



Foraging Behaviour

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1.1 Behaviour of Insect Parasitoids and Predators

In this chapter, we consider practical aspects of the foraging behaviour of insect natural enemies in its widest sense (so wide that we even include a few examples concerning non-insect arthropods, such as mites). Initially, most insect natural enemies must locate the habitat where potential victims may be found. Within that habitat, the victims themselves must be discovered. Once a patch of potential targets is identified, the predator or female parasitoid must choose its victim. Furthermore, in judging host quality, a female parasitoid must decide whether to feed from the host, to oviposit, or to do both. If she does decide to oviposit, then there are questions of sex allocation and offspring number that need

to be addressed (Fig. 1.1). All of these activities fall under the aegis of ‘foraging behaviour’.

Studies of the foraging behaviour of insect natural enemies lie at the heart of much of modern ecology. These studies have taken two broadly defined pathways, where the emphasis is determined by the interest of the researcher (see below). Irrespective of the motivation of the researcher, it is clear that any attempt to understand the foraging behaviour of a predator or a parasitoid will greatly benefit from knowledge gleaned from both approaches. This cross-fertilisation of ideas is something we try to emphasise in this chapter.

In addition, we provide a review of the foraging behaviour of insect natural enemies. This is meant to be illustrative, with stress placed on the experiments used to study the behaviour itself. For greater detail on the behaviour of parasitoids one should refer to Godfray (1994), Quicke

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Which patches to visit

Whether to oviposit and/or feed on a host

How much haemolymph to remove from a host
when feeding

What clutch size to produce for each host
attacked (and whether to oviposit in an
already parasitised hosts, *i.e.*,
superparasitise it)

What sex ratio of progeny to produce

When to leave a patch

Fig. 1.1 Foraging decisions. In adopting either the functional or the causal approach to studying predator and parasitoid behaviour, it is useful to consider that foraging insect natural enemies are faced with a number of consecutive or simultaneous decisions. Listed in this figure are some of the questions that may need to be addressed by a gregarious host-feeding parasitoid

(1997) and Wajnberg et al. (2008) and, for a shorter overview, to Hardy and Godfray (2023). The literature on insect predators is much more diffuse, but New (1991) provides a good introduction to the behaviour of predators in general, while Dixon (2000) reviews the behaviour of ladybird beetles (Coccinellidae), and Davies et al. (2012) provide an excellent introduction to many aspects of animal behaviour in general.

Where possible, we deal with insect predators and parasitoids together, although there are some

sections (e.g., sex allocation, Sect. 1.11) where the examples come exclusively from the parasitoid literature, and other sections (e.g., superparasitism/cannibalism, Sect. 1.9) where both are dealt with, but separately. Nevertheless, many of the approaches to studying foraging behaviour, and the theory underpinning it, are similar for both predators and parasitoids.

In this chapter, we first describe the methodological approaches that underpin studies of the foraging behaviour of insect natural enemies. Second, we discuss how the predators and parasitoids find the habitat patches where potential prey or hosts may be encountered. Third, we reflect on what occurs after the prey or host is found, dealing with issues such as clutch size and sex allocation decisions, and patch defence behaviour. We also deal with considerations such as the cost of reproduction to natural enemies and the resistance of their hosts or prey to being exploited. Finally, we touch briefly upon some of the wider population and ecological consequences of insect natural enemy foraging behaviour.

1.2 Methodology

1.2.1 The Causal Approach

Until the late 1970s, parasitoid foraging behaviour was mostly studied from a proximate (*i.e.*, causal or mechanistic) standpoint, with a strong emphasis on identifying which stimuli parasitoids respond to both in finding and in recognising their hosts. Through this approach, fascinating insights into parasitoid foraging behaviour have been gained, and it has been demonstrated that often an intricate tritrophic relationship exists between phytophagous insects, their host plants and parasitoids. We now know the identities of some of the chemical compounds eliciting certain behaviours in parasitoids. Some of the research in this field has been devoted to the application to crops of chemical substances, as a mean of manipulating parasitoid behaviour in such a way that parasitism of crop pests is increased. Many parasitoid

species display individual plasticity in their responses to different cues. Associative learning (Sect. 1.6.2) of odours, colours or shapes related to the host's environment has been described for many parasitoid species (e.g., Dugatkin & Alfieri, 2003; Meiners et al., 2003a).

Often, causal questions do not involve elaborate theories. Questions of whether an organism responds to a particular chemical stimulus or not, or whether it reacts more strongly to one stimulus than to another, lead to straightforward experimental designs. It is in the technical aspects of the experiment rather than the underlying theory that the experimenter needs to be creative. However, the study of causation can be extended to ask how information is processed by the central nervous system. One can ask how a sequence of different stimuli influences the behavioural response of the animal, or how responses to the same cue may vary depending on previous experience and the internal state of the animal (Putters & van den Assem, 1988; Morris & Fellowes, 2002).

Two different causal approaches have been adopted in the study of the integrated action of a series of different stimuli on the behaviour of a foraging animal:

1. The formalisation of a hypothesis into a model of how both external information and the internal state of the animal result in behaviour, and the testing, through experiments, of the predictions of the model. Waage (1979) pioneered this approach for parasitoids. Artificial neural network models have also been used to analyse sex allocation behaviour in parasitoids (Putters & Vonk, 1991; Vonk et al., 1991).
2. The statistical analysis of time-series of behaviour to assess how the timing and sequence of events influences the behaviour of the organism. An example of this approach is the analysis of the factors influencing patch time allocation of a parasitoid, using the proportional hazards model (Haccou et al., 1991; Wajnberg et al., 1999; Tenhumberg et al., 2001a; Wajnberg, 2003, 2004, 2006 Burger et al., 2006; Parent et al., 2017).

1.2.2 The Functional Approach

The functional approach to the study of parasitoid behaviour is based on Darwinian ideas initially formalised by MacArthur and Pianka (1966) and Emlen (1966). Termed 'natural selection thinking' by Charnov (1982), it asks how natural selection may have moulded the behaviour under study.

Because foraging decisions (Fig. 1.1) determine the number of offspring produced, foraging behaviour must be under strong selection pressures. Assuming that natural selection has shaped parasitoid searching and oviposition behaviour in such a way that it maximises the probability of leaving as many healthy offspring as possible, thus maximising the ability to contribute genetically to the next generations, it is possible to predict the optimised behaviour under given circumstances. In the real world, no 'Darwinian monsters' exist that can produce limitless numbers of offspring at zero cost. Because resources are often limited and because reproduction incurs a cost (e.g., in materials and energy and foraging time, Chap. 2) to an individual, increasing investment in reproduction must always be traded off against other factors decreasing fitness (e.g., more offspring often means smaller individual offspring with shorter lifespans or lower competitive abilities). Thus, producing the maximum possible number of offspring may not be the optimal strategy.

We refer to natural selection thinking as the functional approach, because its aim is to define the function of a particular behaviour. To achieve this goal, it is necessary to show that the behaviour contributes more to the animal's fitness than alternative behaviours in the same situations. The foraging behaviour of female parasitoids has a direct influence on both the number and the quality of their offspring, so it is particularly suited for testing optimisation hypotheses. The functional approach can be applied not only to theoretical problems but also to problems such as the selection, the evaluation and the mass rearing of natural enemies and their efficacy in

biological control (van Lenteren, 2003; Plouvier & Wajnberg, 2018; Chap. 7).

There are several (related) ways of investigating functional problems in behavioural ecology, all using quantitative optimality models. One is to predict the optimised behaviour under given and relatively fixed environmental conditions, considering that the state of the foraging animal (e.g., its egg load, age, energy reserve, etc.) remains fixed throughout its lifetime. These models may be referred to as ‘static’. Other approaches explicitly take into account that the state of the animal can change, essentially due to its foraging activity and its success in finding and exploiting resources. This class of models may be referred to as ‘dynamic’. Usually, for these two types of model, the environment does not contain other competing decision-makers. In this chapter, these two first classes of model will be referred to as ‘classical models’. A third class of models takes into account the possibility that the optimal behavioural strategy will be dependent on what other individuals, attacking the same host or prey population (i.e., competing decision-makers), are doing, since these competitors are also trying to optimise their own foraging decisions. This third class of model is based on game theory. All approaches can be used to inform practical studies of insect natural enemies, and in a similar fashion, the results of practical studies can be used to construct more realistic models.

Classical Optimality Models

Optimality models are used to predict how an animal should behave so as to maximise its fitness in the long term. Classical optimality models do not explicitly take into account the foraging decisions taken by competing decision-makers. They can be designed by determining:

1. What decision assumptions apply, i.e., which of the forager’s choices (problems) are to be analysed. Some of the decisions faced by foraging natural enemies are shown in Fig. 1.1. Sexually reproducing gregarious parasitoids need to make the simultaneous

decision not only of what size of clutch to lay but also of what sex ratio of progeny to produce. The progeny and sex allocation of such parasitoids may be easier to model if the two components are assessed independently; i.e., it is assumed that the female need make only one decision. In a formal model, the decision studied must be expressed as one or more algebraic decision variables (see, e.g., Wajnberg, 2012). In some models of progeny (clutch size) allocation, the decision variable is the number of eggs laid per host, while in most models of patch exploitation the decision variable is patch residence time.

2. What currency assumptions or optimality criteria apply, i.e., how the various choices are to be evaluated. A model’s currency is the criterion used to compare alternative values of the decision variable (in other words, it is what is taken to be maximised by the animal in the short term for long-term fitness gain). For example, some foraging models maximise the net rate of energy gain per time unit while foraging, whereas others maximise the fitness of offspring per host attacked.
3. What constraint assumptions apply, i.e., what factors limit the animal’s choices, and what limits the ‘payoff’ that may be obtained. There may be various types of constraint upon foragers. These range from the phylogenetic, through the developmental, physiological and behavioural, to the animal’s time budget. Taking as an example clutch size in parasitoids, and the constraints there may be on a female’s behavioural options, an obvious constraint is the female’s lifetime pattern of egg production. In a species that develops eggs continuously throughout its life, the optimal clutch size may be larger than the number of eggs a female can possibly produce at any one time. An example of both a behavioural and a time-budget constraint upon the behavioural options of both parasitoids and predators is the inability of the forager to handle and search for prey simultaneously. Here, time spent handling the prey

is at the cost of searching for further prey. For a detailed discussion of the elements of foraging models, see Stephens and Krebs (1986) or Cézilly and Benhamou (1996).

Sometimes the investigator knows, either from the existing literature or from personal experience, the best choices of decision assumption, currency assumption or constraint assumption. If it is impossible to decide on these based on existing knowledge, one can build models for each alternative and compare the predictions of each model with the observed behaviour of the parasitoid or predator. In this way, it is possible to gain insight into the nature of the selective forces working on the insect under study (Waage & Godfray, 1985; Mangel, 1989; Cézilly & Benhamou, 1996).

Classical optimality models assume a static world in which individual parasitoids search for hosts. While these models are still useful research tools, they ignored the possibility that for a forager, today's decision may affect tomorrow's internal state, which may in turn affect tomorrow's decision, and so on. The internal state of a searching parasitoid changes during adult life: its egg load (the number of mature eggs in the ovaries) and its energy reserves may decrease, and the probability that it will survive to another day decreases. The optimal behavioural strategy will depend on these changes. Likewise, the environment is not static. Bad weather or the start of an unfavourable season can also influence the optimal strategy. Dynamic foraging models have been subsequently designed to take into account internal physiological changes and changes in the environment (Mangel & Clark, 1988; Chan & Godfray, 1993; Weisser & Houston, 1993; Tenhumberg et al., 2001b).

Implicit in some optimality models is the assumption that the forager is omniscient or capable of calculation, e.g., that a parasitoid wasp has some knowledge of the relative profitability of different patches without actually visiting them (Cook & Hubbard, 1977).

Behavioural studies on parasitoids have shown, however, that insects can behave optimally by employing very simple quick 'rule' mechanisms such as the mechanism determining patch time allocation in *Venturia canescens* described in Sect. 1.5 and the males-first mechanism used by some species in progeny sex allocation (Sect. 1.11.5 and Fig. 1.19). These mechanisms approximate well the optimal solution in each case.

Evolutionarily Stable Strategies

Almost all parasitoids leave the host in situ. Thus, there is always the possibility that other parasitoids may find the same host and also oviposit in it. The optimal behaviour of the first female thus depends on what other parasitoids may do (i.e., the environment of a focal individual contains other competing individuals), especially since other individuals are also expected to adopt their own optimal reproductive behaviours. Likewise, the best time allocation strategy for a parasitoid leaving a patch in which it has parasitised a number of hosts depends both on the probability that other wasps will visit that patch and on the probability that other parasitoids may have already exploited the patches it visits next. For this reason, problems concerning the allocation of patch time, progeny and sex require models in which the evolutionarily stable strategy (ESS; Maynard Smith, 1974; Mesterton-Gibbons, 2019) is calculated. The ESS approach asks what will happen in a population of individuals that play all possible alternative strategies, and is based on game theory. The fact that individuals lack control over all decision variables affecting their rewards is what makes such situations a game, and what distinguishes them from classical optimisation problems (Mesterton-Gibbons, 2019). A strategy is an ESS if, when adopted by most members of a population, it cannot be invaded by the spread of any rare alternative strategy (Maynard Smith, 1972). In seeking an ESS, theoreticians are looking for a strategy that is robust against mutants playing alternative

strategies. The ESS, like the optimum in models for single individuals, is calculated using a cost-benefit analysis. We refer the reader to Maynard Smith (1982), Parker (1984) and Mesterton-Gibbons (2019) for descriptions of well-explored ESS models, details of how to calculate the ESS and their use in behavioural ecology, and to Hardy and Mesterton-Gibbons (2023) for a recent discussion of game theory in relation to natural enemy behaviour.

Why Use Classical Optimality and ESS Models?

Sometimes, experimental tests of optimality and ESS models will produce results not predicted by the models. At other times, only some of the predictions of the theoretical model are confirmed by empirical tests. Rarely is a perfect quantitative fit between model predictions and empirical test results obtained. Irrespective of whether a good fit is obtained, valuable insights are likely to be gained into the behaviour of the insect. Construction of models helps in the precise formulation of hypotheses and quantitative predictions and allows us to formulate new hypotheses when the predictions of our model are not met. Thus, classical optimality and ESS models are nothing more or less than research tools.

Ideally, both causal and functional questions should be asked when studying the foraging behaviour of insect parasitoids and predators. In the sections on superparasitism (Sect. 1.9.4) and patch time allocation (Sect. 1.5), we will show how, by ignoring functional questions, one may hamper the interpretation of data gathered to establish that a certain mechanism is responsible for some type of behaviour. Ignoring causal questions can likewise hamper research aimed at elucidating the function of a behavioural pattern; e.g., research into causal factors can demonstrate the existence of a constraint, not accounted for in a functional model, upon the behaviour of the parasitoid. Both causal and functional approaches are required for a thorough understanding of parasitoid behaviour.

1.2.3 The Comparative Method

Introduction

Perhaps the approach with the longest pedigree in studying animal behaviour is the comparative method. With this method, data are collated across species, and a search is made for statistical patterns (Harvey & Pagel, 1991). One advantage of this method is that data are often already available (although often widely scattered) in the literature (e.g., see analyses by Blackburn, 1991a, 1991b; Mayhew & Blackburn, 1999; Jervis et al., 2001, 2003). Until recently, sets of species average data were usually analysed in much the same way as within-species data. However, the fundamental assumption of most early statistical analyses—that species-comparative data are independent observations (i.e., are independent of each other)—may not hold. Also, we want to know whether observed interspecific similarities have evolutionary meanings in the present time or whether they derive from common ancestors in the phylogenetic tree. Cross-species data may actually be non-independent, because the species are related through phylogeny (i.e., they share an evolutionary history). Comparative biologists have developed methods which use phylogenetic information in conjunction with species data sets to generate independent values for statistical analysis and to enable a more accurate evolutionary interpretation of interspecific observed similarities or differences (Felsenstein, 1985; Harvey & Pagel, 1991; Harvey & Nee, 1997; Freckleton et al., 2002; Wajnberg et al., 2003).

The Method of Independent Contrasts

Probably the most commonly employed method involves ‘independent comparisons’, also known as ‘independent contrasts’ (originally developed by Felsenstein, 1985: simple examples are given in Harvey & Pagel, 1991; Purvis & Rambaut, 1995; Harvey, 1996; Mayhew & Pen, 2002). The approach assumes that the branches of a phylogeny can be modelled by a Brownian motion

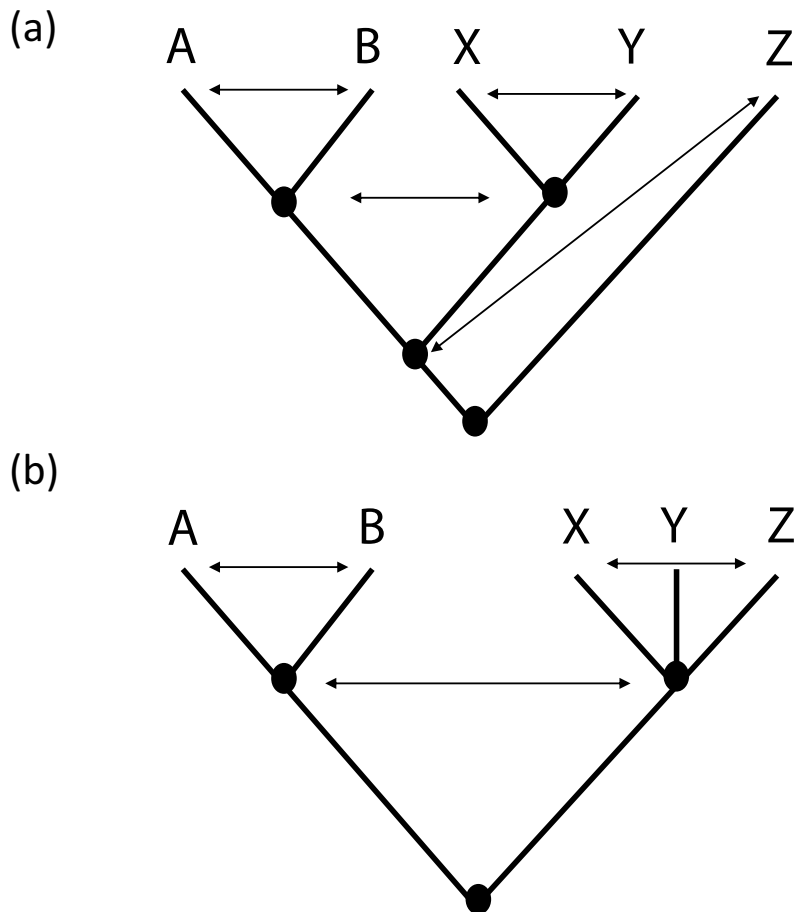
process, such that successive changes are independent of one another and that the expected total change summed over many independent changes is zero. The original method for contrast analysis assumes that the lengths of branches in the phylogeny are known, but often they are not, in which case they can be assumed to be equal (e.g., Jervis et al., 2001, 2003). Branch lengths are estimated by genetic distances (divergence times, in relation to the present, estimated from the fossil record or from molecular clocks) or by the number of character changes, determined from a cladistic analysis (Harvey & Pagel, 1991).

An independent contrast is obtained from each node in the phylogeny for each measured variable. Imagine that you are studying five species (Fig. 1.2a): it is clear that A and B, and X and Y are more closely related to each other than to members of the other clade, and, by comparing

their values, we then only include independent evolutionary trajectories. By calculating an ancestral trait value at the node below A-B and X-Y, we gain another contrast. By comparing this ancestral node value with the value for species Z, we gain another independent contrast. Therefore, we gain four contrasts from five species. If two traits are of interest in the comparative analysis and if they are continuous variables, then typically the data are analysed using a linear regression, constrained to pass through the origin (i.e., there should be no intercept in the regression model, Garland et al., 1992).

