Hardy).

For gregarious species, the optimal clutch size has frequently been considered to be the number of eggs that maximizes the parent females' fitness gain from the whole clutch, often referred to as the Lack clutch size (Lack 1947, Godfray 1994). However, the majority of experimental laboratory studies have observed clutch sizes that are smaller than the Lack clutch size (Godfray 1994, Zaviezo & Mills 2000). This suggests that the lifetime

reproductive success of gregarious parasitoids is not always determined by the size of a single clutch, but can be modified by environmental conditions that influence the likelihood of future reproduction. Thus, the optimal strategy, when the expectation of future reproduction is high, is more toward maximization of the fitness gain per egg (a reduction from the Lack clutch size), a situation that may well apply to parasitoids under laboratory conditions. However, when the expectation of future reproduction is low, the optimal strategy is to maximize the fitness gain per clutch (Lack clutch size), a situation that may be more applicable to insect parasitoids under field conditions. Environmental factors that can influence the expectation of future reproduction include host encounter rates, parasitoid survivorship, and competition (Iwasa et al. 1984, Visser & Rosenheim 1998).

Finally, sex allocation within parasitoid clutches is influenced by local mate competition (LMC) which generates female-biased offspring sex ratios, regardless of whether mothers use a patch of hosts simultaneously or sequentially (Hamilton 1967, Werren 1980, see also Chapter 12 by Ode and Hardy). Hamilton's (1967) theory of LMC predicts that, when mating takes place between the offspring generated by one of a few mothers, sex ratios should be female biased to limit the competition between brothers for mates and that, as the number of mothers increases, the female bias declines. There is considerable experimental evidence that LMC can account for the variation in sex ratios of parasitoids (Godfray 1994). However, in an interesting recent extension of LMC, Shuker et al. (2005, 2006) pointed out the importance of asynchronous emergence of offspring from sequential females visiting the same patch of hosts. Under such circumstances, optimal parasitoid sex ratios can vary for different hosts in the same patch due to differential levels of competition between males that emerge asynchronously within the patch. Thus, optimal sex allocation presents a complex problem for gregarious parasitoids involving host quality, clutch size, and asymmetrical LMC, suggesting that an absence of perfect information may at times constrain their ability to respond accurately (Shuker & West 2004).

1.3.2 Optimal foraging and inundative biological control

The aim of inundative biological control is to release as many insectary-produced parasitoids as needed to generate sufficient mortality to suppress pest densities on a localized scale and prevent crop damage. At such a localized scale, patch use and host use decisions by the parasitoids are of much greater importance than patch choice, both in the context of mass production and impact following release. In the context of mass production, the goal is to produce vast numbers of selected parasitoids in insectaries without compromising their ability to function as intended after release (van Lenteren 2003). The emphasis here is primarily on production, with quality control serving not so much to optimize the fitness of the individuals produced as to maintain an acceptable level of field performance.

One particularly interesting practical application of the host quality model of sex allocation in parasitoids (Charnov et al. 1981) to mass production concerns the manipulation of host size to reduce male-biased sex ratios in *Diglyphus isaea* (Ode & Heinz 2002, Chow & Heinz 2005, 2006). *Diglyphus isaea* is commercially produced for inundative releases against *Liriomyza* leafminers in glasshouses, but the cost of production often prohibits greater adoption of this approach in comparison to insecticides. As is typical for a solitary idiobiont parasitoid, *D. isaea* produces more daughters on larger host larvae and bases its assessment of host size on recent experience of the distribution of host sizes in a patch (Ode & Heinz 2002). *Diglyphus isaea* was found to produce about 60% male offspring

when presented with hosts of an intermediate size over 3 days, whereas a sequence of increasing host sizes each day over the same time period reduced male production to 40% and a sequence of decreasing host sizes increased male production to 74% (Ode & Heinz 2002). Taking this to a more practical level for parasitoid production, Chow and Heinz (2005) showed that *D. isaea* produces 60% male offspring when presented simultaneously with small host and large hosts on separate plants in rearing cages but, when both host sizes were present on the same plants, male bias could be reduced to 48%. Over an 8-week period of simulated mass rearing (Fig. 1.3a), the combination of host sizes on plants produced an equal number of wasps, but with a significantly lower male bias (10% reduction with

