CHAPTER 7

Parasitism and biological control

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7.1 Introduction

Parasites exert negative effects on their hosts, both at the individual and population level. This ecological feature can be used to develop **biological control** programmes, i.e. 'the use of living organisms [called biological control agents] to control the population density or impact on a specific pest organism, making it less abundant or less damaging than it would otherwise be' (Eilenberg *et al.* 2001). More than a thousand biological control agents are currently in use worldwide and most of them are **parasitoid** insects used to control phytophagous insect pests. This chapter aims to describe this particular form of parasitism, highlighting its huge diversity and the associated consequences for demographic interactions between hosts and parasitoids. More specifically, we will detail how the ecological and dynamic features of parasitoid species can be used to control noxious pests, and how recent advances may improve the efficacy of biological control programmes. We will conclude by emphasizing the complex scientific questions raised by the study of these particular species in terms of evolutionary ecology and the associated agronomic applications.

7.2 Ecological features of parasitoids

7.2.1 Overview

Parasitoids are organisms whose larvae develop to the detriment of a single host (Godfray 1994). Their mode of development lies between that of predators and true parasites since the host is generally killed and there is a tight physiological interaction between the two partners (Toft *et al.* 1991). The adult parasitoids are free-living. According to recent estimates, parasitoids represent between 8% and 20% of all insect species. Most parasitoids are **Hymenoptera** (around 50,000 described species) or **Diptera** (around 16,000 species) (Feener and Brown 1997). Some species can also be found within Coleoptera, Lepidoptera, Trichoptera, and Strepsiptera (Quicke 1997). From an evolutionary point of view, 'parasitoidism' appears in a different way within the two main orders. More accurately, it seems that all hymenopteran parasitoids probably originated from a single mycophagous ancestor inhabiting dead wood. In the Diptera, however, parasitoids appear to have arisen independently numerous times from different saprophagous or predatory ancestors (Eggleton and Belshaw 1992). These different evolutionary origins may explain the important interspecific variations, but other factors (including ecological ones) must be taken into account to understand the processes of speciation and diversification.

7.2.2 Host range

Most parasitoids attack other insects, but some species attack other arthropod hosts or even hosts from other phyla (molluscs or even some chordates) (Feener and Brown 1997). Sometimes, the host is itself a parasitoid species leading to a tritrophic interaction between a host, a parasitoid, and a so-called **hyperparasitoid**. The parasitized host stage greatly varies according to the parasitoid biology but we can distinguish parasitoids of eggs, larvae, nymphs, or even adults. In some cases, **oviposition** (i.e. the deposition of an egg in (or on) the host) occurs at an early host stage (for instance the egg) but the development occurs in later stages (larvae or nymphs). Some parasitoid species are also able to infest more than one host stage. The host range greatly varies between species. For example, some tachinids are highly generalist, being able to develop successfully within several dozen species belonging to different families (Stireman *et al*. 2006) whereas numerous species are specialized and restricted to a limited number of host species.

There are numerous reasons for the particular host range (Godfray 1994; Stireman *et al*. 2006). For instance, dipteran parasitoids are generally more generalist than hymenopteran species, suggesting that some physiological constraints or pre-adaptation may favour or restrict the host range. The taxonomy of the potential hosts may also influence evolution of the host range since a parasitoid species can probably adapt more easily to new species that share similar physiological features and defence mechanisms with its original host. Similarly, parasitoids are more likely to infest hosts facing similar ecological constraints. However, the host range may evolve through time and space but, contrary to other organisms with a parasitic lifestyle (Fox and Morrow 1981; Jaenike 1990; Nosil 2002), only a few data are currently available on intraspecific variability in the number of potential hosts that can be attacked or, more generally, on ecological specialization phenomena.

7.2.3 Sex determination

Knowledge of the mechanisms of sex determination is an important point not only for understanding the ecology and evolution of parasitoid species but also for improving their use as biological control agents. Three different systems determine the sex of parasitoids: (1) **diplo-diploidy**, (2) **haplo-diploidy**, and (3) **thelytokous parthenogenesis** (Normak 2003). Diplo-diploidy is the main determinant of sex in dipteran parasitoids and is, for instance, similar to the way in which sex is determined in mammals. Each individual originates from a fertilized oocyte which contains both maternal and paternal genomes. The combination of the sex chromosomes determines the sex. In most of hymenopteran parasitoids, however, haplo-diploidy, also called ‘arrhenotoky’, is the most frequent mechanism of sex determination. In this case, females originate from fertilized oocytes whereas males originate from unfertilized oocytes and are thus haploids. In this case, the parasitoid females can ‘decide’ whether or not to fertilize their eggs and thus produce females or males (cf. Section 7.3.1.5). Finally, numerous cases of **thelytoky** have also been described. Thelytokous females are able to produce diploid females without mating. In some cases, diploidy in the germinal cells may be caused by bacterial symbionts (see Box 7.3). Sexual and asexual species strains can sometimes coexist within the same parasitoid species (Amat *et al*. 2006).

7.2.4 Other life-history traits

Depending on the parasitoid species, immature parasitoids can develop either within or outside their hosts (endo- and ectoparasitoids, respectively). The ability or inability of several parasitoids to develop alone within a single host leads to a distinction between gregarious and solitary parasitoids. However, the distinction must be made with caution since the mode of development of some parasitoids may vary depending on host characteristics or status (species, size, quality). The duration of the interaction between parasitoids and their hosts also varies, and distinction can be made between **idiobiont** parasitoids, which quickly kill their hosts, and **koinobionts** that allow the host to survive for some time (Askew and Shaw 1986).

The availability of mature eggs in adult parasitoids also shows an important interspecific variability. Some so-called **pro-ovigenic** parasitoids have a complete stock of oocytes soon after adult emergence, whereas in **synovigenic** species new eggs continue to mature throughout adult life. Actually, the distinction is not always so clear-cut since a continuum can usually be observed between these two extremes (Jervis *et al*. 2001). Adult nutrition is also an important life-history trait in parasitoids. Numerous species do not feed or have access to sugars only (honeydew, nectar, etc.) (Wäckers 2003), while others ‘host-feed’, consuming host tissues or **haemolymph** (Jervis and Kidd 1986).

Such nutritional input appears to be necessary to prolong the adult lifespan or to increase egg production. Host-feeding behaviour, which has been described in 17 families of Hymenoptera as well as in some Diptera, may cause the death of the host and can thus deeply modify the host–parasitoid dynamics (Heimpel and Collier 1996).

7.2.5 Co-variations among life-history traits

One of the goals in the study of the evolutionary ecology of parasitoids is to understand their challenging diversity, and especially to try to identify more accurately some co-variations between the main life-history traits (Godfray 1994; Mayhew and Blackburn 1999; Jervis *et al*. 2001). Some studies also make a dichotomy between, on the one hand, species that are rather specialized, pro-ovigenic koinobiont endoparasitoids and, on the other hand, species that are generalist, synovigenic host-feeder idiobiont ectoparasitoids. However, the causes of such co-variation are still under discussion, and Godfray (1994), for instance, identified a set of selective pressures that could push one lineage to evolve towards one of the two strategies. Moreover, some phylogenetic constraints can limit certain transitions (for instance from **ectoparasitism** to **endoparasitism**) if some required pre-adaptations are lacking. Finally, it is worth noting that these general co-variational trends show numerous exceptions.

7.3 The different steps of parasitism

As shown in Fig. 7.1, several successive steps must be achieved for successful parasitism (Doutt 1959; Vinson 1975, 1976). These different steps can be divided into two main categories. The first one, so-called pre-ovipositional, depends on the behaviour of females (Vinson 1981). In this case, females use a variety of stimuli leading them to progressively reduce their search area until a host is discovered and attacked. The second category concerns the development of the immature parasitoids and depends on the physiological interactions between the two partners (Vinson and Iwantsch 1980a, b). These categories are described more fully in the following sections.

7.3.1 Pre-ovipositional steps

The mechanisms implied in these steps are based on the ecological and behavioural features of the two partners. At the individual level, they will determine the ability of female parasitoids to find and successfully attack their hosts. At the population level, they will influence host–parasitoid dynamics.