As we have seen, with a perfectly resolved phylogeny of n species, there are $n - 1$ possible contrasts available. This may result in statistical difficulties when data sets are small. While this problem may be alleviated by the addition of

Fig. 1.2 Independent contrasts: For n species, there are $(n - 1)$ independent contrasts which can be calculated for a fully phylogeny that is fully resolved at each node (a). Where the phylogeny is less well resolved, resulting in polytomies at some nodes, the number of possible independent contrasts is diminished (b), reducing the potential power of the analysis. Contrasts are shown by double headed arrows, nodes by dots and the species considered are A, B, X, Y and Z



extra species to the analysis, a more invidious difficulty is introduced when a phylogeny is poorly resolved. While phylogenies usually consist of bifurcating lineages, for some taxa the phylogeny may not be well resolved, and so it will contain polytomies (trifurcations, etc.) and hence fewer nodes for a given number of species. Thus, the number of contrasts obtained is less than with a fully resolved (bifurcating) tree, reducing the size of the data set and also the statistical power of subsequent analyses. Reconsider the figure with species A, B, X, Y and Z (Fig. 1.2a). If we do not know the evolutionary relationships among X, Y and Z, we must assume that they all originated from the same common ancestor (a polytomy; Fig. 1.2b). We now have fewer contrasts and hence lower statistical power in the analysis. Such problems can be overcome by obtaining a sufficiently well-resolved phylogeny. Unfortunately, such phylogenies are not always available. Garland and Díaz-Uriate (1999) provide further discussion.

Although a well-resolved, published taxonomy (more often than not, based exclusively on morphology) can be used to approximate the true phylogenetic tree (e.g., Abram et al., 2023), it is important to be aware that some currently accepted taxonomic groupings may not be monophyletic, i.e., they may not contain all the descendants of a common ancestor. Phylogeny-based comparative methods assume groupings to be monophyletic, so using an incorrect phylogeny will seriously undermine the value of the analyses undertaken. In the absence of molecular-based (i.e., DNA) phylogenies, cladistically-based taxonomies are the most suitable taxonomies for comparative studies as they are intended to closely reflect phylogeny.

There are now a number of software packages available that allow users to perform rigorous comparative analyses, many of which are freely available over the internet (<http://evolution.genetics.washington.edu/phylip/software.html> provides access to many of these packages, and more). Several R packages (R Core Team, 2020) are also available for that, e.g., caper (Orme, 2012), ape (Paradis et al., 2004), geiger (Harmon, 2009), etc.

The comparative method can also be used to make predictions concerning the ecology of a species. Hardy et al. (1992a), used a phylogenetic tree, based solely on morphological characters (now published incorporating molecular data; Schilthuizen et al., 1998), of the six *Drosophila* parasitoid species of *Leptopilina* occurring in Europe, to predict where in the environment *L. longipes*, a species whose hosts and host habitat were unknown, would be found (Fig. 1.3). The five other species are all parasitoids of *Drosophila*. The tree divides initially into two branches. When examining how the character ‘host habitat choice’ is distributed over the tree (i.e., the character is ‘mapped’ onto the tree), it appears that the upper branch of the tree contains the species finding its hosts in fermenting fruits (*L. heterotoma*), while the other branch contains species finding their hosts in fungi and/or decaying plant matter (*L. clavipes*, *L. australis* and *L. fimbriata*). Because *L. longipes* is most closely related to *L. fimbriata*, it was predicted that it is attracted, like its close relative, to decaying plant material. Subsequently, *L. longipes* was trapped with baits comprising rotting cucumber containing *Drosophila* larvae, and during fieldwork it was also found on decaying stalks of the umbellifer *Heracleum* and on fungi.

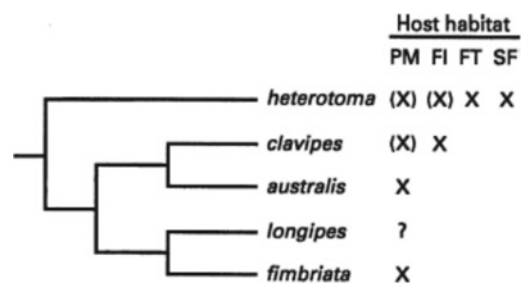


Fig. 1.3 Cladogram, based on adult morphology, of the *Leptopilina* species (Hymenoptera: Eucilidae, parasitoids of *Drosophila*) occurring in northwestern Europe. Microhabitat use is ‘mapped’ onto the ends of the tree branches. X = principal microhabitat, (X) = microhabitat from which a species has occasionally been recovered. PM = decaying plant material; FI = fungi; FT = fermenting fruit; SF = sap fluxes. Microhabitat use by *L. longipes* was predicted from that species’ position on the cladogram

1.3 The Treatment of Parasitoids Prior to Their Use in Experiments

1.3.1 Rearing

The species and quality of the host a parasitoid is reared on can have a marked influence on its subsequent behaviour, for example through its effect on egg load and life expectancy (Sects. 2.7.3 and 2.8.3). While the influence of the host-related phenotypic variation in natural enemy traits on the results of laboratory trials may generally be minimised or even avoided by altering the rearing regime, more insidious problems arise when insect populations are reared in mass culture. The first problem is ubiquitous and unavoidable. Natural selection will operate in the controlled environment room as much as anywhere else, changing the genetic composition of the population and, as a result, potentially influencing the behaviour of the population of interest (e.g., Matos et al., 2000; Simoes et al., 2007; Burke & Rose, 2009; Diamantidis et al., 2011; Hoffmann & Ross, 2018). There are two approaches to avoiding the complications of such adaptation. The first is to simply measure the traits of interest before significant selection occurs, so ideally few generations will have passed between capture and experiment. Second, if one is interested in using selection experiments to probe the nature of the trait, then we recommended that outbred populations of the species of interest be maintained for at least ten generations in the laboratory. This allows adaptation to laboratory conditions to occur and should avoid complications from any inadvertent selection pressures during the experiment. Further, maintenance of separate lines from an initially common population can also be used as a tool to generate and then test the effects of genetic differences (Mathiron et al., 2019).

A more serious problem results from small effective population sizes, leading to genetic drift and inbreeding depression. Testing the variation in an inbred population, at best, results in an

underestimate of the variation in natural populations, and, at worst, provides a skewed view of the true variation present.

1.3.2 Experience

It has been shown for several parasitoid species that an individual's previous experience can modify its behaviour (Sect. 1.6.2). This phenomenon has been observed in all phases of the foraging process and often involves responses to chemical stimuli (Vet & Dicke, 1992). For instance, females *Goniozus nephantidis*, a gregarious ectoparasitoid naturally associated with *Opisina arenosella*, that have developed on the factitious host *Corcyra cephalonica*, prefer *C. cephalonica* when offered a choice between the two host species, but prefer *O. arenosella* after having been exposed to their odour (Subaharan et al., 2005). Previous ovipositions in hosts of a certain species can also influence host species selection in choice experiments (van Alphen & Vet, 1986), while the decision to oviposit into an already parasitised host (i.e., superparasitism) also depends on previous experience with unparasitised or parasitised hosts (Visser et al., 1992b; Hubbard et al., 1999; Chen et al., 2020; Ayala et al., 2021). Thus, when designing experiments, one should always be aware that the previous history of an individual may influence its behaviour (as may the ecological history of the population the individual is drawn from, Vyas et al., 2019). Such history can affect the results of experiments on patch time allocation, superparasitism and also the results of experiments in which interactions between adult parasitoids are studied. Storing parasitoids in the absence of either hosts or host-related cues can have an effect. Visser et al. (1990) showed that it matters whether wasps are stored in a vial singly or with other females prior to conducting an experiment. Such effects have also caused problems when parasitoids and hosts are mass reared for biological control purposes. Rearing the apple pest *Cydia pomonella* on an artificial diet reduced the ability of the parasitoid *Hyssopus*

pallidus to respond to host location cues, as it changed the composition of the kairomones normally found in the host's frass (Gandolfi et al., 2003).

Conditioning parasitoids, by allowing them to search and oviposit for some time before an experiment, can nonetheless be a sensible practice. Inexperienced parasitoids often show lower encounter rates and are less successful in handling their hosts (Samson-Boshuizen et al., 1974). By allowing parasitoids access to hosts before they are actually used in an experiment, one can often save many hours that would otherwise be wasted in observing parasitoids that are 'unwilling' to search. Often, however, it is advisable to use freshly emerged, inexperienced females, for example in choice experiments, either where different host plants, host instars or host species are offered or where the olfactory responses of parasitoids to different chemicals are studied.

Often, one is interested in the performance of natural populations. These comprise individuals with different experiences and/or different degrees of experience, so using only inexperienced females in the laboratory gives a distorted view of what happens in nature. One approach is to collect adults from the field for study in the laboratory. A large enough sample should give a reasonable idea of how individuals in the population behave on average. However, one should be aware of the problems of genotype-by-environment interactions, where not all genotypes respond to changes in environment in the same way. Ideally, the laboratory conditions will reflect what is likely to be encountered in the field, especially in terms of temperature.

Because experience can influence subsequent behaviour, the results of experiments in which an insect encounters two situations in succession can depend on which situation is encountered first. In such cases, one should take care that in half of the replicates one situation is encountered first, while in the other half the sequence is reversed.

1.3.3 Sex Ratio

While such effects of experience can have a great influence on the behaviour of insects, more subtle problems ought to be borne in mind. An often overlooked problem in sex ratio studies is the possible presence of *Wolbachia* and other male-killing bacteria in the study organism (Ode & Hardy, 2008; Chaps. 3, 5 and 6). For example, Majerus et al. (1998) found that almost 50% of females from a Japanese population of the coccinellid *Harmonia axyridis* were attacked by a male-killing bacterium, resulting in a heavily female-biased sex ratio. Those ladybirds from a Mongolian and a Russian population had low (<2%) or no infection. To confirm the presence of bacteria, one can simply 'cure' the experimental individuals by treating them with antibiotics (Sects. 3.4.2 and 6.5).

Selfish genetic elements (regions of the chromosome that are inherited in a non-Mendelian manner during segregation, resulting in their becoming over-represented in gametes) provide another means of sex ratio distortion (Ode & Hardy, 2008; Chap. 3). *Nasonia vitripennis* has been found to commonly carry *psr* (parental sex ratio), a selfish genetic element that results in the production of male-only broods by causing fertilised eggs (normally female) to become male. Such distortion of the sex ratio will have a considerable influence on the population ecology of *N. vitripennis* (reviewed in Godfray, 1994; see also Chap. 5) and could potentially influence the outcome of sex ratio studies if present in a laboratory culture.

More often, changes in sex ratios will result from conditional sex allocation (Sect. 1.11.3) or local mate competition (Sect. 1.11.2). Bernal et al. (1999) found that two species of *Metaphycus*, parasitoids of scale insects, showed much more female-biased sex ratios if provided with larger hosts. This is likely to result from conditional sex allocation (where female parasitoids preferentially place female offspring in larger hosts). Since these parasitoids may be used

as biocontrol agents attacking scale insect pests of citrus trees, using rearing protocols that maximise the proportion of females would be economically sensible (Bernal et al., 1999; Ode & Heinz, 2002; Chow & Heinz, 2005; reviewed in Ode & Hardy, 2008).

1.4 Handling Behavioural Data

1.4.1 Recording Behaviour

The equipment used to record insect behaviour has developed rapidly, driven primarily by advances in computing power. Nevertheless, many (if not most) studies of insect foraging behaviour rely upon direct observation and note-taking. This approach is not without drawbacks, in that it is difficult to avoid bias in recording. The simplest way around this is to use video-recording equipment, so that two independent observers can time and assess the behaviours of interest. A development of such techniques involves 'intelligent' video systems, which have a number of advantages (Chap. 4).

1.4.2 Analysing Behavioural Data

Because insects may change their behaviour in response to experiences gained while foraging, and because their internal state (e.g., egg load) changes during the foraging process, the different behavioural events of the same individual during an observation period are not independent. The standard statistical methods described in numerous textbooks are in general inappropriate for the analysis of some behavioural data because they do not adequately take into account the connection between the succession as well as the duration of acts. Haccou and Meelis' (1992) book on the statistical analysis of behavioural events is recommended as a useful introduction to the most appropriate approach (see also Wajnberg & Haccou, 2008, for additional information).

1.4.3 Behavioural Research in the Field

Whether behavioural research is aimed at answering fundamental questions or deals with the use of parasitoids and predators in biological control, the ultimate goal of interest is the performance of the insects in the field (Heimpel & Casas, 2008). The small size of many parasitoids makes observation of their behaviour in the field often difficult or impossible. This applies particularly to the monitoring of the movements of individuals, for example between patches. Following Hassell and Southwood (1978), patches can be defined either as units of host or prey spatial distribution or as limited areas in which natural enemies search for hosts or prey; often there is a hierarchy of patches, e.g., tree, branch, leaf, leaf-mine. The movements of larger insects, such as ichneumonids and sphecids, can be more easily observed. Dispersal of small parasitoids in the field can be studied by placing patches with hosts (e.g., potted, host-bearing plants) and releasing marked adults. By checking the host plants at regular intervals for the presence of marked individuals, it is possible to obtain information on the speed at which the insects move between host plants, on the time they spend searching each patch and on the spatial distribution of parasitoids over the available patches. When hosts are later examined, the aforementioned data can be related to the amount of parasitism in each patch.

By using marked parasitoid individuals, one can distinguish between insects released for the experiment and those occurring naturally. Large wasps can be marked with paint on the thorax, using a fine paintbrush (acrylic paint was used by, e.g., Driessen & Hemerik, 1992; Petersen & Hardy, 1996; Snart et al., 2018). By using different colours or colour combinations one can distinguish between different individuals, or groups. Small wasps can be marked with fluorescent dusts, but this has the disadvantage that one may need to remove wasps from the

experimental plot to detect the dust mark under ultraviolet light. For some species, it may be useful to mark individuals by rearing them on diet containing deuterium, which alters the chemicals that adults subsequently emit in detectable manner (Goubault & Hardy, 2007). Genetic markers (Chap. 3) have also been used to monitor parasitoids in the field (Kazmer & Luck, 1995). Other workers have suggested that phenotypically distinguishable mutants may prove useful in studying population dynamics, although there are obvious drawbacks with this approach (Snodgrass, 2002).

Many species, when observed in the field, continue foraging normally. Janssen (1989) used a stereomicroscope mounted on a tripod in the field to observe the foraging behaviour of parasitoids on patches (sap streams and fermenting fruits) containing *Drosophila* larvae. Casas (1990) also recorded the behaviour of *Sympiesis sericeicornis* while the parasitoid searched for its leafminer host on potted apple trees in the field. To characterise the relationship between egg loads and sugar availability in actively foraging parasitoids from the field, Segoli and Rosenheim (2013a, 2013b) collected *Anagrus daanei* and *A. erythroneuræ* by shaking the grape canes above a white plastic cafeteria tray (25 × 36 cm) several times at each site during different seasons. The number of cane shakes depended on the number of parasitoids falling on the trays because of the time taken to put them in vials, this also allowed them to estimate the number of parasitoids captured per shake as a primary measure of parasitoid abundance. To study the relationship between oviposition success and body size of female parasitoids, modified collection trays with a system of baffles were used to collect minute parasitoid wasps (<1 mm) of *Anagrus sophiæ* from the field, which forage on *Spartina* foliage for planthopper eggs and, upon death, fall out of the plant canopy (Segoli & Rosenheim, 2015). Other natural enemy species are easily disturbed when approached, and disturbance can be avoided in some cases by using binoculars (Waage, 1983).

1.5 Patch Time Allocation

1.5.1 Introduction

One aspect of parasitoid foraging behaviour where the causal approach and the functional approach have traditionally coexisted is patch time allocation. We will consider first which factors affect patch time allocation and second how one can analyse the interplay of the different factors.

1.5.2 Factors Affecting Patch Time Allocation

Patch time allocation in parasitic wasps is likely to be affected by the following (Wajnberg, 2006):

1. A parasitoid's previous experience;
2. Its internal state (e.g., egg load, energy reserves);
3. Patch kairomone concentration;
4. Encounters with unparasitised hosts;
5. Encounters with parasitised hosts;
6. The timing of encounters and attacks of healthy and already attacked hosts;
7. Whether the females lay a son or a daughter egg;
8. Encounters with the marks of other parasitoids;
9. Encounters with other parasitoid individuals;
10. Superparasitism;
11. Genetic variation.

Some of these factors can be studied through experiments in which all the other factors are excluded. For example, the effect of kairomone concentration can be investigated without involving hosts at all (Sect. 1.6). To eliminate the effects of encounters with other parasitoids and their marks, the experimental design shown in Fig. 1.4 can be used. However, it may be impossible with some experiments to separate the effects of different factors. A notorious problem is the analysis of the factors that determine how

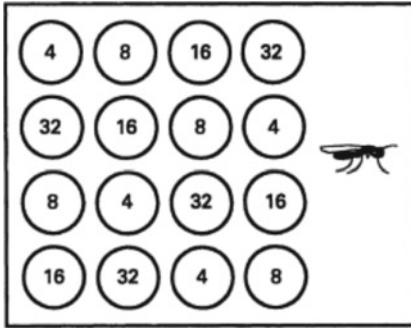


Fig. 1.4 Patch time allocation by individual parasitoids and predators. Schematic representation of one suggested experimental design for an experiment for studying patch time allocation. A randomised arrangement of patches (denoted by circles) is used. Numbers within circles indicate the number of hosts present in each patch. This experimental design can be used in the study of aggregative responses

long a parasitoid will stay on a patch that initially contains only unparasitised hosts. Because the parasitoid oviposits in the unparasitised hosts it encounters, the number of unparasitised hosts decreases while the number of parasitised hosts increases. Thus, with the passage of time, the parasitoid experiences a decreasing encounter rate with unparasitised hosts and an increasing encounter rate with parasitised hosts. Because both the temporal spacing and the sequence of encounters with parasitised and unparasitised hosts are stochastic in nature, encounter rates with both types of host do not alter in a monotonic, smooth fashion. However, modern statistical analysis tools can take into account such situations (see Wajnberg, 2006, for a review), and modelling approaches can also provide some help (see, e.g., Pierre et al., 2012).

In some parasitoid species, encounters with unparasitised hosts have an incremental effect on the time spent in a patch (van Alphen & Galis, 1983; Haccou et al., 1991). This poses the question: ‘What effect do encounters with *parasitised* hosts have on patch time allocation, and how does the relative timing of encounters with parasitised and unparasitised hosts influence the period spent in individual patches?’.

1.5.3 Analysing the Interplay of Different Factors

Two distinct hypotheses can be formulated about the effect of encounters with healthy and parasitised hosts on patch residence times. The functional hypothesis is as follows: given that a parasitoid is able to discriminate between parasitised and unparasitised hosts, encounter rates with both host types provide the parasitoid with information on host density and the degree of exploitation of a patch. This information allows the wasp to determine when to leave the patch, e.g., high encounter rates with parasitised hosts in combination with low encounter rates with unparasitised hosts signal a high level of exploitation of the patch. Because it could be more profitable for the wasp to move on and search for a higher-quality patch, the insect might decide to leave. Van Lenteren (1976) recognised this as one of the functions of host discrimination and showed, through single-patch experiments, that wasps continued to search on patches in which parasitised hosts were immediately replaced by unparasitised ones, whereas wasps allowed to search on similar but unreplenished patches attempted to leave the experimental arena after most of the hosts had been parasitised. The functional hypothesis states that encounters with both unparasitised and parasitised hosts affect patch time, but it does not specify the mechanism involved.

The causal hypothesis formulates explicitly how encounters with healthy and parasitised hosts affect patch time. This hypothesis is an extension of a mechanistic model for patch time allocation proposed by Waage (1979) for the parasitoid *Venturia canescens*. Although this model was shown to be an incorrect description of the behaviour of *V. canescens* (Driessen et al., 1995, see also Pierre et al., 2012), it is still valuable as a conceptual model, and it can be applied to many other parasitoid species. Waage (1979) assumed that a female parasitoid, when entering a patch containing hosts, has a certain motivation level for searching the patch, the level

being set by previous experience and kairomone concentration on the patch. If the wasp does not locate and oviposit in hosts, the motivation level will decrease steadily over time down to a threshold value, whereupon the parasitoid leaves the patch. However, with each oviposition that occurs, an incremental change in motivation occurs. The initial level of motivation, combined with linear decreases of motivation during searching periods and increases in motivation following ovipositions, determines how long the parasitoid will stay in the patch (Fig. 1.5a). The causal hypothesis assumes there is an additional effect of a rejection of a parasitised host, causing a decrease in motivation level (Fig. 1.5b). Like the functional hypothesis, the causal hypothesis predicts shorter patch residence times with increasing patch exploitation, all other things being equal.