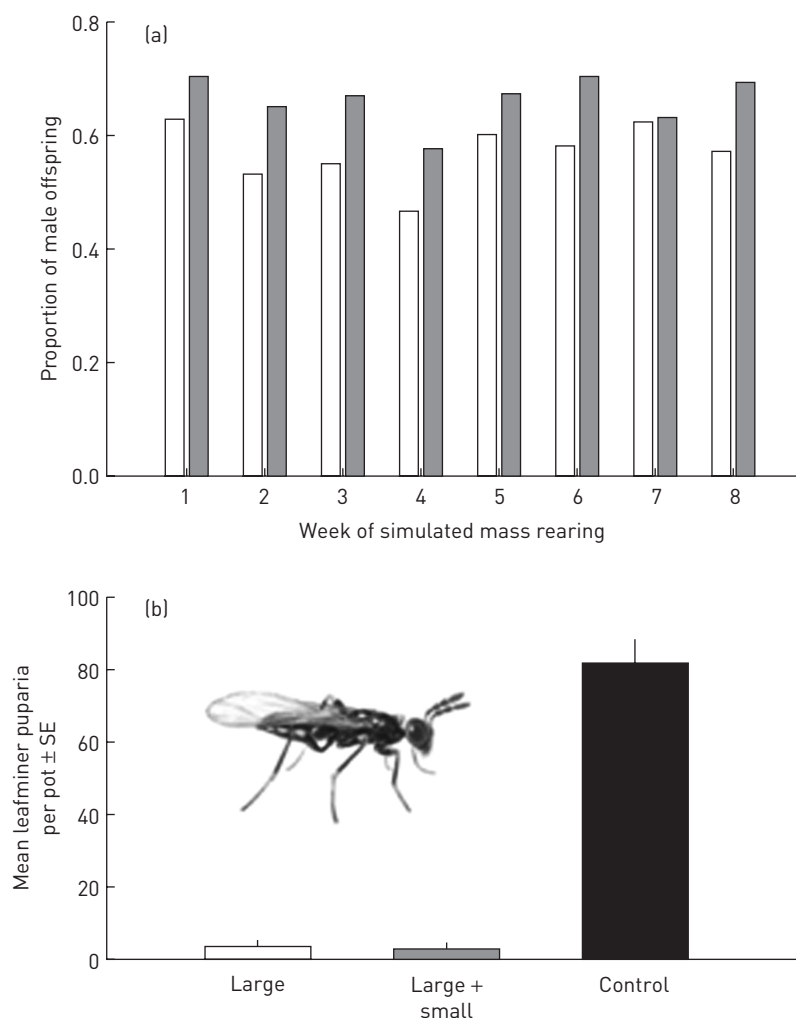


Fig. 1.3 Exposing *D. isaea* to a combination of large and small hosts (white bars) rather than to high-quality large hosts alone (gray bars) can (a) reduce the proportion of male offspring in mass production and (b) produce female wasps that are equally effective in suppressing leafminer densities in relation to untreated controls (black bar) (adapted from Chow & Heinz 2005, 2006).

no reduction in female size) than the standard insectary production procedure of providing large hosts alone (Chow & Heinz 2005). Further, in greenhouse trails, parasitoids produced from the novel host size combination approach to production of *D. isaea* were as effective in reducing survivorship of the leafminer *Liriomyza langei* (Fig. 1.3b) and damage to chrysanthemums as parasitoids produced from large hosts (Chow & Heinz 2006). This example provides a clear indication that the cost-effectiveness of mass production of an idiobiont parasitoid can be enhanced through manipulation of the foraging behavior of the parasitoid. A similar potential has been identified for the production of *Catolaccus grandis* (Heinz 1998), a parasitoid of cotton boll weevil and the approach may be more broadly applicable to idiobiont parasitoids that share the same host-size-based sex allocation behavior.