7.3.1.1 Habitat searching behaviour

A newly emerged parasitoid female is rarely close to its host. Thus, she must first go and find potential hosts to exploit. Numerous studies have demonstrated the important role of visual, acoustic, or olfactory stimuli in the detection of hosts or their habitats (Vinson 1976, 1981). As a consequence, some host species are more frequently attacked not because they are preferred but because their habitat is more actively searched for. For instance, *Leptopilina boulardi* females are attracted by ethanol produced by the fermenting fruits where its hosts (*Drosophila* larvae) develop (Boulétreau and David 1980). More recently, it has been demonstrated that some plants, when attacked by phytophagous insects, emits molecular signals called **synomones** that are used by parasitoids to accurately locate places harbouring potential hosts (Turlings *et al*. 1990). Such 'chemical communication' between different trophic levels raises numerous research questions both at the fundamental (identification of the proximate and evolutionary causes involved) and applied (the use of synomones for crop protection) level.

7.3.1.2 Host searching behaviour

When a host habitat is found, the female parasitoid must find the host through the use of sometimes acoustic or visual but more generally chemical or olfactory stimuli. For instance, sexual pheromones that hosts normally use for attracting or detecting mating partners can be involved. Female parasitoids can behave like spies, tracking host-emitted signals, called **kairomones**, that were originally emitted for another purpose (Noldus 1989). The mechanisms involved are complex and sometimes very highly specific. They are related to strong selective pressures and subtle

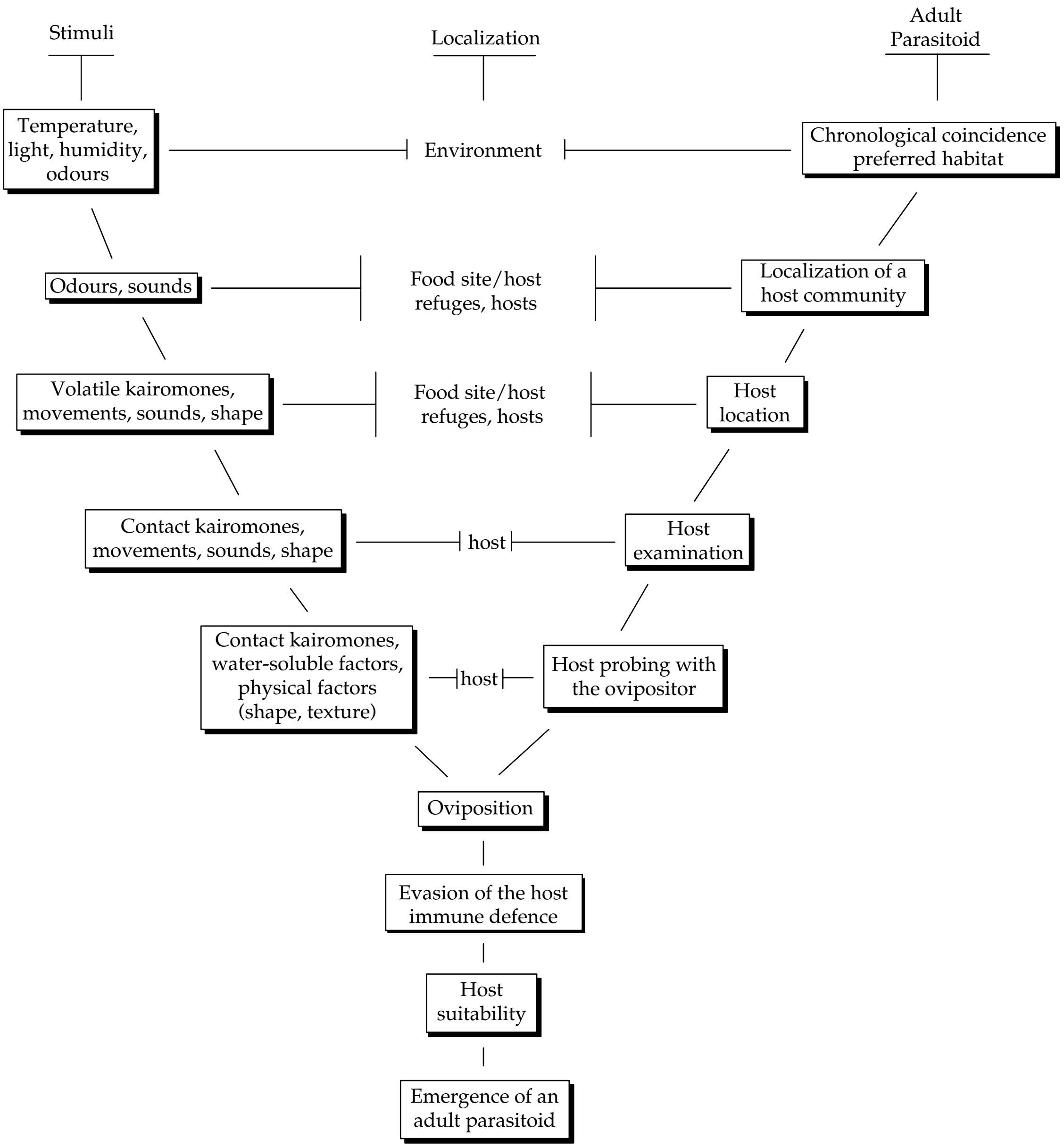

Figure 7.1 Flowchart showing the different steps involved in a host–parasitoid interaction, along with the different corresponding stimuli and their localization. After Vinson (1975).

adaptive mechanisms. For instance, the parasitoid *Cardiochiles nigriceps* is able to use as a cue the chemical 13-methyl dotriacontane that is present in the mandibular glands of its hosts, larvae of the lepidopteran *Heliothis virescens*. A single change in the methyl group of this molecule can entirely destroy its recognition by the females (Vinson *et al*. 1975).

7.3.1.3 Host acceptance

Once a host is found, the parasitoid female should ideally check whether it can ensure the good development of her offspring. Is it of the correct species? Has it reached its correct instar? Is it healthy or has it already been attacked? These questions are answered by examination of the external (shape, size, colour) or internal features of the host. Signals can be detected using the numerous receptors on the antennae (for external host features) or on the ovipositor (for internal host features). Here again, the level of specificity can be very high, leading the female to accept only a particular stage of a well-identified host. All of the mechanisms involved are, again, the result of strong selective pressures. Their study can lead to an explanation of some of the incredible richness in the diversity of parasitoids' behavioural strategies.

For numerous parasitoid species, the information collected during host examination also allows the female to detect whether the host has been parasitized before, either by the female herself or by a conspecific or heterospecific female. The decision to **superparasitize** a host (i.e. to lay an egg in a host that has already been parasitized) is usually risky for a solitary parasitoid, since only one parasitoid can develop in the host in this case. However, several theoretical models predict that the decision could be sometimes profitable under some ecological conditions (van Alphen and Visser 1990; Plantegenest *et al*. 2004). Such a prediction has been confirmed in various experimental works.

7.3.1.4 Clutch size

In the cases of gregarious parasitoids (see Section 7.2.4), the information obtained during examination of the host can be used by the female to accurately adjust the number of eggs she will lay. Bigger or more suitable hosts will enable the development of a greater number of progeny. It has been experimentally demonstrated that females of several parasitoid species are indeed able to estimate the size of their hosts. For instance, before ovipositing, females of the egg parasitoid *Trichogramma minutum* drum with their antennae on the surface of the egg while walking. During such an examination process, the bigger the host the smaller the angle between the first antennal segment and the head of the parasitoid. This angle has been demonstrated to be used by the females of this species as a proximate cue to adjust clutch size (Schmidt and Smith 1986).

7.3.1.5 Sex allocation

In haplo-diploid species, mated females are able to fertilize their eggs or not and thus choose the sex of their offspring (see Section 7.2.3). This may be influenced either by the quality (or suitability) of the host or by the number of other competing females on the host. In all cases, important selective pressures will lead females to optimize the sex ratio (i.e. the proportion of each sex in the offspring) they are producing in accordance with environmental constraints (Box 7.1).