A rigorous test of the causal hypothesis ought to demonstrate whether the mechanism by which shorter patch residence times come about is an

increase in the tendency to leave the patch after a rejection of a parasitised host. Such a test implies that one is able to assess the relative effects on the motivation to search of ovipositions in unparasitised hosts (i.e., increments), of the time interval between encounters, and of rejections of parasitised hosts (i.e., decrements). To illustrate how difficult it is to determine whether the rejection of parasitised hosts causes a decrease in the motivation to search, we will discuss in some detail the experimental evidence given by van Lenteren (1991). In one experiment, individual females of *Leptopilina heterotoma* were allowed to search on a 1 cm diameter patch of yeast containing four unparasitised hosts and sixteen parasitised hosts. Each unparasitised host parasitised during the experiments was immediately replaced by an unparasitised one. As a control, single females of *L. heterotoma* searched a similar patch containing only four unparasitised hosts, and any unparasitised hosts parasitised during the experiment were replaced by unparasitised ones.

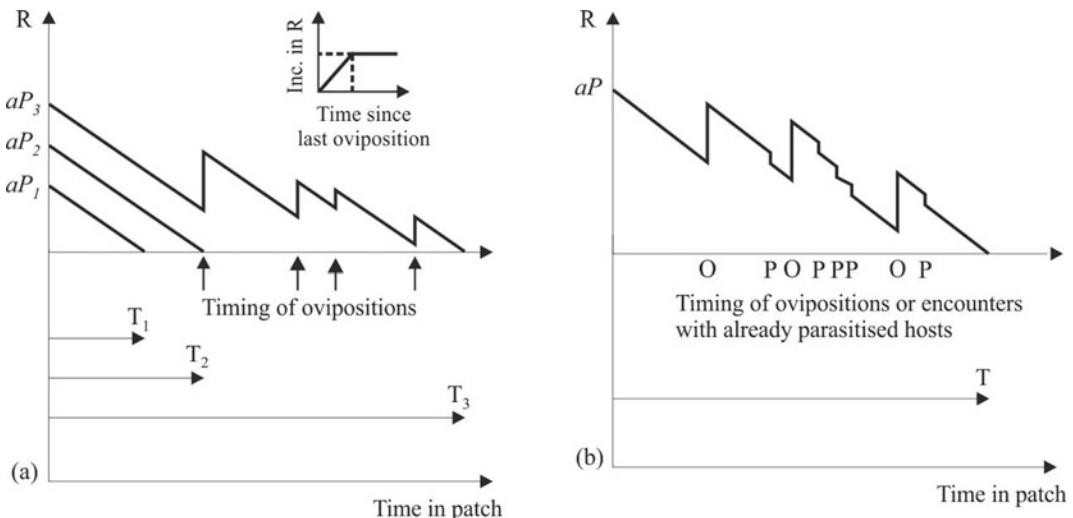


Fig. 1.5 Patch time allocation by parasitoids. **a** Waage's (1979) causal model of patch residence time. R = responsiveness of the female parasitoid to the patch edge (a function of the number of hosts in the patch [P_1, P_2, P_3] and a constant a , the quantity of kairomone produced per host). An oviposition results in an increment of R (inset: the size of the increment depends on linearly on the amount of time that has elapsed since the previous oviposition, and the increment cannot exceed a maximum

value). T_1, T_2 and T_3 are the resulting patch residence times for three different cases. **b** Waage's (1979) model, modified to incorporate the decremental effect of encounters with parasitised hosts. Symbols as in (a) except that O denotes an oviposition, and P denotes an encounter with an already parasitised host. *Source a*: modified from Waage (1979), reproduced by permission of Blackwell Publishing; *b* modified from van Alphen (1993)

Wasps stay longer on patches with four unparasitised hosts than on patches with four unparasitised hosts and sixteen parasitised hosts. Van Lenteren (1991) argued that because there were no significant differences in average time interval between ovipositions in unparasitised hosts in the two treatments, the differences in patch residence times between the treatments can be attributed only to a detrimental effect on patch residence time of encounters with parasitised hosts. First, consider whether it is at all valid to conclude from the observation that average time intervals between ovipositions did not differ between experiment and control, and that there is no difference in the effect of ovipositions on patch residence time between the two treatments. This conclusion would be valid only if the parasitoid itself uses average intervals to assess patch profitability. As Haccou et al. (1991) have shown, the effect of an oviposition on the probability of a wasp leaving a patch depends on its timing; hence it is also important when and where the longest intervals occur. Despite a lack of statistical differences between the average values, important differences in interval times between ovipositions could occur between test and control treatments. An alternative explanation for van Lenteren's (1991) results is that the differences in patch residence time are caused solely by the decrease in motivation over time that results from the extra time spent in rejecting parasitised hosts in the treatment with parasitised hosts. This time could otherwise be spent in ovipositing in unparasitised hosts. Rejection of a parasitised host takes between 2 and 6 s (Haccou et al., 1991), and with on average 33 rejections in the control treatment, this behaviour may account for an important part of patch residence time. If the decrease in the motivation to search (indicated by the sloping lines in Fig. 1.5a, b) continues during the time spent in rejections, these small decrements may accumulate over time, causing the parasitoid to reach the threshold motivation rate for patch leaving sooner than when no parasitised hosts are encountered. Intervals between encounters with unparasitised hosts would, on average, be slightly longer in experiments with parasitised hosts than in those without them, as indeed they were: 84

compared with 79 s. Although these differences are not significant, the time lost in rejection of parasitised hosts gradually accumulates, and so may be responsible for the ultimate differences in patch residence times.

Clearly, one cannot test the causal hypothesis simply by determining whether patch residence times and search times differ significantly between treatments. What is required is an analysis in which the relative weight of effects of the influencing factors and their timing are estimated from the data and tested statistically. For this reason, several authors (e.g., Haccou et al., 1991, Wajnberg et al., 2003, 2004; Wajnberg, 2012, see Wajnberg, 2006 for a review) used Cox's (1972) proportional hazards model (Sect. 1.2.1) to analyse experimental data. Haccou et al. (1991) analysed a new set of experimental data using the model. No effect of encounters with parasitised hosts on the probability of patch leaving was found. If such an effect exists at all, we expect it to be a small one. It might be detected in experiments in which there is a high proportion of encounters with parasitised hosts (as this was the case, e.g., in Wajnberg et al., 2003, 2004, 2006). The first evidence confirming the hypothesis first formulated by Waage (1979) comes from Hemerik et al. (1993) who used the proportional hazards model to analyse their experimental results and demonstrated in female *Leptopilina clavipes* that encounters with parasitised hosts decrease the tendency to search the patch. Finally, the effect of encounters with parasitised hosts may depend on the previous experience of the parasitoid. It is thus possible that encounters with parasitised hosts could also increase the tendency to search on a patch, as is the case when they decide to super-parasitise (van Alphen et al., 1987).

More recently, using a proportional hazards model to analyse patch residence time in *Trichogramma chilonis* females, Wajnberg (2012) discovered that each attack on a host had a significant incremental influence on the tendency of the females to leave patches of *Ephesia kuehniella* eggs. However, such effect depended on the sex of the egg females laid in each host attacked. Laying a daughter had a strong effect while laying a son had no effect. First of all, this indicates that

all previously published studies that were carried out with mated arrhenotokous females and that demonstrated an effect of each host attack should be re-analysed to see whether such effect was due to laying a son or a daughter or both. Moreover, *T. chilonis* females typically lay their sons first ('male-first' strategy; see Sect. 1.11.5). Using a modelling approach, Wajnberg (2012) demonstrated that the result obtained likely enables the females to adjust simultaneously their optimal patch time and sex allocation strategy according to LMC (Sect. 1.11.2).

Studies of patch residence times of insect predators are rare. It is evident that patch residence time may be influenced by the predator's level of satiation, but this is unlikely to be a straightforward relationship. For example, wolf spider (*Schizocosa ocreata*) patch residence time is influenced by hunger, but only in an interaction with spider age and sex (Persons, 1999).

1.5.4 Genetic Variation in Patch Time Allocation

As discussed above, several authors used Cox's regression model to investigate the patch-leaving behaviour of parasitoid wasps (see Wajnberg, 2006, for a review). Using this technique, Wajnberg et al. (1999) studied the behaviour of *Telenomus busseolae*, attacking the eggs of *Sesamia nonagrioides*. Not only did they find that female *T. busseolae* increased their tendency to leave a patch after each successful oviposition attempt, but, using the isofemale lines methods, they also demonstrated that the genotype of the ovipositing female influenced this behaviour. However, most workers consider patch-leaving (and indeed most parasitoid or predator behaviour) rules as a species-specific trait (Driessen et al., 1995; Wajnberg et al., 1999), rather than a variable characteristic among the individuals under study. This is rather short-sighted in many ways, as it assumes: (1) that all populations of a given species will respond in a similar way to different hosts or patches, and (2) that the trait is fixed, whereas it is likely that there is heritable

variation for the trait, and that natural selection may change the response found in a population over time.

1.6 Host and Prey Location Behaviour

1.6.1 Introduction

With the exception of ambush predators, insect predators and parasitoids employ a hierarchy of behaviours that enable them to locate and choose their prey. These behaviours are generally associated with either:

1. Finding the host or prey habitat
2. Finding the host or prey itself.

Within each of these levels, which, of course, are part of a continuum and are only delineated for our convenience, individual parasitoids and predators will generally follow a behaviour pattern that responds to cues. While such a scheme may allow us to visualise the foraging process, it must be remembered that these behaviours will be influenced by learning (a plastic response to experience) and genetic variation (both within- and between-population variation in responses to cues).

During searching, two important types of cue will influence insect natural enemy behaviour. Attractant stimuli induce a change in forager behaviour that results in orientation to areas that either contain, or are likely to contain, hosts. Arrestant stimuli act by eliciting a reduction in the distance or area covered per unit time by the forager within such areas. These stimuli can act at a number of scales, with distinct cues influencing the behaviour of the forager over differing distances.

1.6.2 Host and Prey Habitat Location by Parasitoids and Predators

The literature concerning host habitat location derives largely from studies showing which stimuli (cues) attract parasitoids and predators to

the host's habitat (reviewed by Vinson, 1985). Few studies deal with functional aspects of this step in the foraging sequence (but see, e.g., Le Ru and Makosso, 2001; Gohole et al., 2003). The emphasis on causal aspects of host habitat finding reflects the fact that it is much easier to answer qualitative questions, such as which odour acts as an attractant, than it is to answer the question of why one odour should be attractive, and another not, in terms of the contribution to fitness of the insect natural enemy.

Parasitoids spend a significant proportion of their adult lives searching for places where hosts can potentially be found. They may use visual, acoustic or olfactory cues to locate potential host patches. Certainly, for parasitoids, olfactory cues are more important. Often, visual and acoustic cues can guide a parasitoid to its host over a short distance only, in contrast to olfactory cues that can act over much longer distances.

It is difficult to demonstrate the use of visual cues in host habitat location by insect predators and parasitoids, because the use of other, olfactory and acoustic, cues must be excluded. Van Alphen and Vet (1986) investigated the searching behaviour of *Diaparsis truncatus*, an ichneumonid parasitoid of larvae of the twelve-spotted asparagus beetle, *Crioceris asparagi*. Larvae of the beetle feed inside the green berries of the *Asparagus* plant. It was shown, by placing green-painted wooden beads on *Asparagus* plants, that *D. truncatus* females respond from a distance to the berries of *Asparagus*. The parasitoids landed more often on the slightly larger wooden beads than on the green *Asparagus* berries, which is consistent with the hypothesis that the parasitoids respond to visual cues. Such an approach may be adopted for parasitoids of other insects living in fruits. Visual responses of parasitoids of leaf-rollers and stem-borers could be investigated by presenting females with paper tubes of various colours, sizes and shapes. In this case, it is useful to record the light absorption/reflectance characteristics of the objects used rather than simply their apparent colour.

Coccinellids are perhaps the best-studied insect predators (Dixon, 2000), and it appears

that visual cues can play a large part in longer-distance prey location. Hattingh and Samways (1995) found that the ladybird *Chilocorus nigritus* initially orientated towards a simulated tree line, and then showed a preference for simple ovate leaves over more complex leaf shapes. Hattingh and Samways (1995) studied 'biotope' location behaviour using a flight chamber that comprised a transparent, Perspex cylinder, which was closed at both ends. The chamber itself was situated in a room whose walls and ceiling were covered with white paper. On each of the walls facing the chamber ends were screens, upon each of which was painted a particular image: vertical *versus* horizontal stripes, flat horizon *versus* horizon with a tree line, shape of a tree *versus* vertical stripes, shapes like citrus leaves *versus* squares. Sixty coccinellids were released, per replicate, into the centre of the chamber and the numbers of beetles at either end recorded for up to one and a half hours. To eliminate any bias towards either end of the arena, the chamber was rotated 180° between replicates. Significantly more beetles were recorded at the end of the chamber facing the images of a horizon with a tree line than at the opposite end with a flat horizon, and also significantly more were recorded at the end facing the citrus leaf images than at the end facing the squares. Most of the plants on which *C. nigritus* occurs in nature have ovate leaves. Overall, Hattingh and Samways (1995) found evidence that beetles habituate to visual cues, as predators and parasitoids are known to do for olfactory cues.

Some parasitoids respond to acoustic stimuli produced by the host, and so execute host habitat location and host location in one step, and this appears to be much more common among dipteran parasitoids (Feener & Brown, 1997). Cade (1975), whilst broadcasting the song of the male cricket *Gryllus integer* from a loudspeaker to study the mating behaviour of the crickets in the field, discovered that a tachinid parasitoid (*Euphasiopteryx ochracea*) of the cricket was attracted by the song. Burk (1982) similarly demonstrated this for the tachinid *Ormia lineifrons*. Soper et al. (1976), using tape recordings, showed that the sarcophagid parasitoid

Colcondamyia auditrix finds male cicadas by this means (phonotaxis). Phonotaxis by the tachinids *Ormia depleta* and *O. ochracea* has been demonstrated using synthesised male calling songs (Fowler & Kochalka, 1985; Walker, 1993; Adamo et al., 1995). Both Fowler (1987) and Walker (1993) carried out experiments in which the synthesised calls of a range of several host cricket species were simultaneously broadcast in the field. Allen (1998) found that the parasitoid *Homotrixa alleni*, an ormiine fly, locates the bushcricket *Sciarasaga quadrata* by orientating towards calling males. Gravid female flies were most likely to search when calling was maximal, and by using trapped male *S. quadrata*, it was shown that there was a positive correlation between call duration and the number of flies attracted to the bush crickets (Allen, 1998).

Chemical communication, both between insects and between plants and insects, plays a very important role in determining the behaviour of parasitoids and predators. Any chemical conveying information in an interaction between two individuals is termed an infochemical (Dicke & Sabelis, 1988). Infochemicals are divided into pheromones, which act intraspecifically, and allelochemicals, which act interspecifically. Allelochemicals are themselves subdivided into synomones, kairomones and allomones. A synomone is an allelochemical that evokes in the receiver a response that is adaptively favourable to both the receiver and the emitter; a kairomone is an allelochemical that evokes in the receiver a response that is adaptively favourable only to the receiver, not the emitter; an allomone is an allelochemical that evokes in the receiver a response that is adaptively favourable only to the emitter (Dicke & Sabelis, 1988). The majority of parasitoids and many insect predators respond to volatile kairomones or synomones in the long-distance location of their hosts. These chemicals may originate from (1) the host itself, e.g., from frass, during moulting, during feeding, sex pheromones and aggregation pheromones, i.e., the chemicals involved are kairomones for the parasitoids; (2) the host's food plant, i.e., the chemicals involved are synomones for the parasitoids; or (3) some interaction between host and

food plant, e.g., feeding damage, i.e., the chemicals involved are synomones for the parasitoids.

The attraction responses by parasitoids to odours from any source can be studied using various olfactometers, wind tunnels and locomotion compensators (servospheres), or by observing the responses of parasitoids to odour sources following release of the insects in the field.

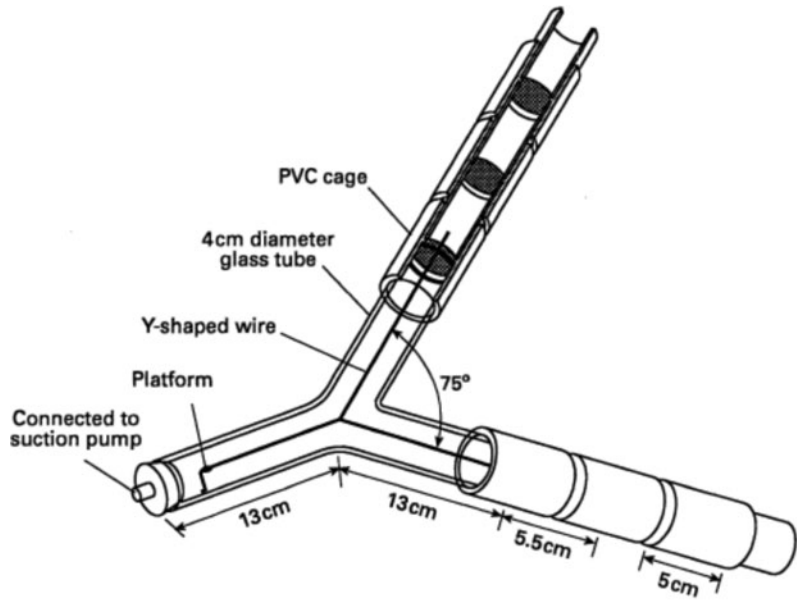
Olfactometers

Two types of airflow olfactometer are commonly used to study responses to olfactory cues. One is the glass or clear Perspex Y-tube olfactometer (Fig. 1.6). The insect can be given a choice either between odour-laden air (test) and odour-free but equally moist air (control) or between air laden with one odour and air laden with another odour. Although Y-tube olfactometers have been criticised because odour plumes may mix where the two arms of the olfactometer meet due to turbulence, and that choice is no longer possible once the insect has passed the junction of the tube, impressive results have been obtained. Smoke can be passed through the apparatus to test for unwanted turbulence, but tobacco smoke must be avoided as it is absorbed by the tubing and it can affect the outcome of future experiments. By passing NH_4OH vapour over HCL, a fine smoke of NH_4Cl crystals can be created and the vapour channelled through the Y-tube. After testing, the crystals can easily be washed from the tubing. Turbulence, if detected, can often be reduced by adjusting the flow speed of the air.

With diurnally active insects, a diffuse light source is often required to illuminate the apparatus to encourage the insects to move towards the fork of the tube. This light should not cause the olfactometer to overheat, and so to avoid this a cold-light source (e.g., fibre optics) ought to be used.

To eliminate the effects of any asymmetry in the apparatus, the chambers need to be alternated for each 'run'. It is recommended that parasitoids be tested individually, rather than in batches, because either interference or facilitation may occur between insects and so bias the results. The apparatus should be washed, first with alcohol

Fig. 1.6 Y-tube airflow olfactometers. The upper panel shows the design used by Sabelis and van de Baan (1983). The Y-shaped wire within the tube cavity provides a walking surface for small predators and parasitoids. For details of operation, see text. The lower panel shows a Y-tube olfactometer being used to assess parasitoid odour preferences. Odour emanated from two pieces of white filter paper, within the arms, which had previously been soaked in extracts of healthy or infested host-plant leaves. Note the regulators which ensured equal flow through the two arms (photograph K. S. Shameer)



and then with distilled water, between runs to prevent any response of parasitoids to any trail left by previous individuals. Finally, consideration needs to be given to the possibility of left- and right-handedness in the insects. By analysing the number of left and right turns in the apparatus, it is possible to test, statistically, whether wasps tend to move more to the right or more to

the left. The null hypothesis will be that the distribution of turns by parasitoids should be equal in both arms irrespective of the position of the chambers. An additional test of turn preference is to perform several runs when both chambers are empty, although insects may be unwilling to move through the apparatus in the absence of any odour. Some parasitoid species

show ‘handedness’, i.e., a tendency to turn more in one direction than another (J. Pritchard, unpublished).