Mass production of gregarious parasitoids necessarily involves the use of rearing cages in which multiple females simultaneously parasitize hosts in close proximity. Under these conditions, it would be expected that LMC might lead to a reduction in the production of female offspring. However, in a study of mass rearing protocols for two soft scale parasitoids *Metaphycus flavus* and *Metaphycus stanleyi*, Bernal et al. (1999) found that the sex ratio was dominated by host quality rather than by interactions with other females. Contrary to expectations, larger-scale hosts produced more females and larger broods than smaller hosts. The larger broods produced on larger-scale hosts not only produced constant sex ratios, but produced offspring of larger size. Although these two parasitoids did not respond to crowding in an optimal way with respect to LMC, their lack of response clearly does not compromise their mass production. The observation that host quality may dominate LMC as an influence on sex ratios in captive parasitoid rearings may be more general, as a similar lack of response to female crowding was found for *Parallorhogas pyralophagus*, a gregarious ectoparasitoid of the stemborer *Eoreuma loftini* (Bernal et al. 2001) and for *Anagyrus kamali*, a solitary endoparasitoid of the colony forming pink hibiscus mealybug (Sagarra et al. 2000). Such a scenario would also be consistent with the previous observation that sex ratios in *D. isaea* can readily be improved through manipulation of host quality despite the multiple foundresses of a mass-rearing environment.

Of interest to note here, in the context of maximizing female production in mass rearing, is the influence of *Wolbachia* infection in *Trichogramma* species. Stouthamer (2003) suggested that the selection of unisexual (i.e. female only) strains of *Trichogramma* could benefit mass production as no hosts would be wasted on the production of males and thus, production costs could be reduced. In a direct comparison of unisexual and sexual (through antibiotic treatment) forms of the same line of *Trichogramma deion* and *Trichogramma cordubensis* in a glasshouse setting, it was found that both forms found host egg patches equally effectively but that the sexual form parasitized more hosts per patch than the unisexual form (Silva et al. 2000). The latter effect is probably due to the lower offspring production of the unisexual form, suggesting that the use of unisexual parasitoids would be most effective against solitary hosts.

In considering the field performance of insectary-produced parasitoids, arguably the most important constraint is that the constancy and simplicity of an insectary environment inevitably selects for a limited set of genotypes that proliferate under rearing conditions, but that are not so well adapted to function effectively under field conditions (Nunney 2003, Wajnberg 2004). While this has led to the development of some valuable recommendations for the maintenance of genetic diversity in the captive rearing of parasitoids (Roush & Hopper 1995, Nunney 2003, Wajnberg 2004), there is less information

on the extent to which captive rearing influences the foraging behavior of parasitoids. Captive rearing did not prevent *T. brassicae* from showing optimal behavior in the exploitation of localized patches of hosts (Wajnberg et al. 2000), but patch-leaving rules that result in parasitoids abandoning a patch before all potential hosts have been attacked are not optimal for inundative biological control. The ideal outcome for biological control would be to maximize host attack in every patch irrespective of patch host density and the marginal gain with respect to other patches. In this way, optimal foraging runs counter to the goal of inundative biological control. Although patch residence times might be increased through use of natural flightless mutants, such as known for the coccinellid *Harmonia axyridis* (Tourniaire et al. 2000), a more widely applicable approach is through use of behavior-modifying infochemicals.

It is well known that parasitoids are responsive to infochemical cues and that learning of such cues plays an important role in parasitoid foraging (Vet et al. 2003, see also Chapter 5 by Hilker and McNeil). This has led to consideration of applications such as the priming of insectary-reared parasitoids with infochemicals prior to field release (Hare & Morgan 1997) and the spraying of crops with compounds that will either stimulate parasitoid search or retain parasitoids in patches where extended periods of search are desired.

The potential for priming is well illustrated by the oviposition behavior of *A. melinus*, a parasitoid of California red scale, for which host recognition is mediated by the presence and quantity of the contact chemical *O*-caffeoyltyrosine present in scale covers (Hare & Morgan 1997). The contact chemical is highest in concentration in the covers of third instar scale, the preferred host stage and the threshold concentration that stimulates ovipositor probing can be reduced either through experience with California red scale covers or with the chemical itself. For mass production, *A. melinus* is reared on an alternative host, the oleander scale on squash and, as this scale lacks the host recognition chemical, mass-reared parasitoids do not have any experience of this contact cue when field released. Hare and Morgan (1997) showed that it is feasible to prime mass-reared parasitoids and that primed parasitoids do show an increased level of probing of California red scale. Subsequently, Hare et al. (1997) showed that this can lead to a 6–11% enhancement of parasitism rates in sleeve cages in the field. Although the recognition chemical can be produced synthetically, commercial application of *Aphytis* priming awaits the development of a mechanical procedure for priming thousands of wasps, the concentration of chemical necessary to ensure effective priming, and verification that such a system would be effective for parasitoid releases in commercial orchards.