Box 7.1 Optimal proportion of males and females in insect parasitoid progeny

Most parasitoid females use a special haplo-diploid sex determination system enabling them to control accurately the sex of each of the eggs they lay (Section 7.2.3). Since parasitoid females are under strong selective pressures, they most likely have to optimize the proportion of sons and daughters (i.e. the sex ratio) in their progeny in order to maximize transmission of their genetic makeup to the following generation. It has been known since 1930 that when mating between males and females occurs randomly the optimal sex ratio should be 50% males, 50% females (Fisher 1930). The reason for such an equilibrium is based on the fact that every mother obtains the same gain in fitness if she produces either a son or a daughter. Moreover, such an equilibrium is known to be a so-called 'evolutionarily stable strategy' (ESS) (Charnov 1982). Indeed, if one of the two sexes is present in the population at a lower percentage, it would be advantaged, having a higher mating opportunity, and this would lead the global sex ratio in the population to return to 50% males, 50% females.

In insect parasitoids, however, mating does not usually occur at random. Indeed, most hosts are geographically concentrated in small patches of a few individuals, distant from each other, and colonized by a few parasitoid females only. Their progeny usually mate together before leaving to search for new hosts to attack. Since the

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Box 7.1 continued

number of parasitoids in a host patch usually remains low, mating occurs between progeny that can have some genetic relatedness. It can be shown that if *n* females are exploiting a host patch, the optimal proportion of sons they should produce should be $(n-1)/2n$. This is the so-called 'local mate competition' of Hamilton (1967) (see figure). When only one female colonizes a host patch ($n = 1$), she should lay, according to this model, only eggs producing daughters. More realistically, she should lay just enough sons to mate with all her daughters, which most likely means a small number of males since each of them can mate with several females. When the number of females exploiting a host patch increases, it becomes more and more worthwhile to produce sons that can then mate with females that are not produced by their mother. In this case, the situation progressively looks like random mating between males and females, and the Hamilton (1967) model indeed converges toward a 50% male, 50% female equilibrium, as in the original model of Fisher (1930).

A number of experimental works have shown that several parasitoid species accurately follow such predictions (King 1993).

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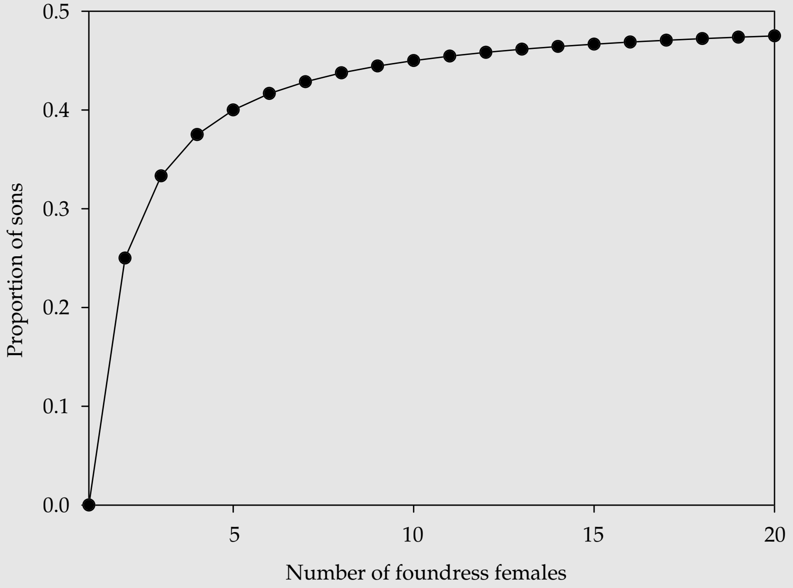

Box 7.1 Optimal proportion of sons parasitoid females should lay as a function of the number of females exploiting a host patch: model of 'local mate competition' from Hamilton (1967).

7.3.1.6 Patch time allocation

The adult lifespan of insect parasitoids is usually short, so females have to maximize their production of offspring per unit time. Moreover, most hosts are usually patchily distributed in the environment (Boxes 7.1 and 7.2). Females thus have to optimize their residence time on each patch they exploit before leaving it. Numerous theoretical works have dealt with this issue in an effort to predict the optimal residence time for a female according to environmental conditions (Box 7.2). Several experimental works indicate that females of different parasitoid species behave according to the corresponding theoretical predictions.

7.3.2 Post-ovipositional steps

After oviposition, the immature parasitoid faces a particular environment: its host. Indeed, the host not only constitutes protection and a source of nutritional resources but may also be hostile and defend itself against the intruder. In order to cope with these different features, several adaptive mechanisms have been selected through time including either the injection of specific products by the female during oviposition or particular adaptations of the immature parasitoids. The mode of action and availability of these different mechanisms vary greatly between species, but they have two main goals: (1) avoiding, destroying, or diverting the immune defense of the host and (2) regulating the long-term development of the host in order to favour development of the parasitoid. Other complementary aspects are also included in so-called host suitability (Vinson and Iwantsch 1980a). For instance, the physiological state of the host greatly influences not only the survival of the immature parasitoid but also the adult phenotype (size, fecundity, adult lifespan, etc.). Moreover, the tight interaction between the two partners can also be modulated by environmental factors, either biotic like the presence of pathogens (Hochberg 1991) or abiotic like temperature (Ris *et al*. 2004).

7.3.2.1 Immune defences

One of the most frequent defence mechanisms of a host against endoparasitoids is the **encapsulation** of the immature parasitoids (Carton and Nappi 1997). The process implies the collaboration of different cell types called haemocytes that will successively identify the intruder, adhere to it, and recruit other cells to form a melanized capsule. The endoparasitoid is then killed, probably by asphyxiation or through the release of toxic compounds. Three different strategies have been shown to be used by parasitoids to evade encapsulation (Strand and Pech 1995). The first is to passively limit the interaction with the host, either through ectoparasitism or through the choice of unprotected instars (eggs for instance) or tissues (muscles, gut, glands, etc.).

Box 7.2 Optimal residence time on host patches

Most parasitoid species attack hosts that are distributed in the environment in patches that are distant from each other. In such a situation, parasitoid females are most likely selected to optimize the residence time on each of the host patches they are exploiting in order to maximize the number of progeny they can produce per unit time. When a parasitoid female exploits a host patch, the number of available, unparasitized hosts progressively decreases and there is a cost, in terms of both time and survival, in leaving the patch to try to find another one in the environment. Without competitors, the optimal time a female should remain on a host patch is provided by the so-called 'marginal value theorem' (Charnov 1976). In this model, the female takes a time T to find the patch in the environment and exploits it during a time t, producing a cumulative number of progeny $f(t)$, a function having a decreasing slope since hosts are progressively depleted. If we call $R(t)$ the number of progeny produced per unit time, then $R(t) = f(t)/(T + t)$. The time t that maximizes this function is the one that leads to a null first derivate, leading to:

$$\frac{\partial R(t)}{\partial t} = 0 \Rightarrow \frac{\partial f(t)}{\partial t_i} = \frac{f(t)}{T+t}.$$

A graphical solution for solving this equation is presented in the figure.