Even when great care is taken in the design of olfactometer experiments and the analysis of data, the results of olfactometry may be difficult to interpret (Kennedy, 1978). This applies especially to Y-tube olfactometers. The Y-tube, when employing a light source, simultaneously presents test insects with two types of stimulus, light and air current, to which the insect might respond by phototaxis and anemotaxis, but presents the two odours (or odour and non-odour) separately at only one point in the apparatus: the fork, which represents the ‘decision point’. Responding by phototaxis and anemotaxis to the common air current, insects might be entrained past the decision point and become behaviourally trapped in the wrong arm (Vet et al., 1983).

One recent use of Y-tube olfactometry first tested the response of the parasitoid *Dolichogenidea gelechiidivoris* (Hymenoptera: Braconidae), an endoparasitoid of larvae of tomato pest *Tuta absoluta* (Lepidoptera: Gelechiidae), towards the headspace volatiles of healthy plants, pest-infested plants, pest larvae and larval frass, and then tested the individual odour attractants present in these (Ayelo et al., 2022). This showed that the pest larvae-infested tomato plants and the host larval frass volatiles were more attractive and that the parasitoids are specifically attracted to the terpenoids α -pinene, β -myrcene, α -phellandrene, α -terpinene, β -ocimene, (E)- β -caryophyllene, and to the benzenoid ester methyl salicylate.

Bertoldi et al. (2019) used two different types of Y-tube olfactometer setups to determine the behavioural responses of female *Trissolcus japonicus* to host-associated cues of *Halyomorpha halys* and *Podisus maculiventris*. In the ‘long-distance’ setup, the air streams passed through a 4-L glass jar (diameter: 10–15 cm; height: 30 cm) containing the odour source and connected to the olfactometer arm through a 40 cm-long plastic tube and, in the ‘close-distance’ setup, the sources of volatiles were placed close to the olfactometer in two small chambers connected with the tubes and placed directly at the

ends of the olfactometer arms. Bertoldi et al. (2019) tested the volatiles from stink bug treated plants in the ‘long-distance’ setup, and those from adults and eggs of the hosts in both setups, because oviposition-induced plant volatiles may be perceived from a longer distance than the volatiles from adult stink bugs and from eggs (Conti et al., 2003; Colazza et al., 2010; Hilker & Fatouros, 2015).

Fрати et al. (2008) used a vertical open Y-shaped olfactometer (originally developed to record aphid behavioural responses to plant odours by Visser & Piron, 1998; Fig. 1.7) to test the response of *Lygus rugulipennis* females to host-plant volatiles. This type of olfactometer is constructed from a brass rod positioned vertically and divided into two arms, over which two separate glass tubes are placed to direct either clean air flow or an air flow containing odour towards the Y-junction. The insect, initially placed on the base of the vertical rod, starts walking upward and chooses between the arms at the junction. For further studies using olfactometers, see, for instance Chiappini et al. (2012) and Rondoni et al. (2017a, 2017b).

Another type of airflow olfactometer, designed by Pettersson (1970) to study the responses of aphids, avoids many of the disadvantages of Y-tube olfactometers. A modification (Fig. 1.8) of the Pettersson olfactometer by Vet et al. (1983) and further developed by others (e.g., Sengonca & Kranz, 2001) has been widely used to analyse parasitoid behaviour. It is constructed mainly of transparent acrylic (Perspex, Plexiglas) and has a central arena with four arms. Air is drawn out of the arena via a hole in the centre of the bottom plate. Air flows into the arena via four arms. Insects in the central arena may therefore be exposed to as many as four different odours. Air speed in each arm can be controlled with a valve and an anemometer and should be equal in all arms. Before an experiment is performed, an NH_4OH smoke test can be carried out to test for unwanted turbulence and to show that a clear, straight boundary exists between odour fields. Diffuse light of equal intensity on all four sides of the arena prevents asymmetric attraction of insects to light.

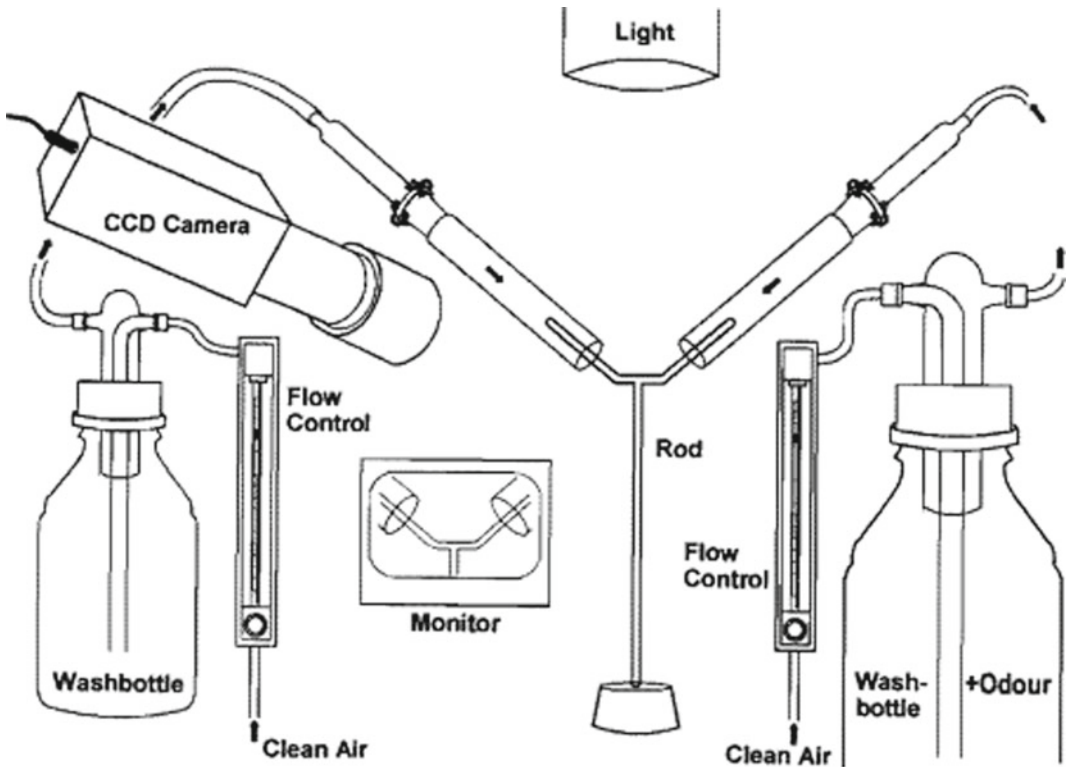


Fig. 1.7 Open Y-track olfactometer. The insect is placed on the base of the vertical rod and starts walking upward. At the junction it will choose between a clean air flow, here at the left, and an air flow loaded with plant odour,

shown at the right. Subsequently the insect is removed and the experiment repeated with another insect (reproduced from Visser & Piron, 1998, with permission from the Netherlands Entomological Society)

Insects are introduced through a hole in the bottom plate by temporarily disconnecting the tube from the air pump. Observations are best made using a video camera placed directly overhead, because any movements by a human observer may disturb the insects. Such systems can be further automated by integrating commercially available components, such as CCD (charge-coupled device) cameras, with a computer program that incorporates a positioning and tracking algorithm (Vigneault et al., 1998; Sect. 4.2.6).

The Pettersson olfactometer thus allows an insect to choose between four different odour fields, and repeated choices by the insect are also made possible. In non-automated versions of the Pettersson olfactometer, the final choice by an insect is usually considered to be made when it enters the narrow tube through which air laden

with odour enters the arena. Both because airflow in this narrow region is strong and because many parasitoids have an aversion to entering narrow crevices, some insect species avoid this area and turn without entering. Other parasitoids react to the odour stimulus by flying vertically upwards. Because flight is impossible in the narrow space between the base and the olfactometer cover, the insects will hit the top plate, and after a number of these aborted flight attempts become so disturbed that they cannot be expected to choose odour fields.

Often, one or more of the odours offered in an olfactometer comprises a mixture of many unidentifiable volatile substances, the concentrations of which in the odour fields are unknown. This does not pose a problem if the responses of an insect to a mixed odour source and a clean air control are compared, because

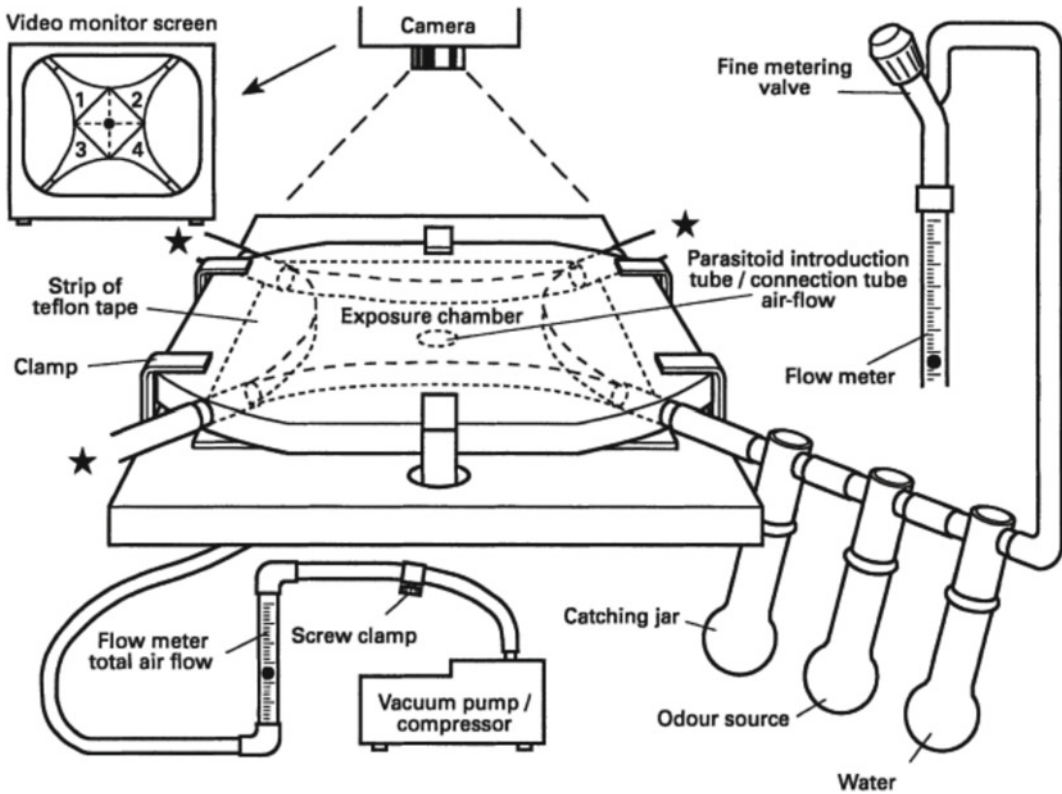


Fig. 1.8 Design of the Pettersson olfactometer, as used by Vet et al. (1983). The catching jar is used to collect any insects that move into an outflow tube. The stars represent

three further odour sources that are not shown. Reproduced by permission of Blackwell Publishing. For a related 6-arm design see Aleosfoor et al. (2014)

only the test odour is the potential attractant. However, when testing for attraction to two odour sources (e.g., the odours of two different food plants of the host), there may be problems of interpretation. One of the odour sources may be more attractive than the other because the insect responds to one or more substances in that odour source that are lacking in the other. Alternatively, both odour sources may be qualitatively similar but the insect may be differentially attracted because of differences in the concentration of an attractant component of an odour. It also needs to be borne in mind that a combination of a qualitative difference and a quantitative difference may be responsible for differential attraction. The ultimate solution to the above problem would be to isolate the attractants and test whether differential attraction to odour sources is due either to differences in

chemical composition between the sources or differences in concentration of their chemical components.

With any airflow olfactometer it is important to ensure, before carrying out any experiments, that air flows through the apparatus at a constant rate (usually the rate is low). With the Y-tube and Pettersson olfactometers, both of which are hypobaric systems (i.e., air is sucked out), a good-quality vacuum pump should be used. Flow meters of the correct sensitivity, i.e., neither over- nor under-sensitive, should also be employed. Static-air olfactometers (i.e., without generated air flow) can be used with predators and parasitoids to measure chemotactic responses to odour gradients (Cusumano et al., 2022a, 2022b; Steidle & Schöller, 1997). One such olfactometer, used successfully by Vet (1983), consists of three chambers (Fig. 1.9): the

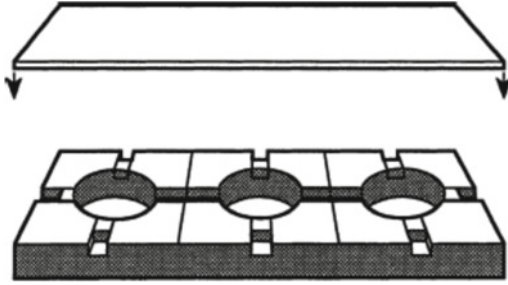


Fig. 1.9 The static-air olfactometer of Vet (1983). The apparatus comprises three Perspex blocks glued together and covered by a single glass lid (a single Perspex block would also suffice, although it may be more difficult to excavate). The excavations (chambers) in the blocks are connected by corridors. The chambers, measured internally, are 50 mm wide and 16 mm deep; the corridors are 10 mm wide and 5 mm deep. Reproduced by permission of E.J. Brill (Publishers) Ltd

parasitoid or predator is released into the middle chamber and its subsequent choice of outer chamber containing a test odour recorded. Vet (1983) also recorded the time taken for females to reach an odour source chamber.

Static olfactometers can also be used to evaluate whether the parasitoid is able to perceive the stimuli as short-range volatile cues (Conti et al., 2010). This is similar to the closed arena experiments, the only difference being a fine mesh placed between the leaf surface and the observation chamber, to prevent direct contact between the parasitoid and the leaf surface. Conti et al. (2010) found that, in the static olfactometer, *Trissolcus brochymenae* reacted to short-range volatiles from cabbage leaves with feeding damage, oviposition and walking paths by *Murgantia histrionica*. Parasitoid arrestment behaviour to the host-insect cues can be investigated in an open arena made of filter paper (185 mm diameter) which allows the parasitoids unconstrained movements (Bayram et al., 2010). The central circular area (10 mm diameter) in the open arena was contaminated with the abdominal scales of virgin females of *Sesamia nonagrioides* and the arrestment responses of naïve female wasps of *Telenomus busseolae* were recorded using a monochrome CCD video camera. A similar

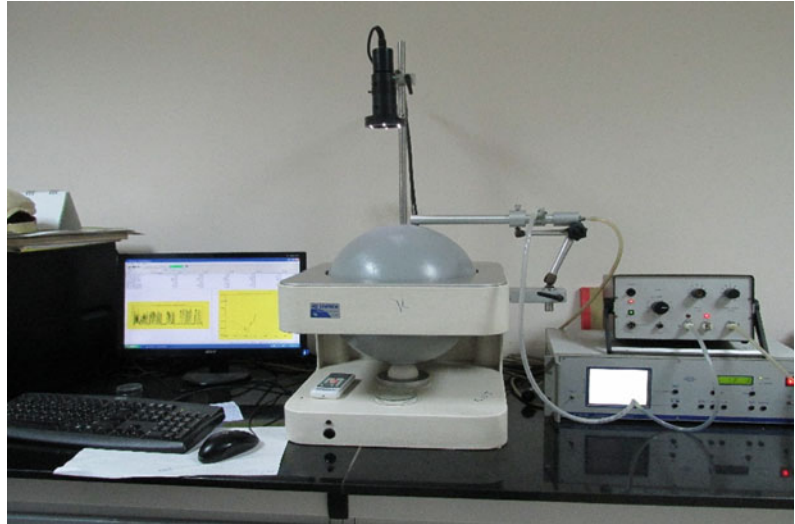
bioassay was used by Bertoldi et al. (2021), but on a large filter paper arena (20 × 20 cm), to assess the behaviour of *Telenomus podisi* to host-associated cues of female *Halyomorpha halys* and *Podisus maculiventris*.

Locomotion Compensators

The analysis of insect behaviour in response to semiochemicals can be difficult when using olfactometers, as the details of walking tracks may not be observable and may be influenced by the confines of the apparatus (Visser, 1996a, 1996b). Locomotion compensators (also called servospheres or trackspheres) for insect studies were first constructed and described by Kramer (1976) and are used for measuring the orientation behaviour of a variety of insects, such as aphids, moths, beetles, bugs, cockroaches, crickets, honeybees and parasitoid wasps (Thiery & Visser, 1986; Vet & Papaj, 1992; Visser, 1996a, 1996b; Geiselhardt et al., 2008; Rouyar et al., 2011; Minoli et al., 2012; Party et al., 2013; Piesik et al., 2013).

The instrument consists of a sphere, on top of which the insect is placed, and which is rotated opposite to the insect's displacements by means of two electric motors (Fig. 1.10). The motors are driven by electrical commands proportional to the displacement of the insect measured by an optical detector (Video CMOS camera with Macro zoom lens) located above the insect. As a result, the insect stays on top of the sphere while walking. The locomotion compensator permits unconstrained movement and thus avoids the behavioural artefacts commonly encountered in more confined experimental setups. The rotational movements of the sphere are detected by two encoders or pulse generators in contact with the sphere. The speed and direction are calculated every second and transmitted to a computer, where the displacements are stored as incremental X and Y coordinates. The computer software program collects and stores the displacement data, reconstructs the walking path and provides track analysis (Vet & Papaj, 1992). The following four track parameters can be used to quantify the insect's behaviour: (1) walking

Fig. 1.10 A locomotion compensator being used to test the responses of host larvae to plant volatiles (photograph K. S. Shameer). Examples of parasitoid walking tracks can be found in Vet and Papaj (1992)



speed (mm/s); (2) straightness of walking, i.e., the ratio of vector length to total track length (ranging from 0 to 1); (3) upwind length (mm), i.e., the net distance from the origin towards the odour source along a straight line; and (4) upwind fixation, the ratio of upwind length to total track length (ranging from -1 to $+1$).

Vet and Papaj (1992) used a locomotion compensator to study the effect of oviposition experience on the upwind movement of the eucoilid parasitoid, *Leptopilina heterotoma* (Thomson), in odour plumes of host microhabitats. The parasitoids were first exposed for 2 h to the host *Drosophila melanogaster* larvae in either fermenting apple yeast or decaying mushroom substrate. They found that females experienced with a particular substrate walked faster and straighter, made narrower turns and spent more time in upwind movement toward the source in a plume of odour, whereas inexperienced females showed little or no difference in response to alternative odours.

Some workers use several bioassay methods together to study the orientation behaviour of insects to host-plant volatiles, pheromones, etc. For instance, Tinzaara et al. (2003) used three different bioassay methods, a locomotion compensator, a dual port olfactometer and double pitfall olfactometer, to study the orientation behaviour of *Cosmopolites sordidus* to host-plant

volatiles and a synthetic pheromone. The results of all three bioassays indicate that *C. sordidus* responds in an additive way to the combination of plant volatiles and the synthetic pheromone.

Wind Tunnels

As noted above, not all parasitoids can be successfully tested in olfactometers, because they are prevented from flying. Flying parasitoids can be tested in wind tunnels (Drost et al., 1986; Keller, 1990; Parent et al., 2017; Fig. 1.11), but it is difficult to keep track of the smaller species. Wind tunnels allow the parasitoid wasps to express their full range of behaviour, especially the searching behaviour towards their host insects, and it also allows observation of the wasp's preflight behaviour, flight behaviour and behaviour after landing on the host (Yazdani et al., 2015). Wind tunnel trials showed that *Aphidius ervi*, a common parasitoid of the pea aphid, *Acyrtosiphon pisum*, preferred to fly towards aphid-damaged bean plants (Du et al., 1996; Powell et al., 1998; see also the discussion below). Wind tunnel experiments also found that flight duration and the profile of foraging behaviours exhibited by the parasitoid *Goniozus jaccintae* depended on the instar of the host light brown apple moth, *Epiphyas postvittana*, a lepidopteran pest of grapevines (Aspin et al., 2021). Using the same wind tunnel, Yazdani et al.