In addition to initial priming of wasps prior to field release, consideration has also been given to spraying crops directly with host recognition chemicals (Prokopy & Lewis 1993), particularly for *Trichogramma* releases (Lewis et al. 1979). However, this approach has met with more variable success and it remains unclear whether a uniform coating of plant surfaces with kairomones would stimulate or disrupt parasitoid foraging behavior. In a laboratory study of the aphid parasitoid *Aphelinus asychis*, Li et al. (1997) showed that the presence of aphid honeydew on leaves could at least double patch residence times, but that this increase applied only to parasitoids with no or limited (1 day) experience with hosts and was not apparent for parasitoids that were more fully experienced (3–4 days with hosts). In many cases, parasitoid mass-rearing protocols do produce naïve female wasps and thus, uniform coatings of inexpensive contact kairomones could lead to foraging patterns that are not optimal for the individuals released, but more effective in terms of suppression of pest densities and crop damage.

1.4 Conservation biological control

Conservation biological control focuses on the enhancement of both introduced and indigenous parasitoid populations through the enhancement of limiting resources or the removal of incompatible pesticides. The potential impact of synthetic pesticides on parasitoids is well documented and has given rise to the well-known phenomena of pest resurgence (Hardin et al. 1995) and secondary pest outbreaks. Although removal of excessive pesticide use or the adoption of more selective pesticide products can lead to effective conservation of parasitoid populations, this aspect of conservation biological control concerns the survivorship rather than foraging behavior of parasitoids in crop production systems and will not be discussed further. In contrast, the provisioning of limiting resources as an approach to the conservation of parasitoids in cropping systems is the least well understood and implemented component of biological control with little documentation of the elements of success (Ehler 1998, Landis et al. 2000). As pointed out by Gurr et al. (2000), many studies of conservation biological control have focused on habitat manipulation, such as crop diversification. Under such circumstances, it becomes difficult to separate the relative importance of the bottom-up influence of resource concentration from the top-down influence of enemies when pest populations change in abundance. While natural enemy abundance often increases in response to crop diversification, there is limited verification that increased enemy abundance leads to greater pest population suppression.

More recently, there has been renewed interest in the provisioning of nectar subsidies as a more specific limiting resource for parasitoids in cropping systems (Heimpel & Jervis 2005, Wäckers et al. 2005). Although extra-floral nectar and honeydew can also be important sugar sources for parasitoids, floral nectar is more readily manipulated in farmer fields in the context of the implementation of conservation biological control. Not only does this approach more specifically target the foraging behavior of parasitoids, it also provides a more focused direction for field-based studies in conservation biological control. This then raises the question of optimal patch choice between hosts and adult food, the distance or ease of access of nectar sources from host patches and the extent to which foraging for food could reduce the time available to search for hosts (see also Chapter 7 by Bernstein and Jervis).

1.4.1 Behavioral context – optimal use of nectar subsidies

As a variant on patch choice, foraging parasitoids also face decisions of whether to stay in a patch of hosts or to select an alternative patch containing plant-provided food (see also Chapter 7 by Bernstein and Jervis). The most important form of plant-provided food for parasitoids is nectar. Not only have parasitoids frequently been observed feeding from flowers (Jervis et al. 1993), but in many cases the longevity and realized fecundity of parasitoids are known to be greatly enhanced in the presence of floral nectar (Wäckers 2004, 2005). Although parasitoids vary in the frequency with which they require carbohydrate sources to sustain survivorship and flight, foraging females must make important decisions of whether to search for nectar subsidies to support future reproduction or for hosts to maximize current reproduction (see also Chapter 6 by Strand and Casas and Chapter 7 by Bernstein and Jervis). Nectar subsidies come with both direct and indirect costs. Direct costs are associated with the potential of increased mortality while foraging on flowers (Rosenheim 1998) and indirect opportunity costs are associated with the time

lost while feeding rather than ovipositing (Sirot & Bernstein 1996). As an initial step, using a stochastic dynamic programming model, Sirot and Bernstein (1996) determined that the optimal solution for the distribution of parasitoids between patches of hosts and food is influenced by both the availability of food sources and the dependence of survivorship on energy reserves (see also Chapter 7 by Bernstein and Jervis). More recently, Tenhumberg et al. (2006) extended this approach to relax some of the assumptions and to include an energy cost for host searching. They found that, in contrast to the Sirot and Bernstein (1996) model, parasitoids should always search for food rather than hosts when energy reserves drop to a low level, even if food availability and rewards are low. However, Bernstein and Jervis (Chapter 7) show that the reason for the contradiction between the two models is more a matter of the parameter values chosen than the assumptions of the model *per se*.