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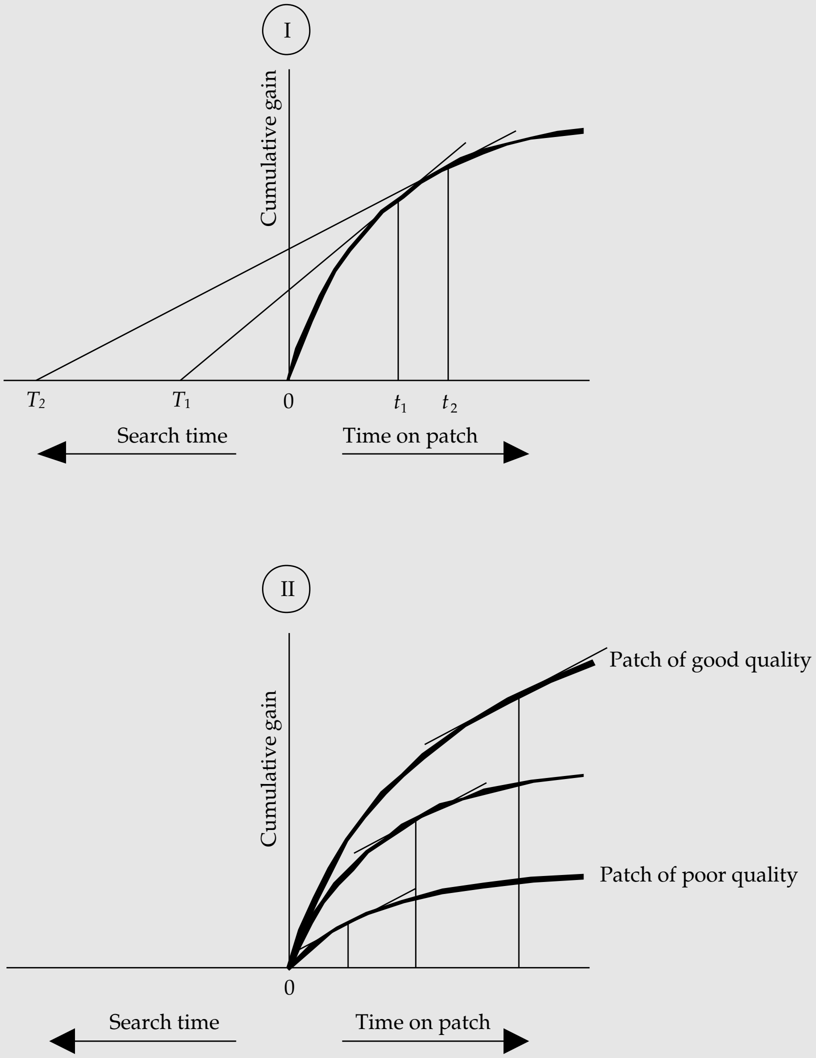
Box 7.2 continued



Box 7.2 Graphical representation of the 'marginal value theorem'. The time used by the parasitoid female to find a host patch to exploit is plotted as a negative x-value. Once the patch is discovered, the cumulative number of progeny produced (which corresponds to the cumulative number of hosts attacked) is represented by a thick curve. The optimal patch residence time corresponds to the x-coordinate of the contact point between the cumulative progeny production curve and a tangent to this curve originating from the time taken by the female to find the patch in the environment. This theoretical model predicts that the optimal residence time on a host patch should be longer when the female took longer to find the patch in the environment (case I). In a heterogeneous environment, this model also predicts that the female should leave the patch she is exploiting when her instantaneous fitness gain (slope of the curve) has decreased to a threshold value that corresponds to the average gain rate that can be achieved on all the patches available in the environment. Such a threshold value should not depend on the quality of the patch exploited, but it will be reached sooner on poorer quality patches. Hence, this model predicts that females should remain for a shorter time of poorer quality patches (case II).

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Box 7.2 continued

According to this theoretical model, all mechanisms that lead to a modification of the rate of host encounters per unit time should influence the optimal time females should remain on host patches. For example, if a female spends a lot of time finding a host patch in the environment, the number of hosts she will attack per unit time will remain low and the marginal value theorem predicts in this case that she should exploit such patch for a longer time before leaving it. Furthermore, if the quality of patches (expressed here as the number of hosts available) varies in the environment, the model predicts that females should remain for longer on better quality patches. A large number of experimental works have shown that parasitoid females usually follow these predictions rather accurately (Wajnberg *et al*. 2000, 2006).

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Another is for the parasitoid to protect itself actively against the immune response. For example, numerous dipteran parasitoids circumvent the host's immune response by building a protective layer around their body while maintaining a respiratory channel to avoid asphyxia. Finally, many species have been shown to destroy the host's immune defences with the help of **virulence** factors. From an evolutionary point of view, all these weapons, defences, and counter-defences, can be viewed as the result of complex co-evolutionary processes and as an arms race between the two partners. This may lead to important intraspecific variation in virulence or resistance in the parasitoid or in its host, respectively (Carton and Nappi 1997; Kraaijeveld and Godfray 1999).

7.3.2.2 Host regulation

Because of the close physiological proximity between the two partners, synchronization of their development is necessary to ensure the survival of the parasitoid. Lawrence (1986) distinguishes two kinds of parasitoid: 'conformers' who use the hormones of the host to adjust their own development and 'regulators' who disturb the host's developmental schedule inducing either supplementary or precocious moults or by definitively blocking the host in an immature stage. These manipulations of the host's physiology imply several regulating factors of the two main hormones (**juvenile hormone** and **ecdysteroids**) that are involved in moulting and metamorphosis (Beckage and Gelman 2004).

7.3.2.3 Virulence and regulation factors

The study of virulence and regulation factors is currently a very active research area and several reviews have been published (Strand and Pech 1995; Beckage and Gelman 2004; Pennacchio and Strand 2006). Venom is probably the 'ancestral weapon' against host defences. Its primary role is to, temporarily or permanently, paralyse the host. Sometimes, it also contributes to host regulation by blocking the moults. In some species, venom can enhance the efficiency of other virulence factors like **polyDNAvirus** (PDV). PDVs are particular symbionts (called braco- or ichneumo-viruses) found in two families of hymenopteran parasitoids, Braconidae and Ichneumonidae, respectively. PDVs have a great similarity with viruses (Box 7.3) but their DNA is integrated as a provirus into the host genome and their replication only occurs in some particular tissues and at precise stages in the development of the female parasitoid. Viruses are injected into the host during oviposition, where they are expressed more or less rapidly and durably depending on the species attacked. PDVs are now known to play a major role in the suppression of the host's immune defence through the

Box 7.3 Parasitoid symbionts

In addition to their hosts, parasitoids interact in the wild with numerous other organisms: predators, pathogens, competitors, etc. Among these, **endosymbionts** have been neglected for a long time. However, their influence on the parasitoid phenotype and their impact on ecological and evolutionary processes have become more and more obvious (Boulétreau and Fleury 2005). These symbionts are mainly viruses or bacteria.

Viruses

Parasitoids, in particular hymenopteran wasps, harbour numerous DNA (e.g. Ascovirus) or RNA (Reovirus) viruses with variable influence (Renault *et al.* 2005; Stasiak *et al.* 2005). In numerous cases, the virus uses the parasitoid as a vector for transmission to its actual host. Then it quickly multiplies, leading to the death of the host and the parasitoid. In this case, the virus can be viewed as a parasite or as a competitor of the parasitoid since its development is detrimental to the parasitoid's offspring. In other cases, the relationship is rather commensal, the virus being either transmitted horizontally (via the parasitic behaviour of the parasitoid) or vertically (from the parasitoid female to its offspring) without having a significant impact on the parasitoid. Finally, the interaction between parasitoids and their viruses has sometimes seemingly evolved towards a real mutualism. In this latter case, the two partners have co-evolved so tightly that some researchers no longer consider the current virus to be a true one but rather an organelle like a mitochondrion (Federici and Bigot 2003). Indeed, they not only play a major role as virulence factors in the development of the wasp (Section 7.3.2.3) but also completely depend on the development of the wasp for their own transmission since their DNA is integrated into the wasp's genome.

More recently, the influence of a virus on superparasitic behaviour, i.e. the decision to lay an egg in an already parasitized host (Section 7.3.1.3), has been demonstrated in a wasp species highlighting the wide range of possible biological interactions between the two partners (Varaldi *et al.* 2003).

Bacteria

Parasitoids are also hosts of numerous bacteria. For instance, the alpha-proteobacteria of the genus *Wolbachia* infect at least 16% of insect species and in particular numerous hymenopteran parasitoids (Werren and Windsor 2000). These rickettsia are endosymbionts and are located within the cytoplasm of their host cells. Their effects on their hosts are complex and variable. One of the most spectacular is undoubtedly the manipulation of parasitoid reproduction. In some haplo-diploid species (Section 7.2.3), some *Wolbachia* strains are able to induce thelytoky, the female parasitoids then being able to produce daughters without mating. Since the parasitoid males have no direct effect on the host populations, such thelytokous strains could be interesting for biological control in order both to limit mass-rearing costs and to increase the efficiency of releases (Stouthamer 2003). In other species, some *Wolbachia* variants induce **cytoplasmic incompatibilities** (CI). Female offspring are then reduced in some crosses involving partners with 'incompatible' variants. The consequences of CI are probably vast and range from reproductive isolation between populations with different variants to the disturbance of clutch size adjustment or sex allocation (Section 7.2.3). The outcome of endosymbiont–parasitoid interactions can be astonishing, as in the braconid *Asobara tabida* where *Wolbachia* has became necessary for oogenesis (Dedeine *et al.* 2001).