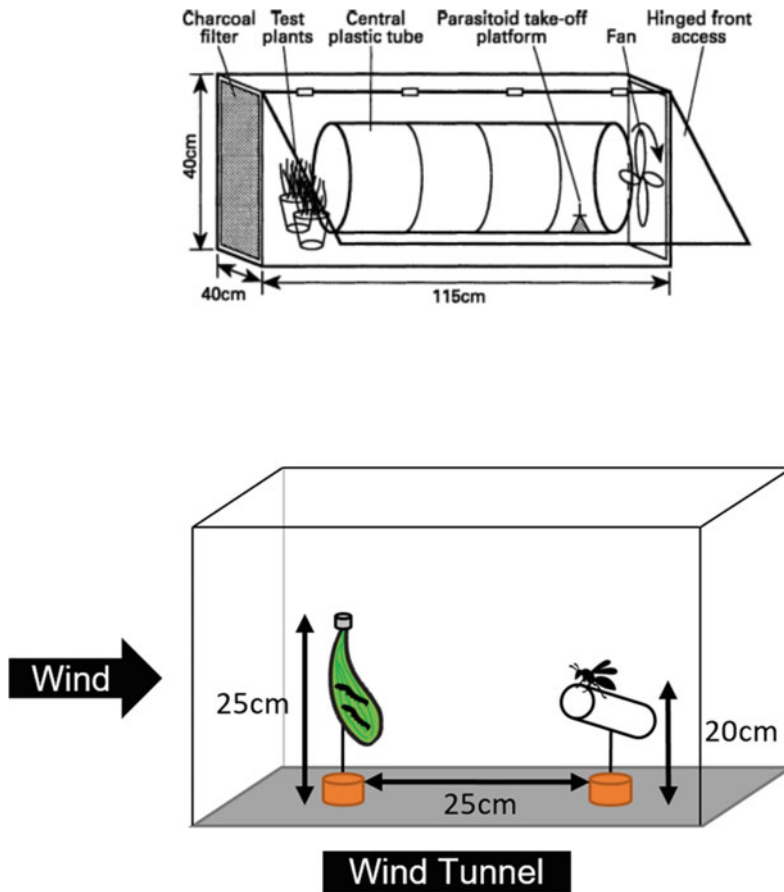


Fig. 1.11 Wind tunnels. Upper panel: Design of the wind tunnel used by Grasswitz and Paine (1993) to study the behaviour of *Lysiphlebus testaceipes* (Hymenoptera: Braconidae), a parasitoid of aphids. The main (rectangular) chamber was constructed of Plexiglass, and the central (cylindrical) test section was constructed of Mylar (biaxially-oriented polyethylene terephthalate). Lower panel: Schematic diagram of the wind tunnel used by

Aspín et al. (2021) to study the sequence of foraging behaviours of female *Goniozus jacintae* (Hymenoptera: Bethyloidea), a parasitoid of lepidopterans attacking grape vines and plantains. Host larvae fed on plant leaves that were suspended from a bar fixed 25 cm above the floor of a wind tunnel and wind speed was set at 20 cm s^{-1} . In each trial, a single female wasp was released 25 cm downwind from the infested leaf

(2015) found similar results for a different parasitoid, *Dolichogenidea tasmanica*, of the same pest species.

Other Methods and Further Considerations

When a wind tunnel cannot be used, one could try the following:

1. Placing potentially attractive odour sources in an array, either in the field, in a large field cage, or in a large controlled environment chamber.

2. Releasing a large number of adult females and examining the odour sources frequently.
3. Removing each insect that lands on the odour sources.

If more individuals than expected, based on a random distribution, land on a particular odour source, this can be taken as evidence that the odour source is attractive. If different odour sources are offered, it may be possible to rank them in terms of their attractiveness. The

problem with this type of experiment is that the number of parasitoids or predators trapped on a particular source is a function both of the number of insects landing on the source and of the time they spend there. Ideally, the test individuals should be caught immediately after arrival on the source, but this is not always possible. Another problem is that the experimental design does not exclude the effect of interactions between individuals. For instance, parasitoids may repel conspecifics, even actively chasing them away (Hardy et al., 2013).

The field release method (involving counting of the numbers of females attracted to uninfested and infested cassava plants) was used successfully in field experiments with *Apoanagyrus* (= *Epidinocarsis*) *lopezi* and to compare the attractiveness of different microhabitats containing *Drosophila* larvae to several species of *Lepidopilina*. The method also allows a functional analysis of habitat choice. If one knows (1) the encounter rates with hosts in the different microhabitats, (2) the species composition of the host larvae in each microhabitat, and (3) the survival rates of parasitoid eggs deposited in each of the host species, one can calculate the relative profitability of each microhabitat for the parasitoid and then predict which ones the parasitoids should visit when given a choice. This approach was employed by Janssen et al. (1991).

Another approach to studying functional aspects of host habitat location by parasitoids is to consider the reliability and detectability of a cue (Vet & Dicke, 1992). This approach contrasts cues having a high detectability but a low predictive value regarding the presence of hosts, with cues having a low detectability but a high predictive value. Cues with a high detectability are odours emitting from potential host plants. Cues with a high reliability are, for example, substances produced by the host plant in reaction to the presence of the host and substances emitted directly from the host. Vet and Dicke (1992) assumed that high reliability cues are produced in smaller amounts than general host-plant odours. Measuring reliability and detectability in a quantitative way is a problem in testing the concept. However, a number of studies

(discussed below) have gone some way to overcoming this problem. A related concern is highlighted by McCormick et al. (2014a), who caution that there could be minor volatile cues, seen as little peaks in chromatography (indicative of low volumes), released from host plants but with important roles in plant–insect interactions, and describe experimental approaches and chemical and statistical methods to detect these minor compounds with major biological activities.

As with all behavioural tests that purport to investigate insect preferences (e.g., for a given odour, host plant, host size, host instar, etc.), statistical concerns abound. Two will be considered here. First, at which point is the test insect provided with too many choices to make effective comparisons and how does this affect the sample size required? In part, the answer depends on whether the experimenter is interested in extremes (whether an insect prefers an odour to the control treatment) or in forming a rank order of preference among odours. Raffa et al. (2002) show that an increased number of replicates is required to show the latter and they provide an excellent guide as to how to maximise experimental power (see also Taborsky, 2010; and Smith et al., 2011, for general discussions of sample sizes and power). Second, what is the best way to analyse the data? There are several established statistical approaches. Data from binary outcomes can usually be analysed using a standard probit or logistic regression approach (Chap. 9) but standard probit models are not suitable for preference assays, and Sakuma (1998) provides an extension of the standard probit method to overcome these problems.

Many studies have shown that parasitoids and insect predators respond to odours produced by the host plants of their potential prey or hosts (reviewed by Vet, 1999). In some cases, parasitoids respond to the odour of host-free (undamaged) plants, but frequently herbivore damage is required before a response to plant cues is observed. Wind tunnel trials showed that *Aphidius ervi*, a common parasitoid of the pea aphid, *Acyrtosiphon pisum*, preferred to fly towards aphid-damaged bean plants. However,

washing the plants to remove aphid cues did not reduce this preference, indicating that induced plant volatiles were being used as cues (Du et al., 1996). When extracts of the plant volatiles were applied to filter paper and placed in a wind tunnel, a similar effect was seen (Powell et al., 1998). If *A. ervi* females are provided with a choice between volatiles collected from pea aphid-damaged plants or from black bean aphid (*Aphis fabae*)-damaged plants, they are much more likely to fly towards the former (Powell et al., 1998). This is evidence that there are host-specific cues in the plant volatiles (Du et al., 1996; Powell et al., 1998; Costa et al., 2010). *Dolichogenidae tasmanica* responded to the volatile cues associated with two related tortricid host species, *Epiphyas postvittana* and *Mero-phyas divulsana*, in a dual-choice wind tunnel experiment (Bui et al., 2020).

Predators also respond to similar cues. In a field experiment, Drukker et al. (1995) found that psyllid-infested pear trees attracted significantly more anthocorid predators than uninfested trees. Scutareanu et al. (1997) collected volatiles from the headspace (i.e., the air directly above the leaf) of attacked and unattacked trees, and using a Y-tube olfactometer found that the anthocorids preferentially chose the airstream containing volatiles from attacked trees. Using mass spectrometry, they found six volatiles that were significantly more common in the headspace of attacked trees (the monoterpene (E, E)- α -farnesene, the phenolic methyl salicylate, and four green leaf compounds). Only the monoterpene and the phenolic compounds elicited the preference in the bugs (Scutareanu et al., 1997). Methyl salicylate has also been shown to influence the behaviour of other predatory arthropods, including phytoseiid mites (Dicke et al., 1990), and anthocorids are attracted to methyl salicylate produced from mite-infested beans (Dwumfour, 1992). However, not all increases in volatile emission following herbivore attack led to an increase in natural enemy recruitment. For example, induced secondary defences in cucumber plants correlate with an increase in volatiles, and this deters predatory mites (Agrawal et al., 2002).

It has been suggested that plants might produce synomones (herbivore-induced plant volatiles, HIPV) as an indirect defence. By actively recruiting natural enemies of their herbivores, the damage suffered by the plant will be reduced over time (Vinson, 1999). This hypothesis is not without critics: van der Meijden and Klinkhamer (2000) point out that plants may not benefit from the presence of koinobiont parasitoids (Sect. 1.6.7), since they do not immediately kill the host and damage continues to occur after the host is attacked. More direct benefits accrue to the plant from the recruitment of predators, and parasitoids may simply be subverting this interaction. The quantity and composition of the volatiles produced by plants may vary with the herbivore species, the plant species and the environmental conditions under which plants are grown. In principle such emissions may be an adaptive response by plants to minimise damage by herbivores (Hare, 2011). The argument that plants benefit most from natural enemies that quickly kill herbivores or cause them to immediately cease feeding (Faeth, 1994; van der Meijden & Klinkhamer, 2000) is substantiated by Hare (2011): predators, which generally have broader diet ranges than parasitoids, and idiobiont parasitoids that immediately terminate herbivore feeding have greater impact on plant fitness than koinobiont parasitoids.

Synomone production by a herbivore-infested plant will depend on the feeding mechanism of the herbivore species. Maize plants attacked by the aphid *Rhopalosiphum maidis* (a phloem feeder) do not increase volatile production, whereas the lepidopteran *Spodoptera littoralis* (a leaf-chewer) and the stem-borer *Ostrinia nubilalis* induced large changes in volatile production (Turlings et al., 1998). However, plants attacked by *O. nubilalis* released a lower quantity of volatiles, and these included several unidentified volatiles that were not induced by *S. littoralis* attack, supporting the hypothesis that herbivore-specific volatiles may be produced by infested plants. The differences in HIPV induction by different herbivores can be very precise but are sufficiently distinct to be recognised by the natural enemies (Turlings & Erb, 2018), and this

allows specialist parasitoids to locate plants that are attacked by their specific hosts (de Moraes et al., 1998; Mumm & Hilker, 2005; Schroder & Hilker, 2008; Webster et al., 2010) and suitable host stages (Takabayashi et al., 1995). Cultivated tobacco, cotton and maize produced qualitatively and quantitatively different HIPV blends when attacked by *Heliothis virescens* and *Helicoverpa zea*, and the specialist parasitoid *Cardiochiles nigriceps* preferred plants damaged by its host, *H. virescens*, to plants damaged by the non-host, *H. zea* (de Moraes et al., 1998). The HIPVs may also differ in response to feeding by different life-history stages of a single herbivore species, as naïve adults of *Cotesia kariyai* differentiated between the qualitatively and quantitatively different HIPV blends of maize induced by different instars of the *Pseudaletia* caterpillars (Takabayashi et al., 1995). Similarly, early and late instar *Lymantria dispar* caterpillars induce different patterns of HIPV emission from poplar trees, which may help the parasitoids to locate a suitable developmental stage of their prey (McCormick et al., 2014b). The infested leaves of coconut palms and frass of larvae produced many herbivore-induced plant volatiles that mediate both direct and indirect defences like attracting foraging carnivorous predators and parasitoids (Shameer et al., 2017).

Of course, a given herbivore species may not necessarily induce the same production of volatiles on different host plants, and different natural enemies may in turn show different responses to these plant-produced cues. A good example of this is provided by the work of Takabayashi et al. (1998) who studied two different tritrophic systems. In the first system, the parasitoid *Cotesia kariyai* was preferentially attracted to plant (corn) volatiles produced by damage from *Pseudaletia separata*. Surprisingly, this attraction was only elicited when the plant was attacked by early larval instars of the host; feeding by late instars did not induce any preference. Plants attacked by younger *P. separata* instars produce higher proportions of terpenoids and indole volatiles. As early instar *P. separata* parasitised by *C. kariyai* consume less leaf material than older larvae, it is beneficial for the plant if the herbivores are

attacked when young (Takabayashi et al., 1995). But host age does not always influence parasitoid behaviour. Gouinguene et al. (2003) showed that *Microplitis rufiventris*, a parasitoid that cannot successfully attack first instar *Spodoptera littoralis*, could not distinguish among maize plants attacked by different instars of the herbivore.

In the second system, the congeneric parasitoid *C. glomerata* preferred volatiles produced by *Rorippa indica* (Cruciferae) plants infested with its host *Pieris rapae* over clean air. However, the parasitoid's preference is for artificially damaged plants over herbivore-damaged plants, although in both cases the plant releases (Z)-3-hexanol and (E)-2-hexenal. The technique used to artificially damage the plant seems to produce larger amounts of those volatiles. Takabayashi et al. (1998) suggest that the parasitoids in these systems use different mechanisms to overcome the reliability-detectability problem. *Cotesia kariyai* responded to volatiles that provide direct evidence of the presence of potential suitable hosts, whereas *C. glomerata* responded to volatiles produced in response to plant damage. *Rorippa indica* has few herbivore species, of which *Pieris brassicae* is one of the most prevalent, so responding to general damage cues is likely to lead the parasitoid to potential hosts.

There may also be differences in the response elicited by such cues between generalist and specialist predators or parasitoids. Röse et al. (1998) found that the specialist parasitoid *Microplitis croceipes* is attracted to insect-damaged cotton plants, whereas artificial damage (i.e., without herbivore kairomones) is enough to attract the generalist *Cotesia marginiventris*. In contrast, Dickens (1999) found that both generalist (*Podisus maculiventris*) and specialist (*Perillus bioculatus*) predators of Colorado potato beetle showed similar responses to the systemic volatiles produced by infested plants. The ability to recognise HIPVs that are associated with their specific hosts may be innate in specialist parasitoids (de Moraes et al., 1998), whereas generalist parasitoids learn to distinguish between different blends of volatiles so that they can focus on the most profitable cues (Vet et al., 1995). The damaged *Brassica*

plants release, in addition to other compounds, typical glucosinolate derivatives (Blaakmeer et al., 1994; Danner et al., 2015) which specifically attract parasitoids of herbivores that feed on the glucosinolate-producing plants (Neveu et al., 2002; Pope et al., 2008; Mumm & Dicke, 2010).

It is advisable to include at least three treatments when studying the potential role of insect herbivore host plants in natural enemy host location. These treatments are based on the following questions: First, does the predator or parasitoid respond to unattacked plants? Second, is artificial damage enough to generate a response (clipping using a sterilised pair of scissors or a hole-punch)? Third, does herbivore damage induce a response (allowing the herbivores to feed, before removing them and washing away any direct cues which may emanate from the host, such as frass)? In addition, one may ask if there is a synergy between host-plant and host-insect cues. Havill and Raffa (2000) showed that gypsy moth (*Lymantria dispar*) larvae fed on an artificial diet were not attractive to a foraging braconid parasitoid, *Glyptapanteles flavicoxis*, whereas caterpillars that had fed on their main host plant, poplar, were attractive.

As an aside, Rutledge and Wiedenmann (2003) attempted to alter the preference for different host plants in the parasitoid *Cotesia sesamiae*, a braconid parasitoid of stem-borers. *Cotesia sesamiae* preferentially attacks hosts in sorghum, and after four generations of artificial selection (attempting to obtain parasitoids with a preference for cabbage plants), no change was found in foraging behaviour. This suggests that there is little genetic variation (in this species at least) in response to plant cues in parasitoids.

Many species of insect herbivore communicate with conspecifics using infochemicals such as sex pheromones. These provide reliable cues to the presence of potential prey/host individuals. Pickett et al. (1992) identified and synthesised several aphid sex pheromones, and these have proved to be highly attractive to *Praon* spp. parasitoids in field trials (Hardie et al., 1994). However, it appears that other species of aphid parasitoid (*Aphidius ervi* and *A. eadyi*) do not

respond to these cues in field-sited pheromone traps. This may result from the behaviour of the parasitoids; these species do not appear to fly towards point sources (Stowe et al., 1995). This may explain why aphids placed on plants near sex pheromone sources in the field suffered significantly greater parasitism than those aphids kept away from the odour source (Powell et al., 1998).

Using a combination of four-way olfactometer (Fig. 1.8) and Observer software (Sect. 4.2.6), Couty et al. (1999) found that *Leptopilina bouvardi*, a parasitoid of *Drosophila melanogaster*, was attracted by a combination of the odours of both rotting fruit and a kairomone left by adult *D. melanogaster* on the substrate tested. Predators also respond to the presence of prey and plant odours. The black bean aphid, *Aphis fabae*, produces a kairomone that attracts *Metasyrphus corollae*, a predatory hoverfly (Shonouda et al., 1998), and the coccinellid *Hippodamia convergens* is attracted by plant cues released when the aphid, *Myzus persicae*, feeds on the plant (Hamilton et al., 1999). However, predators differ from parasitoids in that the host location behaviour may differ between the adult and larval stages, and also within the larval instars. Bargaen et al. (1998) found that first instar larvae of the hoverfly, *Episyrphus balteatus*, were attracted to aphid cues, but not to honeydew. Older larvae did not respond to these volatiles, but aphid extracts, honeydew and sucrose did provide cues.

The olfactory responses of foraging parasitoids and predators may vary with age, nutritional state and experience. It is important to take account of these factors when designing experiments. Ideally, preliminary experiments should be carried out to test for any effects. Synovigenic species (Sect. 2.3.4) may spend the first few days of adult life searching, not for hosts, but for foods such as nectar and honeydew, which supply nutrients for egg development (Chap. 8). Therefore, when young or starved, they may be unresponsive to host plant and host odours. Some parasitoids may even be repelled very early in adult life by an odour, which later on in life is used in host finding. *Exeristes ruficollis* responds

in this manner to the odour of pine oil (Thorpe & Caudle, 1938). Such responses need not be fixed. In an elegant study, Lewis and Takasu (1990) showed that female *Microplitis croceipes* can learn to recognise different artificial odours associated with food and host sources. Starved individuals showed a preference for the odour associated with the food source, whereas well-fed females preferentially moved towards the host-associated odour.

Furthermore, the ecological context of the interaction may need to be considered. Orr et al. (2003) found that the likelihood of a phorid fly parasitoid successfully locating its ant host, *Linepithema humile*, depended on (host) interspecific competitive interactions. Successful host location was more likely when the host was interacting with a species that elicited a chemical, rather than a physical response. Le Ru and Makosso (2001) found that foraging coccinellid predators (*Exochomus flaviventris*) can distinguish between the odours of cassava infested with parasitised and unparasitised mealybugs, preferentially orientating towards the cassava-unparasitised mealybug complex. In a similar study, van Baaren and Nénon (1996) studied two mealybug parasitoids. Both are monophagous species, with *Apoanagyrus lopezi* attacking the cassava mealybug (*Phenacoccus manihoti*) and *Leptomastix dactylopii* attacking the citrus mealybug (*Planococcus citri*). Both parasitoid species readily responded to the odours of infested plants or unattacked hosts, but not to those produced by parasitised hosts. However, rather than the parasitoids ignoring the odour of parasitised hosts, it may be that parasitised hosts have an additional odour, which acts as a deterrent. Such work strongly suggests that simplistic approaches to tritrophic systems may underplay the importance of other species in altering the pattern of the interaction.