While there have been numerous laboratory studies on the impact of floral nectar on the performance of individual parasitoids (Wäckers 2005) and an increasing number of field studies on the influence of nectar subsidies on parasitism (Gurr et al. 2005, Heimpel & Jervis 2005), the consequences of floral nectar for the dynamics of host–parasitoid interactions at a population level are poorly understood. Krivan and Sirot (1997) confirmed the suggestion of Sirot and Bernstein (1996) that the inclusion of floral subsidies can stabilize a host–parasitoid model, but provided no indication of the consequences for host population suppression. Kean et al. (2003) addressed this problem by asking specifically how an increase in parasitoid longevity or fecundity, through provisioning of nectar subsidies, would affect the equilibrium density of a host population. By including parasitoid longevity and fecundity (maximum number of attacks) into a simple extension of a Lotka–Volterra host–parasitoid model, they were able to show that increased fecundity is of less importance than increased longevity and that the effect of increased parasitoid longevity in suppressing a host population depends upon whether a parasitoid is primarily egg or time limited and whether time spent on nectar subsidies is likely to result in a reduction in the search rate for hosts (Fig. 1.4). In other words, parasitoids that are more pro-ovigenic (with a high ovigeny index *sensu* Jervis et al. 2001) are less likely to benefit from increased longevity, whereas those that are more synovigenic (low ovigeny index) could provide enhanced pest suppression in the presence of a nectar subsidy as time spent searching for food should not limit the daily number of hosts attacked for a time-limited parasitoid (see also Chapter 7 by Bernstein & Jervis for further details).

1.4.2 Optimal foraging and conservation biological control

Infochemicals originating from a damaged host plant (synomones) or from the host itself (kairomones) are well-known signals that aid parasitoids in the location of suitable hosts. Although less well known, there is also increasing evidence that parasitoids also respond to floral odors in their search for sugars to support maintenance and flight (Wäckers 1994, Jacob & Evans 2001). The responsiveness of parasitoids to host-related versus food-related cues then depends upon the level of hunger, with starved females responding preferentially to food odors and well-fed females responding preferentially to host-associated odors (Jervis et al. 1996, Lewis et al. 1998, Desouhant et al. 2005). This responsiveness can lead to parasitoids maintaining a fairly constant level of energy under field conditions in the presence of an abundant adult food supply, as shown for *Venturia canescens* (Casas et al. 2003).

The concept of using floral nectar subsidies to enhance the abundance or activity of parasitoids is based on three important observations: (i) crop monocultures are often devoid of sugars; (ii) parasitoid longevity is often greatly enhanced when fed on sugars;