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Box 7.3 continued

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modification or destruction of some targeted cells. In numerous cases, PDVs can also modify the endocrine system by either inducing precocious moults or metamorphosis or blocking the development of the host. In other species, 'virus-like particles' play a similar role to PDVs. However, they do not contain nucleic acids.

Some parasitoid species also exhibit teratocytes, particular cells originating from an extra-embryonic membrane. Soon after hatching of the egg they differentiate and are released freely in the host's haemolymph. Their role is still not totally clear but they could be used as a nutritional source for the parasitoid. Other functions, like host regulation, are also cited. Finally, some immature parasitoids can directly contribute, through their own secretions, to host regulation. Several experimental works have demonstrated that some parasitoids are also able to release hormones into the host in order to modify its development.

7.4 Demographic characteristics of host–parasitoid interactions

There are now a large number of works, some experimental but mainly theoretical, that have tried to describe, understand, and thus explain temporal fluctuations in the number of parasitoids and their hosts. There are several reasons why such a research effort has been maintained over several decades. The first is that the ecological features of parasitoids, as has briefly been described in the previous sections, are relatively easy to formalize mathematically. For example, in contrast to what can be observed in predators, only female parasitoids seek and attack hosts. Moreover, since a host that has been attacked almost always dies, there is a direct relationship between the search efficiency of parasitoid females and the host mortality rate. Similarly, the reproductive success of female parasitoids is directly linked to the number of hosts attacked. Finally, hosts and parasitoids have similar generation times. Also, insect parasitoids can be used to control pests on different crops, and the goal in this case is to reduce the number of hosts (see Section 7.5). For this, an accurate understanding of the mechanisms involved in host–parasitoid dynamics is needed.

7.4.1 A basic demographic model

Several modelling approaches have been developed over the years (see Hassell 1978; Nisbet and Gurnet 1982; Begon and Mortimer 1986). Here, we will present the developments arising from the Nicholson and Bailey (1935) model only. All the corresponding models are based on the following basic equations:

$$\begin{cases} H_{t+1} = \mathrm{e}^{r}(H_t - H_a) \\ P_{t+1} = H_a. \end{cases} \tag{7.1}$$

In this model, H_t and P_t are the size of the host and parasitoid populations, respectively, at generation t and H_a is the number of hosts attacked in this generation. Without parasitism, the host population shows exponential growth with rate r. At generation $t+1$, the size of the host population is the number of hosts escaping from parasitism in the preceding generation, taking into account its exponential growth, and each host attacked at generation t gives rise to a parasitoid at generation $t+1$.

Let us suppose now that female parasitoids search for their hosts randomly and that each host found is attacked. If R_t is the number of host–parasitoid encounters at generation t and A is the proportion of hosts encountered by each parasitoid at this generation (A is sometimes called the 'area of discovery' of the parasitoid), then $R_t = AH_tP_t$, and the number of host–parasitoid encounters per host is thus $R_t/H_t = AP_t$. The hypothesis that parasitoids are searching for their hosts randomly implies that the proportion p_0 of hosts that are not encountered by parasitoids corresponds to the first term of a Poisson distribution having the number of host–parasitoid encounters per host as an average value. Thus, $p_0 = \exp(-R_t/H_t)$ leading to $p_0 = \exp(-AP_t)$. The number of hosts attacked at generation t thus becomes $H_a = H_t[1 - \exp(-AP_t)]$ and, substituting this in the equation system describing the dynamics of host–parasitoid interaction, we obtain:

$$\begin{cases} H_{t+1} = H_t \exp(r - AP_t) \\ P_{t+1} = H_t[1 - \exp(AP_t)]. \end{cases} \tag{7.2}$$

This is the Nicholson and Bailey (1935) model whose properties are well known. More accurately, for each value of r and A, there is an equilibrium demographic situation that is actually unstable since a slight disturbance from this equilibrium leads to divergent oscillations, leading both populations to disappear (see Fig. 7.2). In real situations, host–parasitoid associations are generally demographically stable since both partners can persist during the course of time. The aim of several theoretical works was thus to modify the original Nicholson and Bailey (1935) model in order to increase its stability.

7.4.2 Effect of competition between hosts

An obvious improvement of the Nicholson and Bailey (1935) model is to replace the exponential growth of the host population by a **density-dependent increase** resulting from intraspecific competition between hosts. For this, the constant growth rate r of the host population can be replaced by a growth rate that is inversely proportional to the size of the population: $r(1—H_t/K)$. This growth rate decreases linearly from the value r, when $H_t = 0$, down to zero when $H_t = K$. K is the

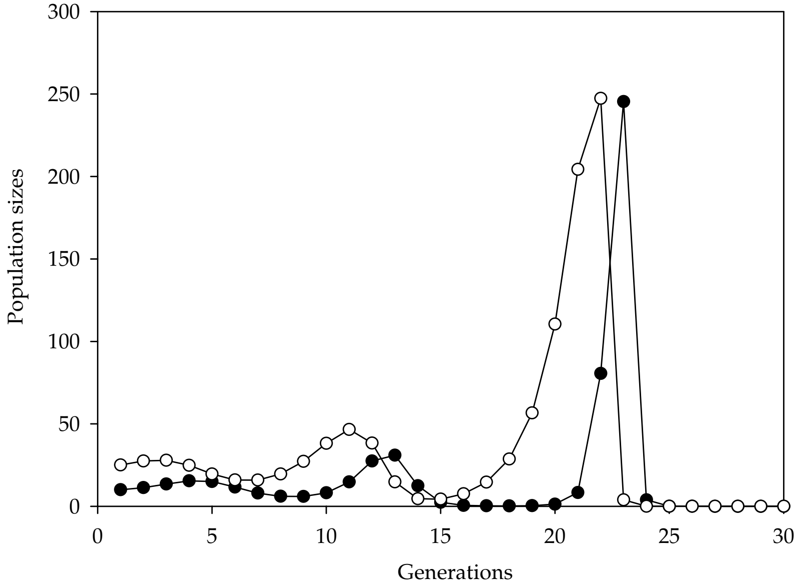

Figure 7.2 Example of demographic fluctuations between hosts (open circles) and their parasitoids (black circles), as computed from the Nicholson and Bailey (1935) model (Eqn 7.2), with $r = 0.693$ and $A = 0.6$.

'carrying capacity' of the environment corresponding to the maximum size the host population will reach without parasitism. The modification leads to the following equation system:

$$\begin{cases} H_{t+1} = H_t \exp\left[r\left(1-\frac{H_t}{K}\right) - AP_t \right] \\ P_{t+1} = H_t[1-\exp(-AP_t)]. \end{cases} \tag{7.3}$$

This the Beddington *et al.* (1975) model that, in contrast to the original Nicholson and Bailey (1935) model, can produce stable demographic equilibria for specific values of the parameters, as can be seen in Fig. 7.3. More accurately, the conditions for stability depend on both the value of r and on the efficiency of the destructive effect parasitoids have on their hosts. The competition between hosts seems to be a non-negligible factor in the demographic stability of host–parasitoid interactions.