There is one frequently overlooked aspect of experimental design associated with studies of natural enemy responses to odours. Not only do the enemies themselves show both phenotypic and genotypic variation in response to cues, the plants and prey insects themselves show variation in the signal. For example, the parasitoid

Diaeretiella rapae shows different responses to the volatiles released by two near-isogenic strains of *Brassica oleracea*, which differ only in the production of isothiocyanates (Bradburne & Mithen, 2000). Such results also hold across cultivars of the same plant species (Gowling & van Emden, 1994). Plants emitting terpenoids, a highly diverse group of compounds, show great variability in their emission among different genotypes (Gershenzon & Dudareva, 2007; Degenhardt et al., 2009). Each plant species and plant genotype releases its own particular blend of terpenoids (Degen et al., 2004) in different quantities and ratios in response to herbivore feeding and even the time of the day that feeding occurs (Loughrin et al., 1994; de Moraes et al., 2001; Shiojiri et al., 2006; Shimoda et al., 2012).

Genetic variation in kairomone production is also found among aphids. Not only will parasitoids show differential responses to different clones of aphids, the clones themselves will also show variation in response to alarm pheromone (Müller, 1983). It cannot be overemphasised that researchers studying aphid–natural enemy interactions should work with several different clones of aphids. To be pedantic, since aphids within a clone are for all practical purposes genetically identical, the clone is the replicate. Many studies of aphid–natural enemy interactions are essentially performed without replication, since only one clone is used.

There are many studies that show learning in parasitoid wasps. Cues that elicit no response in naïve females can induce a response when they have been experienced in association with host contact (e.g., Fukushima et al., 2002; Meiners et al., 2003). This is known as associative learning, defined as a response to a stimulus that usually does not induce a response, after that stimulus has been experienced in combination with another stimulus to which the animal already shows an innate response. The behavioural plasticity allowed by associative learning provides considerable flexibility in parasitoid foraging strategies.

Associative learning modifies the foraging behaviour in many parasitic wasps, as they adapt their responses to specific cues in accordance

with the rewards they receive (Costa et al., 2010). Female *Cotesia marginiventris* showed increased attraction to a specific plant odour in a six-arm olfactometer after the wasps perceived one of the herbivore-induced odours of three plants either (1) without contacting any caterpillars, (2) while contacting the host caterpillar *Spodoptera littoralis*, or (3) while contacting the non-host caterpillar *Pieris rapae* (Costa et al., 2010).

If *Aphidius ervi* females are allowed to experience oviposition on the plant-host complex (here the pea aphid, *Acyrtosiphon pisum*, on broad bean, *Vicia faba*), then they are significantly more likely to orientate towards the plant-host complex than naïve females. Naïve females will orientate towards a source of host volatiles (Du et al., 1996; the innate response), but experienced females will also show an increased response to volatile cues from uninfested plants, which is likely to be an example of associative learning (Guerrieri et al., 1997).

The effect of learning on behaviour may depend on the experience and physiological state of the parasitoid. Female *Leptopilina boulardi* (a eucoilid parasitoid of *Drosophila melanogaster*) will associate odour cues with host presence, increasing ovipositor searching when exposed to the cue (Pérez-Maluf & Kaiser, 1998). This increase in searching behaviour was not associated with mating or prior oviposition experience, although both factors did influence some parameters of host searching. Females with prior oviposition experience showed a higher latency and reduced probing duration, whereas mated females tended to have a reduced latency and increased probing duration (Pérez-Maluf & Kaiser, 1998). Female *L. boulardi* show heritable variation in these responses to learned cues (Pérez-Maluf et al., 1998).

The likelihood of learning appears to be related to the nature of the substrate the parasitoid is searching. Duan and Messing (1999) suggested that parasitoid acceptance of less preferred hosts may be more likely to change with experience, than if the parasitoid is allowed to learn cues associated with preferred host-substrate complexes. If this is the case, then it is possible that associative learning will not be

equally likely to be found with all potential host species. Therefore, the absence of learning in one situation may not reflect what will be found with other potential hosts. For example, Morris and Fellowes (2002) found that natal host influenced the likelihood of learning in the pupal parasitoid *Pachycrepoideus vindemmiae*. Females that emerged from *Musca domestica* only showed a preference for that host species after gaining experience attacking it. Experience gained in attacking *Drosophila melanogaster* did not change their preference. In a similar manner, wasps that emerged from *D. melanogaster* only showed a preference for that host when allowed to gain experience in attacking *D. melanogaster* pupae and experience gained on *M. domestica* did not alter their preference.

In experiments investigating learning in parasitoids, it is often best to use novel cues, which can be controlled and measured by the investigator. In studies of associative learning, odours such as vanilla and strawberry essence have been successfully used. Iizuka and Takasu (1998) used this approach to show associative learning by the pupal parasitoid *Pimpla luctuosa*. In addition, they found that females ceased attacking dummy hosts which had the previously learned odour after several failed oviposition attempts, which suggests that parasitoids can also learn to ignore cues (Iizuka & Takasu, 1998). Similarly, female *Microplitis croceipes* that had antennated host frass or oviposited in a host in the presence of vanilla odour responded to the odour in the wind tunnel and the parasitoids oviposited in the presence of the odour responded to the odour even at 24 h after experience (Takasu & Lewis, 2003). This shows that oviposition in the host in the presence of odours strongly affects associative learning and the persistence of learned response to the odours (Takasu & Lewis, 2003; Giunti et al., 2015). *Lariophagus distinguendus*, the ectoparasitoid of *Sitophilus granarius*, after being trained by being kept on infested grains in the presence of an odorant furfurylheptanoate (FFH) preferred the odour field containing FFH in olfactometers (Müller et al., 2006). In this case, the reaction to FFH is caused by associative learning due to host experience as an

unconditioned stimulus, and this learning experience in wasps induced a memory equivalent to the long-term memory found in *Apis mellifera* and *Drosophila melanogaster* (Müller et al., 2006). Studies on the effect of associative learning of plant chemicals on host-searching behaviour in *Ascogaster reticulata*, an egg-larval parasitoid of *Adoxophyes honmai*, revealed that the female wasps conditioned with tea leaf preferred tea leaf over the other plant species (Seino & Kainoh, 2008). Similarly, Kawamata et al. (2018) studied the innate colour preference and associative colour learning ability of *Ascogaster reticulata*, a braconid parasitoid of the tortricid *Adoxophyes honmai*, and reported that the wasps trained to associate black or blue colour with the presence of a host egg mass showed increased preference for these colours.

1.6.3 Host Location by Parasitoids

Inferring Behaviour from Morphology

Perhaps one of the more straightforward means of deducing how a predator or parasitoid may locate its prey is to pay close attention to the insect's morphology. For example, pipunculid flies have extremely well-developed compound eyes, and in the females the forward-facing facets are considerably enlarged (Jervis, 1992), so it can be inferred that host finding in these parasitoids relies on vision (confirmed by Forbes P. Benton, see Waloff & Jervis, 1987). However, some caution should be used when inferring behaviour from morphology, and, ideally, the insect would be studied carefully to confirm that the trait does aid predation or parasitism. Nevertheless, a small amount of basic biology and natural history will provide a huge amount of help in understanding the species of interest.

Genetic Variation in Foraging Behaviour

Wajnberg and Colazza (1998) used a combination of automated recording and statistical techniques to study the foraging behaviour of the parasitoid *Trichogramma brassicae* and found not only that the searching efficiency of females within a patch

determined the number of hosts they encountered, but also that there was significant genetic variation among females in this trait. Whether such genetic variation plays a role in allowing populations to adapt to different habitats is a question that deserves a great deal of attention (see Wajnberg, 2004, for a review). Van Nouhuys and Via (1999) studied variation among populations of the parasitoid *Cotesia glomerata* attacking small cabbage white butterfly (*Pieris brassicae*) caterpillars in wild and agricultural habitats. These habitats present very different environments to the foraging parasitoids, as in the agricultural habitat every plant that a parasitoid lands on may carry its host. Wasps that originated from the wild habitat tended to move more between plants, perhaps reflecting the spatial characteristics of wild host populations. Jia et al. (2002) found genetic variation in response to herbivore-induced plant volatiles in the predatory mite, *Phytoseiulus persimilis*. Isofemale lines (Sect. 3.2.3) showed a negative correlation between the likelihood of patch location and patch residence time, suggesting a trade-off between prey location and reproduction.

Kairomones

Having arrived in a potential host habitat, a parasitoid begins the next phase in the search for hosts. Often, insects show arrestment in response to contact with kairomones of low volatility deposited by their hosts on the substratum. Materials containing such kairomones (sometimes referred to as 'contact chemicals') have been shown to include host salivary gland or mandibular gland secretions, host frass, and homopteran honeydew and cuticular secretions. Several herbivore species have evolved traits which reduce the build-up of frass near to where they feed, reducing the likelihood of their location by foraging parasitoids. This is a relatively common behaviour in caterpillars dwelling in leaf shelters, who can eject their frass with considerable force, depositing it some distance from the potential host (Weiss, 2003).

Kairomones present on the host itself have also been shown to induce oviposition behaviour by several parasitoid species. For example, the

parasitoid *Aphidius ervi* shows strong responses to pea aphid (*Acyrtosiphon pisum*) siphuncle secretions, but only at very short range or on actual contact, and the presence of these kairomones alone is enough to induce oviposition behaviour (Battaglia et al., 2000). A similar response is shown by the parasitoid *Diadromus pulchellus*. This wasp responds to the presence of soluble polypeptides present in the cocoons of its host, the leek moth *Acrolepiopsis assectella* (Benedet et al., 1999).

Because stronger responses may be found to a kairomone after prior oviposition experience in the presence of the substance, an initial experiment ought to be performed using parasitoids with previous oviposition experience. The next series of experiments would involve comparing the response of parasitoids to patches of potential host habitat, within which hosts have never occurred (e.g., clean host plant leaves), with the response to patches within which hosts have previously occurred for some time. The following changes in behaviour might be observed in the searching insects: a decrease in walking speed, an increase in the rate of turning, a sharper angle of turn at the patch edge, an increase in the number and frequency of ovipositor stabs, an alteration in position of the antennae, an increase in the amount of drumming with the antennae and an increase in the amount of time spent standing still. Video-recording equipment, together with the computer software discussed in Chap. 4 (Sect. 4.2.6) can be used to record and analyse alterations in these behavioural components. Path tortuosity can be evaluated by measuring the angle between tangents drawn at intervals along the path.

A useful additional analysis that can be carried out involves designating areas of an arena, e.g., the kairomone-treated area and the clean area, and measuring the proportion of the total time available that the insect spends searching each area. If the parasitoid or predator can be shown to have spent a greater proportion of its time in the treated area, then it can be considered as having been arrested by the kairomone.

Once it has been demonstrated that patches within which hosts have occurred contain a

stimulus to which parasitoids respond by arrestment, further experiments can be performed to elucidate the nature of the stimulus. To eliminate the possibility that the arrestment response is due to some physical property of the patch (e.g., the texture of the wax secretions left by mealybugs, or depressions caused by feeding larvae), one can attempt to dissolve the putative kairomone either in distilled water, hexane or another suitable solvent, and then apply the solution to a surface, for example a leaf or a glass plate, which has never borne host larvae. If an arrestment response is still observed, it can be concluded that the soluble substance is a kairomone. For a detailed experimental study of the arrestment response in a parasitoid, conducted along these lines, see Waage (1978) and Fig. 1.12.

Kairomones provide quantitative, in addition to qualitative information. Several parasitoid species, when presented with several patches of kairomone in different concentrations, have been shown to spend longer periods searching those patches with the higher kairomone concentrations than the patches with the lower concentrations, at least over part of the range of concentrations (Waage, 1978; Galis & van Alphen, 1981; Budenberg, 1990; Hare & Morgan, 2000). Because kairomone concentration varies with host density, parasitoids can obtain information concerning the profitability of a patch, even before they encounter hosts. Honeydew produced by the aphid *Brevicoryne brassicae* provides not only a qualitative cue in host location, but also is a source of information on the density of hosts within a patch for the parasitoid *Diaeretiella rapae* (Shaltiel & Ayal, 1998).

1.6.4 Responses to Parasitoid Odours and Patch Marks

Parasitoid Odours

Janssen et al. (1991) showed, using olfactometer experiments, that *Leptopilina heterotoma* is attracted to the odour of stinkhorn fungi containing larvae of *Drosophila phalerata*. When these patches are offered in an olfactometer together with similar patches on which searching females

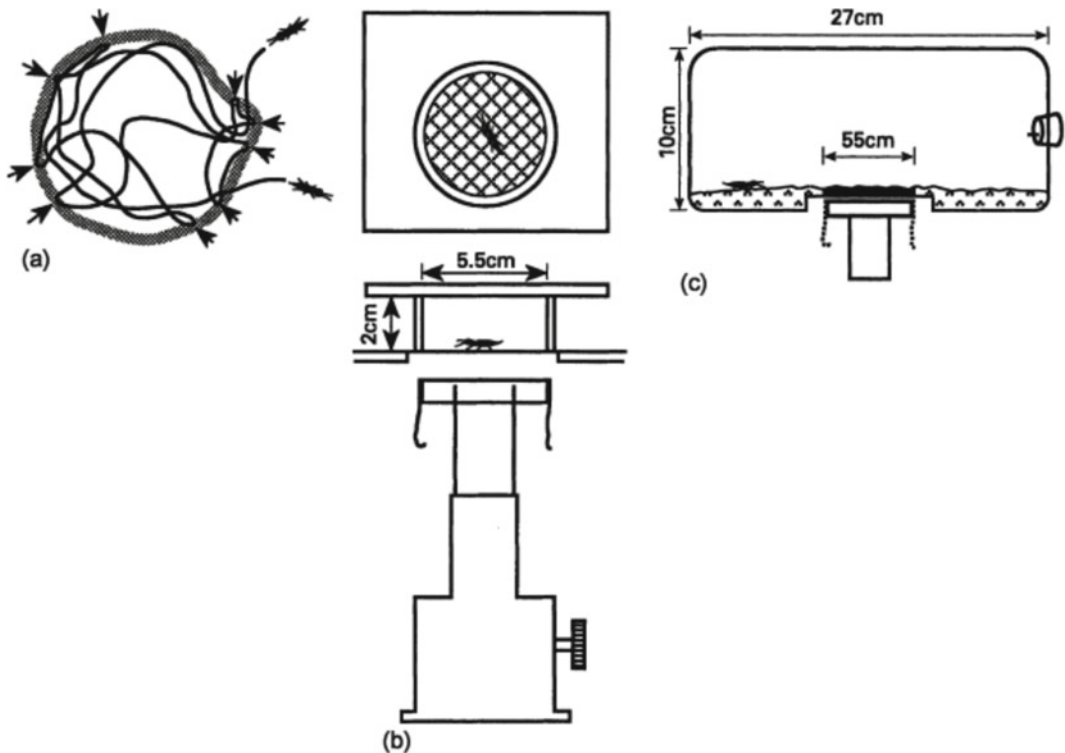
of *L. clavipes* are present, *L. heterotoma* avoids the odour fields of patches containing *L. clavipes* females. The conclusion from these observations is that *L. clavipes* produces an odour whilst searching, which repels its competitor *L. heterotoma*, at least when the latter is presented with the choice between host-containing patches emitting this odour and host-containing patches that lack the odour. Price (1981) suggests that the function of the strong odour emitted by some female ichneumonids, which may be noticed when these insects are handled, likewise signals the insects' presence to other parasitoids. Furthermore, kairomones combined with odours from conspecifics may help parasitoids avoid intraspecific competition. *Venturia canescens* will normally orientate towards host kairomones but will avoid the odour plumes which contain both host kairomones and the odour of conspecific females (Castelo et al., 2003).

Höller et al. (1991) found evidence that foraging primary parasitoids of aphids are repelled by odours produced by adult hyperparasitoids.

Furthermore, individuals of the aphid *Sitobion avenae* that have been attacked by a primary parasitoid, *Aphidius ervi*, show differential responses to odours released by a hyperparasitoid, *Alloxysta victrix*. At 120 h after attack, the aphids are attracted to the volatiles, yet at 160 h after attack they are repelled by the same cue. Since unattacked aphids show no responses to these cues, Guerra et al. (1998) suggest that, as behavioural control passes from aphid to parasitoid over time, the adaptive benefits of responding to these cues will also change.

In cases where the odour of a parasitoid repels conspecifics, the substance is a pheromone, whereas in cases where heterospecific competitors are repelled, there is some justification in describing the substance as an allomone. However, because of similar problems to those mentioned below when discussing patch marking, the use of the term allomone should be avoided here.

It is not known how widespread the use of repellent odours is among insect parasitoids,



◀ **Fig. 1.12** Arrestment and patch time allocation in parasitoids: Waage's (1978) classic study of *Venturia canescens*. **a** An experiment carried out to investigate arrestment behaviour of *V. canescens* in response to contact with a kairomone. The path of a walking female was observed on a glass plate, upon which 1 ml of ether extract of ten pairs of host (the lepidopteran *Plodia interpunctella*) mandibular glands had been placed and allowed to evaporate. Stippling denotes the edge of the patch. Upon encountering the patch edge from the outside, a female stops and begins to apply the tips of its antennae rapidly upon the substratum. It then proceeds onto the patch at a reduced walking speed (inverse orthokinesis). Within the patch, the wasp occasionally stops walking and probes the substratum with its ovipositor. When the wasp encounters the patch edge from within the patch, it turns sharply away from the edge. The wasp eventually leaves the patch, presumably due to waning of the arrestment response, e.g., through habituation or sensory adaptation to the chemical stimulus. **b** Apparatus used to test the hypothesis that the patch edge response of *V. canescens* is to the removal of the chemical stimulus, and not to the patch edge *per se*. The terylene gauze screen was impregnated with host mandibular secretion by confining ten fifth instar host larvae between two sheets of gauze. The lower sheet was then stretched over a Petri dish, as in the figure. By raising and rapidly lowering the contaminated screen, Waage (1978) could precisely control when a wasp (in the upper chamber) was 'on' and 'off' the patch. A wasp's movements were traced with a felt-tipped pen on the plate glass roof of the chamber (nowadays this could be done using video recording coupled with analysis of movements using computer software, Sect. 1.4). Over the first centimetre travelled following stimulus removal, most wasps made a reverse turn, which may be considered to be a klinotactic (i.e., directed) response because the turn oriented the wasps back towards the point from where the stimulus was removed. Thus, Waage (1978) concluded that the patch edge response of *V. canescens* is due to the removal of the chemical stimulus, not to the patch edge *per se*, i.e., his hypothesis was supported. **c** Apparatus used by Waage to test the effect of kairomone concentration on patch

residence time. 'Patches' were made by confining different numbers of host larvae, together with food medium, between terylene gauze sheets for several hours. The larvae were then removed. For each kairomone concentration, the contaminated patch of food medium (minus the hosts) was held over the central part of the floor of the chamber (blackened area). An empty Petri dish was raised beneath the patch (see next experiment). Two arbitrary time intervals (14 s and 60 s continuously off a patch) were used as criteria for determining patch leaving by wasps. Application of either of these criteria indicated that the duration of the first visit to a patch increased markedly with increasing kairomone concentration. The apparatus was also used to test the effect of ovipositions on patch residence time. A patch of host-contaminated food medium was stretched over the central part of the chamber floor, and at the onset of the experiment a dish containing 30 host larvae was raised beneath the patch. Each wasp was allowed to make an oviposition into a host as soon as she entered the patch. During the resting period following that oviposition, the dish containing host larvae was replaced with an empty one. Oviposition was found to produce a marked increase in the duration of the first patch visit by a wasp. Another experiment was carried out by Waage (1978), which demonstrated that oviposition does not elicit a significant arrestment response in the absence of the kairomone. This experiment employed apparatus (**b**). A host-contaminated terylene gauze screen, with or without host larvae beneath it, was raised beneath the chamber. A single wasp was exposed either to the chemical stimulus alone for the duration of one bout of probing, or to the chemical stimulus with hosts present for one oviposition of similar duration. The screen was then lowered, so removing the kairomone stimulus, and the time taken for the wasp to leave the chamber floor and then climb onto one of the chamber sides was recorded (this behaviour being interpreted as the cessation of any response elicited by the contact chemical). No significant difference in the amount of time taken to abandon the host area was observed between the treatments with oviposition and those without. From Waage (1978), reproduced by permission of Blackwell Publishing

largely because this issue has not been studied in a systematic way. Like other infochemicals used by parasitoids, odours produced by adult parasitoids can potentially have a profound effect on patch choice and time allocation by individual wasps and thus on the distribution of parasitoids over a host population.