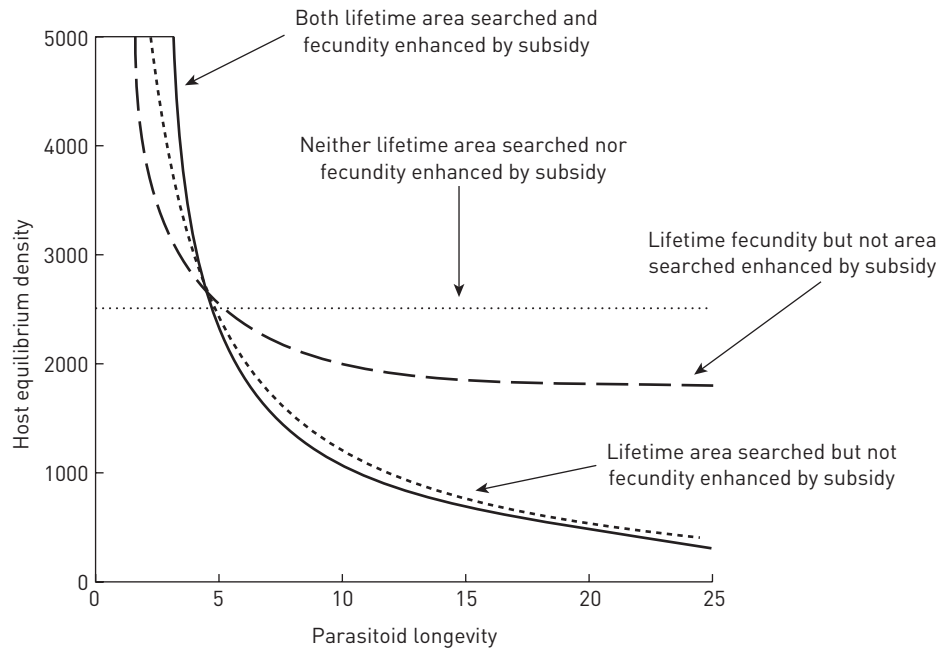


Fig. 1.4 The potential influence of nectar subsidies on the ability of a parasitoid to reduce the equilibrium density of a host population based on an extended Lotka–Volterra model in relation to parasitoid longevity (adapted from Kean et al. 2003). Four possible scenarios are presented, depending upon whether the subsidy has an influence on lifetime fecundity or area searched by the parasitoid (see text for details).

and (iii) parasitoids often use floral nectar under natural conditions. In reviewing the experimental evidence for improved parasitoid performance in the presence of floral nectar, Heimpel and Jervis (2005) noted that there was evidence of increased parasitism in 7 of 20 field studies, but that only one of these 7 showed a simultaneous reduction in pest density, while 2 did not and 4 did not monitor host density. Since this review, several other studies have shown enhanced rates of parasitism under field conditions in the presence of floral nectar (Tylianakis et al. 2004, Lavandero et al. 2005, Berndt et al. 2006, Winkler et al. 2006), but there have been no further reports of a reduction in pest densities. An increase in parasitism in the presence of floral nectar can result from a combination of two effects: an increase in parasitoid density due to greater attraction or retention of parasitoid females and an increase in the per capita performance of the parasitoids. It is not clear which of these factors may have been more important, but it is interesting to note that increased rates of parasitism were reported for both host-feeding and non-host-feeding parasitoids, suggesting that host feeding alone may not compensate for a parasitoid's need for sugars to fuel flight and support longevity (but see Giron et al. 2004). It should also be noted here that sucrose sprays have been shown to be sufficient to increase the abundance of the alfalfa weevil parasitoid *Bathyplectes curculionis* and weevil parasitism during the first crop of alfalfa in fields where aphids are not abundant (Jacob & Evans 1998). Nonetheless, despite increasing evidence for the importance of flower feeding for parasitoids (Wäckers

2005), it appears that there is far less evidence that the presence of floral nectar will translate to improved biological control.

Observations of increased parasitism in the presence of floral subsidies has been sufficient, however, to generate considerable interest in the possibility to enhance parasitoid populations and their performance in agricultural crops that tend to lack natural sources of suitable sugars (Landis et al. 2000, Gurr et al. 2005). In the context of conservation biological control, two important questions arise: which floral subsidies to use and how close they need to be to the crop? To answer the first question it is important to consider five different features of the flowers of a particular plant species: availability in space and time, apparency in terms of olfactory and visual cues, accessibility in relation to parasitoid mouthpart morphology, chemical composition with respect to sugars, stimulants and deterrents, and specificity in enhancing parasitoids rather than pests or higher order predators (Gurr et al. 2005, Wäckers 2005). Although annual buckwheat (*Fagopyrum esculentum*) has become something of a model plant for floral subsidy studies, Wäckers (2004) has shown that the flowers of different plant species can differ considerably in both olfactory attractiveness and accessibility for three different species of parasitoid. Some nectar constituents can also either act as deterrents or be toxic to parasitoids (Wäckers 2001, 2005). Thus, the selection of flowering plant species as insectary mixes for use in conservation biological control, not only needs to take these features into consideration, but also needs to be tailored for variation among parasitoid species.