7.4.3 Effect of the number of hosts

The Nicholson and Bailey (1935) model assumes that the number of hosts attacked by each parasitoid increases linearly with host density, which is rather unlikely. Indeed, numerous experimental works have demonstrated that female parasitoids need a certain amount of time, that differs among species but that can be important, to attack each host that is encountered. When the number of hosts is important, such time constraint can limit the impact of parasitism on the host population, and the relationship between the number of hosts attacked by each parasitoid and host density (the so-called 'functional response') is concave down. Taking into account such a phenomenon leads us to modify the parameter A describing the proportion of hosts encountered by each parasitoid. If a is the instantaneous rate of host searching by each parasitoid and T_h is the time taken to attacked each host, then it can be demonstrated that adding a concave down functional response leads to $A = (aT)/(1 + aT_hH_t)$, where T is the total time available for each female. Such a new formulation of the parameter A leads to a modification of the initial Nicholson and Bailey (1935) model and the new

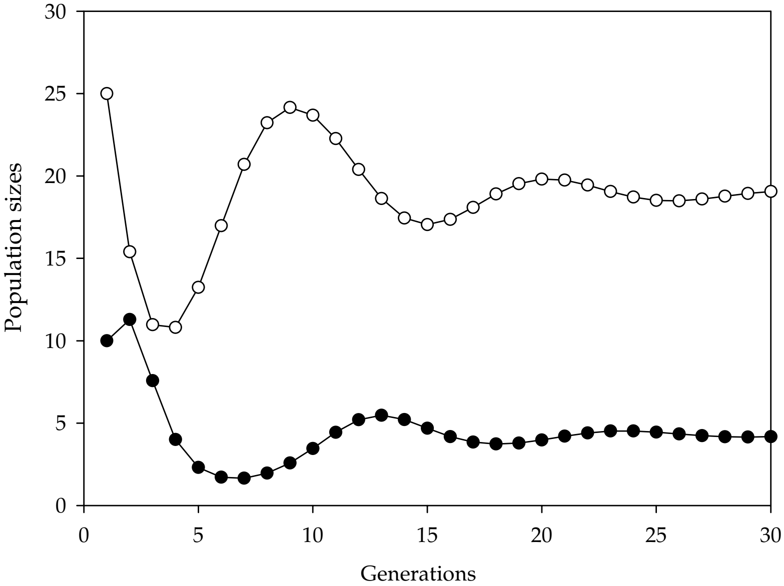

Figure 7.3 Example of demographic fluctuations between hosts (open circles) and their parasitoids (black circles), as computed from the Beddington *et al.* (1975) model (Eqn 7.3), with $r = 0.693$, $A = 0.6$ and $K = 30$. In this case, it is possible to demonstrate that both host and parasitoid population sizes converge to stable values, through oscillations that are getting smaller and smaller.

equation system:

$$\begin{cases} H_{t+1} = H_t \exp\left(r - \dfrac{aTP_t}{1 + aT_h H_t} \right) \\ P_{t+1} = H_t \left[1 - \exp\left(\dfrac{-aTP_t}{1 + aT_h H_t} \right) \right] \end{cases} \tag{7.4}$$

The dynamic properties of this model were examined by Hassell and May (1973). In all cases, such models are even less demographically stable than the original Nicholson and Bailey (1935) model, that can be regained when $T_h = 0$. This is due to the fact that the modification implies a destructive effect of parasitoids on their hosts that is weaker at higher host densities, in contradiction to what we would expect for a stabilizing mechanism.

7.4.4 Effect of host distribution

The Nicholson and Bailey (1935) model also assumes that host–parasitoid encounters occur randomly, despite the fact that numerous experimental works have demonstrated that female parasitoids are mostly aggregated where there is a high density of hosts. In this case, the use of a Poisson distribution to describe the number of host–parasitoid encounters is no longer correct. A so-called 'binomial distribution' seems to work better in describing observed situations (May 1978). In this case, the probability p_0 of escaping parasitism corresponds to $(1 + AP_t/k)^{-k}$, where k determines the level of aggregation of host–parasitoid encounters. The lower k is, the higher the parasitoid aggregation for higher host densities. Reciprocally, when k tends to infinity, we get back to a Poisson distribution describing randomly occurring host–parasitoid encounters. By simultaneously taking into account such an aggregation factor and competition between hosts (Section 7.4.2) we get the following equation system:

$$\begin{cases} H_{t+1} = H_t \exp\left[r\left(1 - \dfrac{H_t}{K} \right) \right] \left(1 + \dfrac{AP_t}{k} \right)^{-k} \\ P_{t+1} = H_t \left[1 - \left(1 + \dfrac{AP_t}{k} \right)^{-k} \right] \end{cases} \tag{7.5}$$

Analysis of the dynamic properties of this model shows that decreasing values of k (i.e. increasing the level of aggregation of host–parasitoid encounters) increases the number of situations in which host–parasitoid demographic interactions are stable over the course of time. Aggregation of host–parasitoid encounters is now still considered to be the most powerful mechanism leading to stability of host–parasitoid demographic interactions.

More accurately, the analysis of this model globally shows that host–parasitoid demographic interactions should be stable as soon as $k < 1$ (May 1978). The mechanism of aggregation taken into account in this model is based on spatial heterogeneity in the distribution of hosts that are located in patches in the environment. May (1978) actually demonstrated that there is a tight relationship between the distribution of attacks on hosts and the spatial distribution of the hosts. The relationship leads to $k = (1/CV)^2$, where CV is the coefficient of variation of host density between patches. Hence, host–parasitoid demographic interactions should be stable as soon as $CV^2 > 1$, a condition described in the literature as the 'CV^2 rule' (Hassell and Pacala 1990). An important number of experimental and theoretical works have demonstrated that such a rule, which appears to be particularly simple, would be valid, although it is still being intensively debated (Bernstein 2000).

7.4.5 Effect of the number of parasitoids

The original Nicholson and Bailey (1935) model also assumed that the host searching efficacy of each parasitoid female remains constant, despite an important number of experimental works demonstrating that such efficacy apparently decreases when the number of parasitoid females increases. Such a decrease, which is the result of competition between females, is usually linear on a log–log scale. Thus, in an empirical way, $\log(A) = \log(Q) - m \log(P_t)$, leading to replacement of the parameter A by QP_t^{-m}, where Q is the intercept of the plot (searching efficiency of parasitoids when they are alone) and m is the slope describing the intensity of the phenomenon (Hassell and Varley 1969).

Taking account of this new modification leads to the following equation system:

$$\begin{cases} H_{t+1} = H_t \exp(r - QP_t^{1-m}) \\ P_{t+1} = H_t[1 - \exp(-QP_t^{1-m})]. \end{cases} \tag{7.6}$$

This model returns to the Nicholson and Bailey (1935) model when $m = 0$. Analysis of its stability conditions shows that competition between parasitoid females can represent an important stabilizing factor. It should be noted that this phenomenon is tightly linked to the mechanisms of aggregation of host attacks described in the previous section. This probably explains its important stabilizing effect (Hassell 1978; Begon and Mortimer 1986).

7.5 The use of parasitoids in plant protection

As shown in the previous sections, the successful development of parasitoids usually causes the death of their hosts. At the population level, this feature contributes to the regulation of host populations. Parasitoids can therefore be used as a means to reduce the impact of crop pests. This is the aim of biological control, broadly defined as 'the use of living organisms [called biological control agents] to control the population density or impact on a specific pest organism, making it less abundant than it would otherwise be' (OILB-SROP 1973). It is worth noting that parasitoid species are not the only biological control agents that can be used. Other natural antagonists can be used: predators, true parasites (like viruses), pathogens, or even competitors. Moreover, biological control is not restricted to the regulation of noxious arthropods but can also be used against weeds or even vertebrates. From an agronomic point of view, biological control constitutes one facet of crop protection programmes in addition to (or as a replacement for) other means like chemical and physical controls or the use of naturally resistant or transgenic plants. Four different strategies of biological control can be distinguished (Eilenberg *et al.* 2001), each of them being associated with specific scientific questions.

7.5.1 Classical biological control

This strategy aims to introduce an exotic biological control agent into the agrosystem, with the hope that it will become permanently established and provide durable control of the targeted pest. Historically, such a strategy seems to have been used for the first time at the end of the 19th century against the cottony cushion scale, *Icerya purchasi*. This insect had previously been inadvertently introduced from Australia and rapidly became a severe pest in Californian citrus groves. A screening of its natural enemies in Australia indicated the presence of a predatory beetle, *Rodolia cardinalis*. This beetle was consequently introduced to the USA, mass-reared in quarantine, and released into the citrus groves. Two years after its introduction, damage caused by the pest became almost negligible. After this first success, the introduction of exotic natural enemies has been repeatedly used worldwide with numerous other successes. As suggested by this case study, the pest is usually an exotic species which causes outbreaks in the absence of natural enemies or for other ecological reasons (Colautti *et al.* 2004). The introduction of one or several **sympatric** antagonists is thought to restore a demographic balance with a low level of the pest population in a new ecological context ('original classical biological control' *sensu* Eilenberg *et al.*, 2001). In other cases, an exotic biological control agent can be used against either an indigenous pest or an exotic but allopatric one. In such cases, the challenge is to create a new ecological interaction between two species which have never co-evolved ('new association classical biological control').