Patch Marking

Some parasitoid species are known to leave chemical marks on surfaces they have searched (Galis & van Alphen, 1981; Sheehan et al., 1993;

Couchoux & van Nouhuys, 2014). This marking behaviour can have a number of functions. By leaving a scent mark on the substratum, a parasitoid can avoid wasting time and energy in searching already visited areas. A female can also use the frequency with which she encounters marks to determine how well she has searched the patch, and so assist in the decision when to leave the patch. When encountered by conspecific or heterospecific competitors, marks sometimes induce the competitor to leave an area. *Pleolophus basizonus*, *Orgilus lepidus*,

Asobara tabida, *Microplitis croceipes*, *Halticoptera rosae*, *H. laevigata* and *Hyposoter horticola* (Price, 1970; Greany & Oatman, 1972; Galis & van Alphen, 1981; Sheehan et al., 1993; Hoffmeister, 2000; Hoffmeister & Gienapp, 2001; Couchoux & van Nouhuys, 2014) mark areas they search, and females spend less time in areas previously searched by conspecifics. In the case of a heterospecific competitor, the marker substance could be termed an allomone. However, leaving the patch may not always be in the interest of the competitor; the competitor may stay and superparasitise the hosts parasitised by the first female (Sect. 1.9.4). Thus, the use of the term allomone should be avoided in this context.

The use of patch-marker substances can be demonstrated by offering patches containing kairomone, but not hosts, to a parasitoid. After the parasitoid has left the patch, a second parasitoid is introduced on to the same patch. If the second insect stays on the patch for a shorter period than the first, the existence of a mark left by the first has, given sufficient experimental replication, been demonstrated.

Predators may also patch-mark. Nakashima et al. (2002) showed that the insect predator *Orius sauteri* avoids patches where they have recently foraged, although this behaviour is not exhibited when the predator has not recently fed. The patch marks appear to be relatively short lived (<1 h) and may simply prevent the females from foraging in an area previously searched.

It is not only insect natural enemies that respond to such cues. The prey themselves may also respond to odour cues left by foraging predators or parasitoids. For example, spider mites (*Tetranychus urticae*) will avoid foraging in patches that have previously held predators, and this avoidance is greater if the predators have been feeding on *T. urticae* (Grostal & Dicke, 2000). Most studies of predator and parasitoid foraging behaviour assume that such avoidance does not take place.

1.6.5 Search Modes Within a Patch

While kairomones and other cues can arrest parasitoids and predators in host/prey patches and so increase the probability of encounter, host/prey location is itself likely to be in response to non-chemical, e.g., visual and tactile cues. For example, in coccinellid predators, prey honeydew acts as an arrestant stimulus for adults (van den Meiracker et al., 1990: *Diomus* sp., *Exochomus* sp.; Heidari & Copland, 1993: *Cryptolaemus montrouzieri*), but the prey are located in response to visual cues (Stubbs, 1980: *Coccinella septempunctata*; Heidari & Copland, 1992: *C. montrouzieri*). Stubbs (1980) devised a method for calculating the distance over which prey are detected (see also Heidari & Copland, 1992). Another method was designed to calculate the distance over which insect parasitoids detect their hosts (Bruins et al., 1994). In the coccinellid *Coccinella septempunctata*, honeydew acts as arrestant stimulus that increased exploitation of prey patches by larvae, but location of the prey occurs only upon physical contact (Carter & Dixon, 1984).

It has been shown for a number of predators that arrestment occurs as a consequence of prey capture (Dixon, 1959; Marks, 1977; Nakamura, 1982; Murakami & Tsubaki, 1984; Ettifouri & Ferran, 1993). In this way, the insect's searching activities are concentrated in the immediate vicinity of the previously captured prey, increasing the probability of locating another prey individual. The adaptive value of such behaviour for predators and parasitoids of insects that have a clumped distribution, such as aphids, is obvious. Predators also show arrestment after capturing a prey individual but failing to feed on it, even a failed encounter with prey is an indication that a clump of prey has been found (Carter & Dixon, 1984). Carter and Dixon (1984) argued that the latter behaviour is particularly important for early instars of coccinellids, since the prey capture efficiency of these instars is

relatively low. In final instar larvae of the coccinellid *Harmonia axyridis*, arrestment in response to prey capture occurs only if the predators are provided with the same prey species as they were reared upon, indicating a strong conditioning effect (Ettifouri & Ferran, 1993). Arrestment of the aboreal ponerine ant *Platythyrea modesta* is affected by prey size. Small prey required contact, whereas larger prey, such as grasshoppers, elicit arrestment at a distance (Djieto-Lordon et al., 2001). Following arrestment, the ants attacked without antennation. Small prey species are killed using pressure from the mandibles, whereas larger prey are stung.

Arrestment in the above cases can be studied in the same way as arrestment of natural enemies in response to kairomones, i.e., by analysing the search paths of predators and parasitoids and by measuring the proportion of the total time spent searching designated unit areas within an arena.

Species of parasitoid attacking the same hosts may differ in the way they search a patch. In parasitoids of concealed anthomyiid, calliphorid, drosophilid, muscid, phorid, sarcophagid and sepsid fly larvae, at least three different search modes exist (Vet & van Alphen, 1985). Wasps may either: (1) probe the microhabitat with their ovipositors until they contact a host larva (ovipositor search); (2) perceive vibrations in the microhabitat caused by movements of the host and use these cues to orient themselves to the host (vibrotaxis) which is then probed with the ovipositor; or (3) drum, with their antennae, the surface of the microhabitat until they contact a host (antennal search).

To determine which search mode a parasitoid species uses is easy in the case of ovipositor search or antennal search, where brief observation of a searching female suffices to classify her search mode. However, it can be difficult to prove that vibrotaxis occurs, because of the possibility that the parasitoid locates its hosts by reacting to a gradient in kairomone concentration or some other chemical cue, or to infrared radiation from the host. Therefore, we will consider this search mode in more detail.

Parasitoids have been shown to respond to vibratory stimuli issuing from foraging hosts

when they are searching for potential victims. Meyhöfer et al. (1994, 1997) found that the leafminer *Phyllonorycter malella* produces vibrations while feeding, and that the parasitoid *Sympiesis sericeicornis* responds to these cues by increased rates of turning in the vicinity (vibrokinesis). There is also some evidence for vibrotaxis, but this is more circumstantial. For example, *Asobara tabida* and *Leptopilina longipes*, two common parasitoids of *Drosophila* species, will fail to locate immobilised hosts (van Alphen & Drijver, 1982; van Dijken & van Alphen, 1998). Indeed, it has been suggested that the rover/sitter polymorphism in larval *Drosophila melanogaster* (Alwash et al., 2021) may be maintained by frequency-dependent selection resulting from the relative proportions of vibrotactic parasitoids within the community of larval parasitoids (Osborne et al., 1997; see also Hodges et al., 2013).

In a valuable review, Meyhöfer and Casas (1999), however, pointed out some pitfalls in the study of the use of vibratory stimuli by parasitoids searching for hosts. Many of these are associated with experimental design, where the use of immobilised larvae (e.g., by freezing, dipping in hot water, needle insertion) introduces the confounding factors associated with reduced metabolic rate (influencing heat or CO₂ output) and changes in the chemical cues emanating from potential hosts. Unless these confounding factors are controlled for, it is difficult to confirm that changes in parasitoid behaviour are the result of responses to vibratory cues. A second issue they raised is the need to confirm that the host does indeed produce vibratory cues to which the parasitoid can and does respond. Very few studies satisfactorily deal with these issues, although techniques such as laser vibrometry are available to characterise these vibrational signals (Meyhöfer et al., 1994).

Wäckers et al. (1998) used laser vibrometry to infer the ability of the pupal parasitoid *Pimpla turionellae* to locate potential hosts. Clearly, the host pupae themselves do not produce vibrations; instead, the parasitoid itself appears to generate vibrations that can then be used, in a manner analogous to sonar, to locate hosts. The

technique used by Wäckers et al. (1998) was particularly ingenious: by using paper cylinders of differing thickness and a cigarette filter to serve as a 'host', the authors were able to show that, as the thickness of the substrate increased, the number of oviposition attempts decreased. They suggest that the parasitoid responded to differences in resonance between hollow and solid sections of substrate, and that increasing thickness of paper reduced the ability of the parasitoid to distinguish between sections.

Vibrations may also be used by potential hosts as a warning that a parasitoid may be about to attack. Bacher et al. (1997), again using laser vibrometry, showed that the late instar larvae and pupae of the leafminer *Phyllonorycter malella* reacted defensively to certain frequencies produced by oviposition insertion by the parasitoid *Sympiesis sericeicornis*. Such ability to avoid attack may prove to be common among leafminers. Using the same system, Djemai et al. (2001) used artificial vibrations matched to the frequencies resulting from *Sympiesis sericeicornis* attack, and this elicited the same defensive behaviours in the host. This provides excellent empirical support for the conclusions drawn by the earlier study.

The reason why it is important to determine the search mode of a parasitoid or a predator is that different search modes lead to different encounter rates with hosts in the same situation. Thus, a parasitoid using vibrotaxis as a search mode may be more successful in finding hosts when the hosts occur at low densities, while ovipositor search may be more profitable at high host densities. Antennal search results in encounters with larvae on the surface, while ovipositor search can also result in encounters with hosts buried in the host's food medium. However, Broad and Quicke (2000) showed that the use of vibrotaxis is positively correlated with host depth in the substrate, controlling for parasitoid size. This suggests that in substrates where ovipositor searching is time-consuming (e.g., where the host is relatively deep in the substrate), vibrotaxis may be more common than the aforementioned argument suggests. Often, the

searching behaviour of a parasitoid comprises a combination of search modes, as the insect responds to different cues while locating a host. It is therefore not always possible to place the behaviour of a parasitoid in one category.

Predators may employ a combination of search modes. The larvae of the predatory water beetle *Dytiscus verticalis* may either behave as sit-and-wait predators when prey density is high, or hunt actively for prey when prey density is low (Formanowicz, 1982). Such variety is common, and many species that are traditionally considered to be ambush predators (e.g., mantids, see below) frequently actively search for prey.

Pit-dwelling antlion (*Myrmeleon* spp.) larvae provide the classic example of an ambush predator. The larvae excavate funnel-shaped holes in loose sand, and it is the latter that prevents potential prey from escaping. The spatial distribution of the antlion *Myrmeleon immaculatus* reflects that of prey density, minimising the need to move to a new pit location (Crowley & Linton, 1999). The antlion larva waits at the base of the pit, with only its relatively large mandibles projecting from the sand. Once a victim becomes trapped, the larva suddenly grabs its prey and drags it under the sand. This has the advantage of rendering physical defences, such as biting or formic acid, useless (New, 1991). Given that the ambush strategy is risky (i.e., the presence of food is unpredictable) and that manufacturing and maintaining the pit is costly (Lucas, 1985; Hauber, 1999), it is unsurprising that antlions have relatively low metabolic rates (van Zyl et al., 1997). Larvae can survive for relatively long periods without food, albeit at the cost of a long development period.

In contrast to situations where camouflage is critically important, some 'sit-and-wait' predators employ conspicuous colouration, e.g., several species of orb-web spider. The spiny spider, *Gasteracantha fornicata*, has a strikingly coloured yellow-and-black-striped dorsal surface. Spiders which were dyed black captured fewer prey individuals, supporting the hypothesis that bright colours helped attract visually orienting prey (Hauber, 2002).

1.6.6 Host Recognition by Parasitoids

Generally, specific (although not necessarily host species-specific) host-associated stimuli need to be present for triggering of oviposition behaviour by parasitoids following location of a prospective host. The role these stimuli play in host recognition has been investigated mainly by means of very simple experiments.

For many parasitoids, host size appears to be important for host recognition. In a classic experiment, Salt (1958) presented female *Trichogramma* with a small globule of mercury – smaller than a host egg—and observed that the parasitoid did not respond to the globule. However, Salt (1958) then added minute quantities of mercury to the globule, whereupon a female would mount it, examine it and attempt to pierce it with her ovipositor. When Salt (1958) continued adding quantities of mercury to the globule, a globule size was reached where a wasp again did not recognise it as a prospective host.

Host shape can be important in host recognition. A number of workers have placed inanimate objects of various kinds inside either hosts or host cuticles from which the host's body contents have been removed and have shown that some host shapes are more acceptable than others.

One needs to be cautious in interpreting the results of experiments where hosts or host dummies of various sizes and shapes are presented to parasitoids. If a parasitoid is found to attempt oviposition more often in large dummies than in small ones, or in rounded dummies than in flattened ones, the stimuli involved could be visual, tactile or both. Some investigators have failed to determine precisely which of these stimuli are important (but see Bruins et al., 1994). Similar caution needs to be applied to experiments in which dummies of different textures are presented to parasitoids.

As can often be inferred from direct observations on the behavioural interactions of parasitoids and hosts, movement by the host can be important in triggering oviposition behaviour. A simple experiment for investigating the role of host movement in host recognition involves killing hosts, attaching them to cotton or nylon

threads, moving both these and similarly attached living hosts before parasitoids, and determining the relative extent to which the dead and living hosts are examined, stabbed, drilled or even oviposited in by the parasitoids.

Kairomones play a very important (although not necessarily exclusive) role in host recognition by parasitoids. In an elegant series of experiments, Strand and Vinson (1982) showed how, if glass beads the size of host eggs are uniformly coated with material present in accessory glands of the female host (host eggs normally bear secretions from these glands) and are presented to females of *Telenomus heliothidis* (Scelionidae), the insects will readily attempt to drill the beads with their ovipositors. Female parasitoids, when presented with either clean glass beads or host eggs that had been washed in certain chemicals, were, on the whole, unresponsive. Strand and Vinson (1983) analysed the host accessory gland material and isolated proteins from it (by electrophoresis); two proteins were shown to be particularly effective in eliciting drilling of glass beads. It cannot be assumed from these findings that *T. heliothidis* will recognise any object that is coated in kairomone as a host: host size and shape are also important criteria for host acceptance. Similar findings have been reported for several other species (e.g., Conti et al., 2003: *Trissolcus brochymenae*; Takasu et al., 2003: *Ixodiphagus hookeri*). In some cases, the active compound has been identified: O-caffeoylserine, produced by the cassava mealybug, elicits host-acceptance behaviour in the encyrtid parasitoids *Acerophagus coccois* and *Aenasius vexans* (Calatayud et al., 2001).

Weinbrenner and Völkl (2002) took a different approach to understanding the importance of contact kairomones in host recognition by *Aphidius ervi*. Wet pea aphids were not accepted as hosts, which the authors suggest resulted from the parasitoids being unable to detect the host's kairomones. Another useful approach to studying the role of kairomones would be to take a polyphagous parasitoid species and determine whether the recognition kairomone is different or the same for each of its host species. Van Alphen and Vet (1986) showed that the braconid

parasitoid *Asobara tabida* discriminates between the kairomone produced by *Drosophila melanogaster* and that produced by *D. subobscura*. Acceptance of a prospective host for oviposition also depends upon whether the host is already parasitised. This important aspect of parasitoid behaviour is dealt with later in Sect. 1.9.

1.6.7 Host and Prey Selection

Host Species Selection

Many parasitoid species are either polyphagous or oligophagous. Strictly monophagous species are relatively uncommon. When different potential host species occur in different habitats, a parasitoid ‘decides’ which host species is to be attacked by virtue of its choice of habitat in which to search. Sometimes, potential host species can be found coexisting in the same patch (e.g., two aphid species living on the same host plant, larvae of different fly species feeding in the same corpse, etc.). In these cases, experiments on host species selection are relevant, and can demonstrate whether the parasitoid has a preference for either of the species involved. Preference is defined as follows: a parasitoid or predator shows a preference for a particular host/prey type when the proportion of that type oviposited in or eaten is higher than the proportion available in the environment. This is the traditional ‘black box’ definition (Taylor, 1984), so called because it does not specify the behavioural mechanisms involved. For example, a parasitoid may encounter a host individual and accept it, but the host may then escape before the parasitoid has an opportunity to oviposit (likewise, prey may escape from a predator following acceptance). If host types differ in their ability to escape, they will be parasitised to differing extents even though they may be accepted at the same rate. Conversely, they may be accepted at different rates but be parasitised to the same extent. It could be argued that preference, to be more meaningful behaviourally, ought to be defined in terms of the proportion of hosts or prey accepted. However, it may not be possible

in experiments to observe and score the number of acceptances (one reason being that the insects do not display obvious acceptance behaviour).

Often experiments designed to test for a preference score the number of hosts parasitised, or prey fed upon, after a certain period of exposure where equal numbers of each species have been offered (Sect. 1.12 describes a different approach). There is, however, a problem with this approach: the number of hosts oviposited in, or prey eaten, depends on the number of encounters with individuals of each species, and the decision to oviposit, or feed, on the less preferred species may be influenced by how often the female has the opportunity to oviposit, or feed, on the preferred species. Encounter rates (Sect. 1.7) may also be unequal for two host, or prey, species, due to factors such as differences in size or activity. Therefore, species selection should preferably be investigated in such a way that encounter rates with both species are equal. This requires pilot experiments, with equal numbers of each species offered simultaneously, to calculate the ratio in which both types should be presented so as to equalise encounter rates.

Mathematical formulae used for quantifying preference (whether for species or for stages) are many and varied (Chesson, 1978, 1983; Cock, 1978; Settle & Wilson, 1990), but the most widely used measure of preference is the following (Sherratt & Harvey, 1993):

$$\frac{E_1}{E_2} = c \frac{N_1}{N_2} \quad (1.1)$$

where N_1 and N_2 represent the numbers of two host, or prey, types available in the environment, and E_1 and E_2 represent the numbers of the two host, or prey, types oviposited in or eaten. The parameter c is the preference index and can be viewed as a combined measure of preference and encounter probability (Sect. 1.12). A value of c between zero and one indicates a preference for host, or prey, type 2, whereas a value of c between one and infinity indicates a preference for host, or prey, type 1. Mathematical formulae used in testing whether preference varies with the

relative abundance of the different host or prey, types are discussed in Sect. 1.12.

A rather more sophisticated approach has been suggested by Sakuma (1998), using probit analysis. This method overcomes the problems associated with standard probit analysis (an all-or-nothing approach), taking into account differences in the strength of the stimulus (e.g., number of hosts or quantity of odour cues). The program (available from Masayuki Sakuma, Graduate School of Agriculture, Kyoto University, Kyoto 606–8502, Japan), involves a regression of the probit-transformed number of responses against the log of the dose (or here, number of hosts). Such an approach would be suitable also for analysing preference data from olfactometer experiments.

Optimal host selection models predict that the acceptance of a less profitable host species depends on the encounter rate with the more profitable host species. The less profitable species should always be ignored if the encounter rate with the more profitable species is above some threshold value but should be attacked if the encounter rate with the more profitable species is below that threshold value (Charnov, 1976; Stephens & Krebs, 1986). Note that if recognition of prey is not instantaneous, then acceptance of the less profitable host species depends on the encounter rates with both of the host species and on the time taken for recognition to take place. Often, for the convenience of the researcher, relatively high densities of hosts, resulting in high encounter rates, are offered in laboratory experiments. This will produce a bias towards more selective behaviour. For example, in laboratory experiments with high encounter rates, the *Drosophila* parasitoid *Asobara tabida* is selective when offered the choice between two host species differing in survival probability for its offspring (van Alphen & Janssen, 1982) and avoids superparasitism (van Alphen & Nell, 1982). However, in the field, when encounter rates are equal to or lower than one host per hour, wasps always generalise and superparasitise (Janssen, 1989). If one is interested in knowing the performance of a parasitoid species in the field, where host densities are often very low, in

the laboratory one should use host densities equivalent to those occurring in the field. The high densities often offered in the laboratory may allow the researcher to obtain much data over a short period of observation but the insect's behaviour in such experiments may not be representative of what happens in the field.

To understand the adaptive significance of host preferences, the relative profitability of different host species can be assessed, in the first instance, by recording the survival rates of parasitoid progeny in the different hosts. Even if no differences in the probability of parasitoid offspring survival are recorded, one cannot automatically assume that the host species concerned are equally profitable. Handling times may vary with host species, as may the fecundity and other components of the fitness of parasitoid progeny, and ideally, these should be measured.