The question of how close a floral subsidy needs to be to a crop, to be readily found and used by adult parasitoids, remains largely unknown. In an interesting study of parasitism of grain aphids by *A. rhopalosiphi* in the presence of annual buckwheat, Tylianakis et al. (2004) showed that parasitism declined exponentially from 36% immediately adjacent to a floral patch to zero beyond a distance of 14 m (Fig. 1.5), suggesting that the foraging distance of this parasitoid may be relatively small. While foraging distance is likely to increase

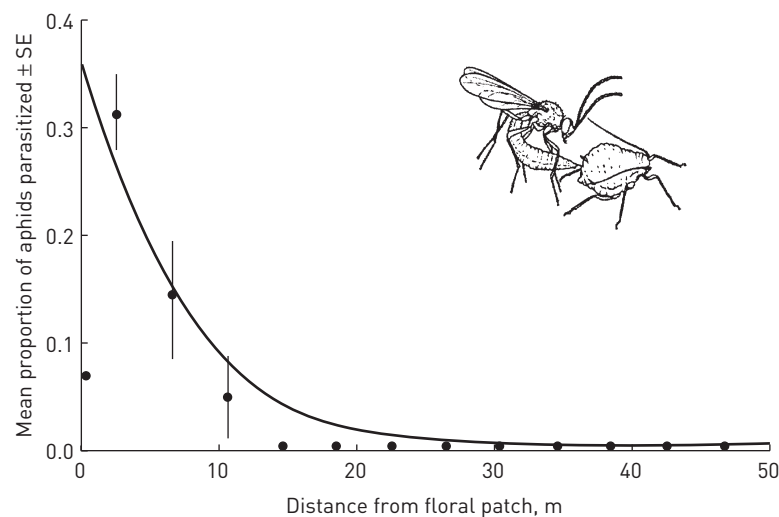


Fig. 1.5 Parasitism of grain aphids by *A. rhopalosiphi* in relation to distance into the crop from a patch of buckwheat flowers that acted as a source of floral nectar (adapted from Tylianakis et al. 2004).

with parasitoid size, there have been few studies of parasitoid foraging distance and the majority of these are concerned with movement in relation to hosts rather than food sources (Desouhant et al. 2003). However, Lavandero et al. (2005) found that *Diadegma semiclausum* could be trapped at distances of 80 m from a source of floral nectar marked with rubidium. Nonetheless, there remains insufficient data from which to base any assessment of the necessary proximity of floral subsidies. Similarly, the question of how much floral nectar is needed to support a suitable population of parasitoids in an agricultural crop has yet to be addressed. However, these examples suggest that proximity might be more important than quantity and that, to reach to the middle of agricultural fields, floral subsidies may need to be integrated into a crop in the form of headland plantings or strips rather than being confined to perimeter plantings.

1.5 Conclusion

Behavioral ecology and optimal foraging theory provide a valuable basis for developing improvements in the application of biological control. As the four main approaches to biological control differ in both temporal and spatial scale, however, it is important to consider the corresponding scale of foraging decisions that are most applicable to each approach, with larger-scale processes likely dominating smaller-scale processes. A behavioral approach also appears promising in more formally linking measurements at the individual level to processes at the population level and helping to shift the implementation of biological control away from its traditional roots of trail-and-error toward a more exact science in which success can be more readily predicted.

Host patch choice is the appropriate scale of behavior for biological control importations and inoculations and, while such behavior offers little opportunity for manipulation to improve success, it could help to clarify the differences between success and failure. Additional theoretical studies that focus on host suppression rather than stability would provide a better basis for understanding to what extent inefficiencies in the distribution of foraging effort could enhance or compromise the success of biological control. In this respect, initiation of field observations on the spatial distribution of foraging effort for established parasitoids would fill a current vacuum and inform the continued debate that aggregation to patches of higher host density is a beneficial aspect of biological control. Patch and host use decisions are the appropriate scales of behavior for inundative biological control, with opportunities to improve both mass production of parasitoids and their subsequent impact following field release. Manipulating sex ratios through host quality and use of uniparental (i.e. female only) strains can reduce the production costs for mass-reared parasitoids. Similarly, patch residence times and consequent parasitism can be increased for inundative releases using infochemicals as crop sprays or for priming parasitoids with host recognition cues prior to release. Although not yet adopted by insectaries and biological control practitioners due to insufficient practical development, these techniques offer considerable potential that could readily lead to commercial application. In the case of conservation biological control, the provision of nectar subsidies for adult parasitoids has attracted considerable attention in recent years, involving patch choice decisions that influence the trade-off between current and future reproduction. While nectar subsidies are used by adult parasitoids in the field and have been shown to increase parasitism, at least locally, there is little experimental evidence that this has

translated to reduced pest densities, indicating the need for additional and more critical field tests.

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