From an economic perspective, classical biological control is very interesting: for the durable control achieved, with no further need for human intervention, the associated costs of development and use are small. Nevertheless, it is noteworthy that the success of such strategies varies greatly. Greathead (1995) estimated that only 10% of the 4500 introductions of biological controls against noxious insects gave economically acceptable control. Consequently, one of the major goals for researchers and practitioners of biological control is to identify the causes of success or failure. This can be done by the use of specific databases (like BIOCAT) containing data from all realized biological control programmes (Greathead and Greathead 1992). Meta-analyses have been carried out to test the importance of numerous features of the biological control agent such as taxonomic origin (Lane *et al.* 1999), fecundity (Lane *et al.* 1999), host feeding behaviour (Jervis *et al.* 1996), functional response (Fernandez and Corley 2003), host specificity (Stiling and Cornelissen 2005), or the relevance of 'multiple species' versus 'single species' introductions (Denoth *et al*. 2002; Stiling and Cornelissen 2005).

Independently of the efficiency of the biological control programme against the targeted host, the impact of biological control agents on potential non-target species should also be studied in order to limit post-release ecological risks (Section 7.5.5.2).

7.5.2 Inoculation biological control

When pests attack non-perennial crops, the biological control agent released cannot usually become permanently established. In such cases, inoculation biological control aims at establishing a biological control agent for an acceptable but temporary period of time. This strategy is used worldwide, especially in greenhouses. Van Lenteren (2000) estimated that pests in 5% of the 300,000 ha of greenhouses are controlled using **integrated pest management**, which favours the use of inoculative releases of parasitoids. This proportion should reach 20% in the near future. The success of inoculation biological control can be explained by the wide range of available biological control agents (more than a thousand).

Contrary to classical biological control, inoculation biological control (and also inundation biological control) requires a continuous supply of large numbers of biological control agents. However, this leads to new difficulties that have to be solved. The production and storage conditions must protect the quality of the biological control agents as well as their fecundity, longevity, dispersal ability, etc. Moreover, numerous authors have highlighted the possible genetic impact that mass-rearing conditions could have on biological control agents (van Lenteren 2003; Wajnberg 2004). As indicated in Table 7.1, the conditions during the mass-rearing step are usually very different from those encountered in real agrosystems. Knowing whether or not (and if so how) some identified selective pressures, drift events, or inbreeding can modify the genetic makeup of the initial strain of the biological control agent is also of utmost importance.

7.5.3 Inundation biological control

Here the aim is to control the pest population through a one-off impact of the released biological control agents. Unlike in the first two strategies, the primary goal is here a drastic and time-limited impact on the pest population. The impact of the offspring of the biological control agent can also be interesting, but is usually not a goal *per se*. This method greatly modifies the criteria used for the selection of efficient parasitoid species. For instance, idiobionts (Section 7.2.4) attacking their hosts at precocious stages or highly fecund species are very interesting for this purpose. These features explain the success obtained with the use of egg parasitoids in general, and more particularly with the inundative releases of *Trichogramma* spp. (Wajnberg and Hassan 1994). *Trichogramma* are minute Hymenoptera that lay their eggs within the eggs of Lepidoptera. Several species (e.g. *Trichogramma brassicae*, *Trichogramma cacoeciae*,

Table 7.1 Comparison between mass-rearing and post-release environmental conditions encountered by biological control agents. After van Lenteren (2003)

	Mass-rearing	Agrosystem
Abiotic factors (temperature, photoperiod, humidity, etc.)	Stable, homogeneous	Varying, heterogeneous
Host presence	High density. Uniform distribution and quality	Variable density and quality. Aggregative distribution
Interspecific interactions (competition, predation, etc.)	Limited	Important
Mating	Facilitated	More difficult
Dispersal	Limited	Necessary

Trichogramma dendrolimi, *Trichogramma evanescens*, etc.) are used for the biological control of pests of different crops (e.g. cereals, cotton, sugar cane, vegetables) over a total area of between 15 and 30 Mha (Li-Ying 1994; van Lenteren and Bueno 2003). For instance, more than 80,000 ha of corn are protected each year in France against the European corn borer, *Ostrinia nubilalis* thanks to the inundative release of *T. brassicae*. About 200,000 *Trichogramma* per hectare are required in this case (Frandon and Kabiri 1999). This clearly highlights the need for optimization of both the mass-rearing and the field release steps. This not only implies technological advances but also scientific work dealing with several fields of parasitoid biology. Ecophysiological studies are needed, for instance, to understand the role of abiotic (e.g. temperature, humidity, photoperiod) or biotic (host species) factors. It is worth noting that spectacular advances have been achieved in this field, leading for instance to the ability to produce some parasitoid species on artificial diets (Thompson 1999). The behavioural ecology of parasitoids should also be investigated in order to understand host searching behaviour or dispersal patterns. More generally, ecological work must lead to an accurate description of the demographic impact of the biological control agents on the target hosts as well as on related species in the community.

7.5.4 Conservation biological control

The aim of this strategy is to modify the agrosystem or agricultural practices in a way that will favour the action of a pest's native natural enemies. To date, this method is probably less developed than the others. Nevertheless, it offers some practical solutions and raises numerous scientific questions dealing with community ecology (Landis *et al*. 2000). Three non-exclusive tactics can be distinguished. The first one relies on the availability of shelters or microclimates that will favour the perennial presence of the biological control agent(s). Indeed, extreme temperatures are unfavourable for their activity or even dangerous to their survival. Neighbouring shaded areas (hedges for instance) can be used as temporary refuges. The use of sites for overwintering can also promote the establishment of parasitoids during harsh conditions and favour more precocious pest control efficiency. The second tactic is to provide sources of food for the biological control agents. This can be done by growing some plant species producing pollen and nectar that can be used by the adult parasitoids. For instance, the influence of several flowers on the parasitoid *Diadegma insulare* has been investigated for biological control of the diamondback moth, *Plutella xylostella* (Idris and Grafius 1995). A last possibility is to provide or maintain a supply of hosts within or close to the crop. This will slow down the post-harvest escape of the biological control agent. The persistence of some generalist parasitoids can also be ensured through the use of plants that will be infested by other host species. These so-called 'plant banks' are currently used in greenhouses or near outdoor crops. Around 3 Mha are planted with spatially alternating wheat and cotton (Landis *et al*. 2000). The wheat is used as a source of natural biological controls in order to protect the cotton plantation more efficiently.

From an ecological point of view, all these practices favour both plant and animal biodiversity within the agrosystem. However, this is not a specific goal, and an increased biodiversity can even sometimes produce an unfavourable effect. For instance, Baggen and Gurr (1998) and Baggen *et al*. (1999) observed contradictory results between the positive influence of a flower on the parasitoid *Copidosoma koehleri* in laboratory conditions and the failure of its pest control efficacy during field trials. They finally observed that the selected plant was not only beneficial for the parasitoid but also for the pest. Only an accurate screening finally allowed the identification of a plant species with a differential impact on the two species. This shows how and why conservation biological control can depend on complex ecological interactions.

7.5.5 The limits of biological control

As previously seen, biological control can be an efficient way to protect crops, human health, and, in most cases, the environment. However, sometimes it is uneconomic. Moreover, unintended negative effects must also be avoided.

7.5.5.1 Economic and social costs

Both the economic and social costs of biological control depend on the strategy used. Unfortunately, most studies deal with classical biological control only (Tisdell 1990). The costs of inoculation or inundation biological control greatly vary according to different factors including: (1) the cost of the method itself (shipment, release, etc.); (2) the actual reduction in damage caused by the pest; (3) the correlated increase of yield and total production of the system; (4) the increase in harvest quality and corresponding price; (5) the relative gain compared with other methods; (6) the social or even health gains (Huffaker *et al*. 1976; Tisdell 1990). Despite this complexity, the ecological and economic benefits associated with biological control seem very high compared with chemical control (Table 7.2).

7.5.5.2 Unintended effects

During the last 120 years, more than 2000 arthropods have been introduced as biological control agents in around 200 countries or islands. Only 1.5% of these introductions have been followed by negative effects on the environment (van Lenteren *et al*. 2006). Nevertheless, the question of unintended ecological risks is currently being intensely debated from both a scientific and a political point of view. As a consequence, several countries have set up legislation governing the introduction of biological control agents (Wajnberg *et al*. 2001; Louda *et al*. 2003; van Lenteren *et al*. 2006). Potential risks associated with biological control programs can appear when the released biological control agents: (1) are attacking one or several non-target species and are dangerously affecting their demography; (2) are competing with one or several species of the same trophic level; (3) are harbouring pathogens that are noxious for **endemic** species. Such unintended effects can also create economic costs if the released agents disturb other useful species (for instance, natural enemies of weeds). Health problems like allergies can also occur during the mass-rearing of some biological control agents. Although rare, such negative side-effects can tarnish the image of biological control and also limit its actual development. This is why the international scientific community has suggested different approaches in order to check, as far as possible, the innocuousness of the released agents. Accurate experimental designs and guidelines have been established for several key points.

The most sensitive point is of course the specificity of the biological control agent, which is not a simple point to resolve. Indeed, host range is not necessarily known as only partial data are usually available in the literature or museum collections. Laboratory experiments are thus required, during which several potential hosts are offered to the parasitoids. The presence or absence of parasitism is then checked in each case. In order to limit such a time-consuming task, Wapshere (1974) proposed a 'centrifugal phylogenetic testing method' or the successive testing of potential hosts from species closely related to the target pest to progressively more distantly related species until the host range has been adequately circumscribed. Such experimental trials can be done in choice or non-choice conditions which respectively correspond to cases

Table 7.2 Comparison of the relative performance of biological and chemical control of crop pests. Data for chemical control were established by the pesticide industry. After van Lenteren (1997)

	Chemical control	**Biological control**
Number of tested products or agents	More than a million	Around 2000
Success rate	1:30,000	1:10
Development costs	Around US$160 millions	Around US$2 million
Development time	10 years	10 years
Gain/cost ratio	2:1	20:1
Risk of acquisition of resistance	High	Very low
Specificity	Weak	Good
Noxious side-effects	Numerous and important	Almost nil

where several or only one species are offered during a trial. The collected data can be then adequately analysed using specific statistical tools (Prince *et al*. 2004; Babendreier *et al*. 2005). Field studies should also be realized in order to compare the dynamics of the target pest inside or outside the area where the biological control agent has been released. In some cases, non-target hosts are also released in order to estimate if or by how much they are attacked by the parasitoids (Mills 1997).

Since biological control agents could also outcompete species of the same trophic level, faunistic survey must be carried out in order to quantify their impact inside the release area in comparison with the pre-release state or surrounding areas. This work should also be linked to laboratory experiments in order to identify more accurately the mechanisms of interspecific competition. This is undoubtedly a difficult task, because the outcome of competition between two parasitoids varies greatly with the biological features of the two protagonists like host range, searching efficiency, host discrimination, competitive ability of the larvae, adult life-history traits, etc.

Finally, it is necessary to verify that the biological control agent will not disperse from the targeted crops to invade new environments. This can be done using experimental designs where traps are regularly placed around the release area. Powerful statistical methods have been developed to analyse results obtained from such studies (Mills *et al*. 2006).

7.5.6 Improving biological control through ecological- and population-based approaches

Optimization of biological control methods simultaneously implies improvement in the pest control efficacy, decrease in the associated costs, and minimization of potential unintended effects. Within this context, much progress on different aspects has been made during recent years: (1) mass-rearing conditions and quality control of the biological control agents; (2) their storage and methods of transporting; and (3) the release strategies. In addition to this empirical process, it seems more and more obvious that there is a need to accurately understand the underlying mechanisms. Biological control is thus nowadays recognized as a real ecology- and population biology-based method (Waage 1990). From this point of view, improved biological control using parasitoid species should be reachable using all the different concepts, information, and tools that have been introduced in this chapter. The main objective of this approach is to scientifically explore both the parameters linked to the efficiency of a parasitoid and their determinants. This is of course a central problem which is not easy to solve, since it varies with the features of the pest, the agrosystem, and more generally the abiotic and biotic environmental factors (Waage 1990).

As described in previous sections, the sequence of parasitism can be divided into successive steps from the search for a potential habitat with hosts to the emergence of the adult offspring. The pre-ovipositional steps are mainly determined by the ability of the females to detect cues from their biotic and abiotic environment. An adequate response of parasitoid females to this different information is necessary for finding a mate, for finding hosts, and finally for efficient control of the targeted pest. In this context, improvement of biological control must be based on ecological studies of the parasitoid, with the objective of analysing and understanding the different mechanisms and their sources of variability. Our brief description of the theoretical approaches to host–parasitoid demographic interactions has also shown how ecological and behavioural features of the parasitoids can affect the host population. Once the parameters of parasitoid efficiency have been defined, the next step is to choose the species to use as a biological control agent. It requires complementary and modern approaches or tools such as comparative analysis that can be used to identify the relative role of the **phylogeny** and the ecological determinants of the parasitoid life-history traits (Harvey and Pagel 1991; Martins 1996). The biological features of the parasitoids that affect their pest control efficiency should also be investigated at the intraspecific level, since strong genetic variability for these parameters can occur both within and between populations.

This shows how the aim of improving the efficacy of biological control programmes is deeply rooted in the disciplines of evolutionary biology and, particularly, behavioural ecology. The biological features of parasitoids are considered to be important components of their adaptive strategies under given environmental conditions. In the particular case of parasitoids, reproduction is directly linked to the destruction of the host, so that identification of factors and strategies that optimize their **fitness** should also improve their pest control efficacy in biological control programmes. Finally, the necessary comparisons of faunistic surveys before and after biological control agents have been released as well as the practices in conservation biological control are also directly connected with the current concern about biodiversity in natural or cultivated areas.

7.6 Conclusion

Parasitoid insects have several biological, ecological, and evolutionary features that make them an ideal model for addressing questions in population biology, from behavioural ecology to population dynamics. We have seen that the study of their reproductive strategies, which show important interspecific variation, raises several problems that can only be solved though the use of tools and methods from several diverse fields like molecular biology, biochemistry, and physiology, but also organism biology, population genetics, and even theoretical or community ecology.

Moreover, the particular mode of development of parasitoid insects enables us to use them in pest control strategies to protect crops. In recent decades this application has seen progressive uptake all over the world as the economics become favourable, leading to increasing avoidance of chemical pesticides that are noxious to both the environment and human health. The design of efficient biological control programmes against phytophagous pests on a given crop system implies the identification of potential biological control agents for production and release, along with an accurate understanding of their biology. This needs both pragmatic, empirical studies and a more formal approach based on evolutionary biology and ecology. Such combined fundamental and applied scientific work explains why a significant number of research laboratories worldwide are currently working on insect parasitoids. These research laboratories are producing on a regular basis fascinating results demonstrating—contrary to what this chapter might suggest—that several important mechanisms involved in host–parasitoid associations still remain to be discovered. The aim of this chapter is to give the reader basic knowledge to enable an understanding of what parasitoid insects, their biology, and ecology are and how they can be used as biological control agents for controlling crop pests. It would be wonderful if readers were inspired to start a scientific research programme focusing on these fascinating organisms.

Important points

- Parasitoids are insects whose pre-imaginal development occurs by eating vital tissues from other living beings, mainly other insects. This usually implies that their development leads to the death of their hosts.
- Under the influence of strong selective pressures, different reproductive strategies and modes of interaction with their hosts have progressively appeared, leading to important interspecific variations.
- The use of mathematical models for analysing the dynamic interactions between parasitoids and their hosts has led to the identification of several key features (for both partners) that influence the demographic stability of their interaction and the ability of parasitoids to control the size of the host population.
- Due to the fact that parasitoids usually kill their hosts, they can be used for biological control programmes to control phytophagous pests on crops. It is now fully recognized that improving the efficacy of such a pest control strategy requires the use of concepts and tools developed in ecology and evolutionary and population biology.

Questions for discussion

- What are the differences between parasitoids and ‘real’ parasites, both in their biology and in the corresponding ecological consequences?
- According to the theoretical models in this chapter describing the demographic interactions

between parasitoids and their hosts, what are the behavioural mechanisms influencing the stability of such interactions and those that should not have any effect?

- According to the ecology of insect parasitoids, what could be done to improve their efficacy to control insect pests when they are released for biological control programmes.

Further reading

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