Experiments on prey choice by predators are influenced by prey densities offered in a manner similar to that described above for parasitoids. Because searching activity is influenced by the amount of food in the gut (more precisely, the degree of satiation), a predator's feeding history may determine the outcome of experiments on prey choice (Griffiths, 1982; Sabelis, 1990; but this may not always be the case, e.g., see de Kraker et al., 2001).

So far, we have considered innate host and prey preferences. Preferences may change with experience (Sect. 1.12) Preferences may also change with the physiological state of the predator or parasitoid. For example, Sadeghi and Gilbert (1999, 2000) found that the hoverflies *Episyrphus balteatus* and *Syrphus ribesii* both preferentially attacked pea and rose aphids over nettle aphids, and that the strength of this relationship weakened with time. This is likely due to the influences of host deprivation and egg load on oviposition rates differing between the species.

One crucial, yet almost completely ignored, factor in parasitoid host choice behaviour concerns the presence of genetic variation within a given population. Without this variation, populations will not be able to evolve in response to changes in the host community. Genetic variation

explains the variation among parasitoid individuals in host preference. Rolff and Kraaijeveld (2001) found that virulent lines of the parasitoid *Asobara tabida* were more likely to accept *Drosophila melanogaster*, a host species with a strong immune response, than control lines which preferentially attacked the non-resistant species, *Drosophila subobscura*. Host species selection is further discussed in Sect. 1.12.

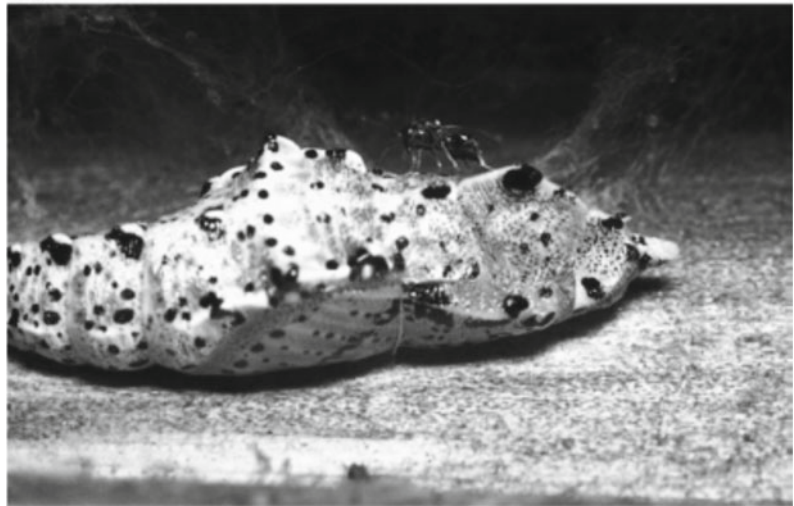
Host Stage Selection

Parasitoids may encounter different developmental stages of the host within a patch. Those

stages potentially vulnerable to attack may differ in their profitability. For idiobionts (parasitoids in which the host does not grow beyond the stage attacked and which therefore is a fixed 'parcel' of resource, Fig. 1.13a), small host stages may provide inadequate amounts of resource to permit the successful development of offspring. Even where successful development of idiobiont progeny is possible in small hosts, the resultant offspring are small and therefore oviposition constitutes less of a fitness gain (in parasitoids, body size can determine components of fitness, such as fecundity, longevity, searching efficiency

Fig. 1.13 Idiobiont and koinobiont parasitoids (both gregarious) of the same host species, *Pieris brassicae* (Lepidoptera: Pieridae): **a** *Pteromalus puparum* (Pteromalidae) ovipositing into host's pupal stage. For the parasitoid's progeny, the pupa is a 'fixed' parcel of resource, as it is a non-feeding, non-growing stage. This parasitoid is therefore an idiobiont. **b** *Cotesia glomerata* (Braconidae) ovipositing into newly hatched host larvae which will continue to feed, grow and develop during parasitoid development. This parasitoid is therefore a koinobiont. Source Premaphotos, UK

(a)



(b)



and competitive ability; Hardy et al., 1992b, 2013; Visser, 1994; Guerra-Grenier et al., 2020). Although they exploit a growing amount of host resource, koinobionts (parasitoids that allow their hosts to continue to feed and develop, Fig. 1.13b) also may display a positive relationship between adult body size and host size, although the relationship may not be linear (Sequeira & Mackauer, 1992; Harvey et al., 1994, 1999).

For both idiobionts and koinobionts, smaller hosts may require less time for handling and represent less of a risk of injury resulting from the defensive behaviour of the host (Sect. 1.20.3). For koinobionts (most of which are endoparasitoids), small hosts may present parasitoid progeny with lower mortality risk from encapsulation (van Alphen & Drijver, 1982; Sagarra & Vincent, 1999; Sect. 2.10). Females of both idiobionts and koinobionts may also gain in fitness from ovipositing in, or on, older larvae, owing to the fact that, under field conditions, host mortality resulting from predation and/or intraspecific competition is more severe in early host stages than in late ones (Price, 1975). Thus, it is often the case that parasitoids prefer to attack certain host stages and even avoid or reject other stages for oviposition. Nevertheless, for several idiobiont parasitoids of fly pupae, there is evidence that older hosts are not preferred, since these provide fewer resources for their developing offspring (e.g., King, 1998).

The distribution of hosts of different size over the host plant may influence encounter rates and thus host stage selection behaviour. Later instars of mealybugs are often surrounded by earlier instars. Encounter rates with younger instars may be higher, and those with larger ones lower than predicted, based on their densities. Young larvae of calliphorid and drosophilid fly species feed near the surface of the substrate, while older larvae may burrow deeper, possibly out of the reach of parasitoids.

Often, hosts are not passive victims of their parasitoids (Sect. 1.20.3). Behavioural defences of hosts (which are often more effective in later host stages) can cause a problem of data interpretation. Should encounters that do not result in parasitism of the host be scored as acceptances or

as rejections? If the parasitoid clearly displays behaviour that is normally associated with host acceptance, such as the turning and stinging shown by encyrtids (Fig. 1.14), the encounter should be classified as an acceptance.

The ability of late-stage hosts to defend themselves from attack better than early-stage hosts may account for a host stage preference. The cost in terms of lost ‘opportunity time’ (time that could be spent in more profitable behaviour) when attacks on late-stage hosts fail, may outweigh the fitness gain per egg laid (Kouame & Mackauer, 1991). Defence against parasitoids may also incorporate an immune response. It is generally the case that the risk of encapsulation is higher in later compared with earlier host larval instars (Sect. 2.10). This suggests that foraging endoparasitoids should preferentially attack host stages with a weaker immune response, whereas ectoparasitoids, which are not exposed in a similar manner to the host’s immune response, should show a host stage-based preference.

Host size selection by parasitoids is not limited to the decision of whether to oviposit or reject the host. It also involves the decision of which sex the offspring ought to be, and, for gregarious parasitoids, how many eggs to lay



Fig. 1.14 Host-acceptance behaviour in the encyrtid parasitoid *Apoanagyrus lopezi*: The female examines the host with its antennae. Acceptance is indicated by the wasp turning towards the host to insert its ovipositor. Sometimes, the host escapes whilst the wasp is turning—acceptance therefore does not necessarily lead to oviposition

(Fig. 1.1). For practical reasons, we analyse those decisions as isolated steps, but one should bear in mind that they are interrelated, and that it is wise to study host size selection in combination with clutch size and sex allocation decisions. Host size selection in relation to clutch size is discussed further in Sect. 1.10.

Predators are usually less specific in their choice of prey than parasitoids, although some predators show a preference for larger prey or certain instars (Cock, 1978; Thompson, 1978; Griffiths, 1982). Prey size selection in predators may also change with the size of the predator (Griffiths, 1982).

Host selection decisions by one female may alter over time during an experiment because these decisions are affected by experience, egg load and stochastic variation in encounter rates. Such changes in decisions are one of the reasons why partial preferences are always found instead of the absolute, i.e., all-or-none preferences predicted by static prey choice models. If one is interested in questions such as how egg load should influence host selection, one should construct dynamic optimisation models as described by Mangel and Clark (1988; see Heimpel et al., 1998, for an example).

1.7 Measuring Encounter Rates

The encounter rate of individual parasitoids with hosts is an important parameter in many optimality models. Because not every encounter will be followed by oviposition, and because not every oviposition will be in an unparasitised host, encounter rate is not equal to the number of hosts parasitised per time unit. Encounter rates can be used to calculate predicted rates of offspring deposited per time unit with a particular optimal foraging model.

Optimality models divide the time budget of a foraging animal into searching time, recognition time and handling time. Encounter rate is expressed and measured as the number of encounters per unit of searching time, thereby excluding recognition time and handling time. Because encounter rates are not always a linear

function of host density, it is necessary to measure them at a range of host densities.

To measure encounter rates, observe a female parasitoid continuously during some time period and make a complete record of her behaviour. From this record, the number of encounters and the net period of time spent searching can be calculated. The encounter rate of a parasitoid searching a patch containing a number of hosts may not be constant over the foraging period for the following reasons:

1. Parasitised hosts are encountered at a lower rate and the number of parasitised hosts increases during the observation period. A lower encounter rate with parasitised hosts may occur because hosts are paralysed by the wasp, and so move less (van Alphen & Galis, 1983).
2. The search effort of the wasp decreases, either in response to contact with its own marker substance (Sect. 1.6.4) or because its supply of mature eggs dwindles.

One method of eliminating some of the causes of decreased encounter rate is to replace each parasitised host with an unparasitised one during the course of an experiment. This is not always possible, e.g., sessile hosts such as scale insects cannot easily be removed and replaced. Replacing parasitised hosts may also affect encounter rate: it may disturb the searching wasp, and so decrease encounter rate, or it may increase encounter rate when the parasitoid is of a species that reacts to host movements and the freshly introduced hosts move more than those already present. Finally, a parasitoid may learn, during the experiment, that the observer is introducing better-quality hosts and simply walk towards the forceps or paint brush used to introduce the new host, as has often been observed with alysiine braconid parasitoids. Therefore, when measuring encounter rates, one should not replace parasitised hosts but instead keep the period of observation short, in order to avoid accumulation of parasitised hosts and marker substance.

Measuring encounter rates using a single-patch experimental design will overestimate the encounter rates that would be recorded in a

multi-patch, i.e., more natural, environment, because the time spent in inter-patch travel is not accounted for. Since it is often difficult, or impossible, to measure inter-patch travel times, the simplest approach is to measure, over a fixed period, the attack rate of a known number of parasitoids foraging in a spatially heterogeneous environment (Waage, 1979; Hassell, 1982).

1.8 Host Feeding

The females of many synovigenic parasitoids (Sects. 1.16.2 and 2.3.4) not only parasitise hosts but also feed on them (Jervis & Kidd, 1986, 1999; Heimpel & Collier, 1996; Jervis, 1998; Ueno, 1998a, 1998b, 1999a, 1999b, 1999c; Yang et al., 2012; Abram et al., 2019; Zhang et al., 2019; Miksanek & Heimpel, 2020; Cusumano et al., 2022a, 2022b). Host feeding supplies the females with materials for continued egg production and for somatic maintenance (Bartlett, 1964; Jervis & Kidd, 1986, 1999; Pérez-Lachaud & Hardy, 1999). Giron et al. (2002) showed that the parasitoid *Eupelmus vuilletti* host fed upon the host's haemolymph. The haemolymph is rich in proteins and various sugars, and it is these sugars that are responsible for the increased longevity of *E. vuilletti*. In some parasitoid species, host feeding causes the host to die (so-called 'destructive' host feeding), rendering it unsuitable for oviposition. Even with those species that remove small quantities of host materials such that the host survives feeding ('non-destructive' host feeding), the nutritional value of the host for parasitoid offspring may, as a result of feeding, be reduced and the female may lay fewer (gregarious species), or no eggs in it. For example, lepidopteran hosts previously host-fed upon by *Pimpla nipponica* produced fewer and smaller wasps when subsequently parasitised (Ueno, 1997). Thus, while host feeding potentially increases future fitness via subsequently increased egg production, the fitness gain is at the cost of current reproduction.

Most authors have supposed that host feeding has a short-term effect on parasitoid fecundity. However, by using radioactively labelled amino

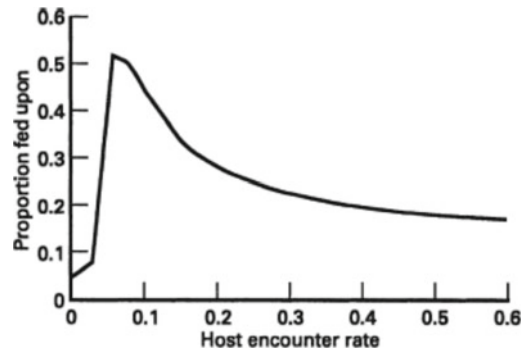


Fig. 1.15 Host feeding by parasitoids. Most models predict that the relationship between the fraction of hosts fed upon and host availability should be dome-shaped, increasing at low levels of host availability and decreasing at moderate to high levels. [The monotonic decline over the mid to high range is supported empirically, e.g., Sahragard et al. (1991).] The functional explanation for the small fraction of hosts fed upon at low host encounter rates is that the female adopts a 'cutting of losses' tactic—the encounter rate is too low to meet (via host feeding) the wasp's energy requirements, and so the female oviposits in every host encountered (Jervis & Kidd, 1986). Models also predict that host feeding is more likely when nutrient reserves and/or gut contents are at or below a critical level. Low nutrient levels and low gut contents presumably warn of the impending risk of starvation and/or egg limitation. In general, the critical level of nutrient reserves/gut contents depends on the current egg load and vice versa (Heimpel & Collier, 1996)

acids, Rivero and Casas (1999) showed that a significant proportion of the resources gained by the aphelinid *Aphytis melinus*, a parasitoid of scale insects, were stored and used gradually throughout the life of the wasp. Such techniques are particularly under-utilised in studies of parasitoid behaviour (Sect. 2.13).

A general prediction of models of destructive host-feeding behaviour is that the fraction of hosts fed upon by female parasitoids should increase with decreasing host availability, at least over the upper range of host densities (Fig. 1.15; Jervis & Kidd, 1986; Chan & Godfray, 1993). This is a prediction borne out by empirical studies (DeBach, 1943; Bartlett, 1964; Collins et al., 1981; Bai & Mackauer, 1990; Sahragard et al., 1991; Thu & Ueno, 2002).

Given that the fitness gains from ovipositing may vary in relation to host stage (Sect. 1.6.7), it is likely that the decision either to host feed or to

oviposit also depends on host stage (Kidd & Jervis, 1991; Rosenheim & Rosen, 1992). Indeed, observational and experimental studies of destructively host-feeding parasitoids show a tendency to feed preferentially or exclusively on earlier host stages and to oviposit preferentially or exclusively on/in later ones (Kidd & Jervis, 1991; Rosenheim & Rosen, 1992; Yang et al., 2012). A similar relationship is likely to apply to different-sized hosts of the same developmental stage.

Furthermore, environmental factors such as temperature may influence rates of host feeding (Urbaneja et al., 2001; Zhang et al., 2019). For example, the egg parasitoid *Trichogramma turkestanica* host feeds on *Ephestia kuehniella* at a greater rate when reared at lower temperatures, although it is not clear why this is so (Hansen & Jensen, 2002). Zhang et al. (2019) found that the temperatures that parasitoids experienced as immatures and as adults affected their host-feeding rates as adults, with the overall amount of host feeding by individuals being highest at intermediate temperatures, but with instantaneous rates being higher at higher temperature as the parasitoids became more active.

Models predict that the decision to host feed *versus* oviposit depends on the parasitoid's egg load: host feeding is more likely when egg load is low (Chan & Godfray, 1993; McGregor, 1997; see Heimpel & Collier, 1996, and Jervis & Kidd, 1999, for reviews). Rosenheim and Rosen (1992) tested this prediction experimentally using the scale insect parasitoid *Aphytis lingnanensis*. Egg load was manipulated by using wasps of different sizes (egg load being a function of body size) and also by holding parasitoids, prior to their exposure to hosts, at different temperatures (the rate of oöcyte maturation and therefore the rate of accumulation of mature eggs in the ovaries being a function of temperature, Sects. 2.3.4 and 2.7.4). Manipulating egg load in this way ensured that previous history of host contact could be eliminated as a possible confounding variable. Alternative methods of manipulating egg load, e.g., depriving parasitoids of hosts or allowing them to oviposit, do not separate the effects of egg load

and experience. Rosenheim and Rosen (1992) found in their experiments that egg load did not significantly affect the decision to host feed or oviposit on (small) hosts. However, although egg load was not directly manipulated, more recent work does support the hypothesis that the likelihood of host feeding is related to egg load (e.g., Heimpel & Rosenheim, 1995, Heimpel et al. 1996, Ueno, 1999b). The decision whether to host feed or oviposit may also depend on the wasp's nutritional state (Heimpel & Collier, 1996).

1.9 Host Discrimination

1.9.1 Introduction

Salt (1932) was the first researcher to clearly demonstrate the ability of a parasitoid to discriminate between hosts that contain the egg of a conspecific and hosts that have not been parasitised, and later (Salt, 1961) he showed that this ability, known as host discrimination, occurs in the major families of parasitoid Hymenoptera. Females of some parasitoid species are able to discriminate between: (1) parasitised hosts and unparasitised hosts (numerous published studies have shown this, although the conclusions drawn in some are questionable, see below); (2) parasitised hosts containing different numbers of eggs (Bakker et al., 1990); or (3) hosts containing an egg of a conspecific from one containing their own egg.

Notwithstanding such sophisticated abilities, superparasitism, the laying of an egg in an already parasitised host (Sect. 1.9.4), is a common phenomenon among insect parasitoids. The occurrence of superparasitism or, expressed statistically, the occurrence of a random egg distribution among hosts, has often led to the erroneous conclusion that a parasitoid is unable to discriminate between parasitised and unparasitised hosts (Hemerik & van der Hoeven, 2003, and see below). Dipteran parasitoids rarely show host discrimination abilities, primarily as the females of many species never come into contact

with potential hosts, instead often relying on host-seeking larvae (reviewed in Feener & Brown, 1997; but see Lopez et al., 1995). The effects of superparasitism on progeny development and survival are discussed in Chap. 2 (Sects. 2.9.2 and 2.10.2).

1.9.2 Indirect Methods

There are two approaches to determining whether parasitoids are able to discriminate between parasitised and unparasitised hosts. One is to dissect hosts (Sect. 2.6) and calculate whether the recorded egg distribution deviates significantly from a Poisson (i.e., random) distribution (Salt, 1961). Van Lenteren et al. (1978) have shown that such a procedure is not without pitfalls. They point out that, if the method is applied to egg distributions from hosts collected in the field, there is a risk that mixtures of samples with regular (i.e., non-random) egg distributions but different means may add up to produce a random distribution (Fig. 1.16). This is one of the reasons why a random egg distribution does not constitute proof of the inability to discriminate. Another problem van Lenteren et al. (1978) identified concerning the analysis of egg distributions is that with gregarious parasitoids the distribution of eggs depends not only upon the number of ovipositions but also on the number of eggs laid per oviposition.

There are further problems associated with the use of egg distributions. Van Alphen and Nell (1982) recorded random egg distributions when single females of *Asobara tabida* were placed with 32 hosts for 24 h. Because not all replicates produced random distributions and because other experiments had unequivocally shown that females of this species are able to discriminate between parasitised and unparasitised hosts, the random egg distributions could not be explained by a lack of discriminative ability.

In van Alphen and Nell's (1982) experiments the replicates with a high mean number of eggs had random distributions, whereas replicates with lower means had regular ones. It was therefore concluded that *A. tabida* discriminates

between unparasitised and parasitised hosts but is unable to assess whether one or more eggs are present in a parasitised host. Egg distributions are a mixture of the regularly distributed first eggs laid in hosts and of the randomly distributed supernumerary eggs. At lower means, the contribution of the regular distribution of the first eggs is not masked by the random distribution of the supernumerary eggs, whereas at higher means it is.

Even when egg distributions more regular than a Poisson distribution are found, one cannot establish with certainty that a parasitoid is able to discriminate between parasitised and unparasitised hosts. The recorded egg distribution could result from parasitised hosts having a much lower probability of being encountered, either because they move less than healthy hosts or because they leave the host plant. It is also possible that encounter rates with parasitised hosts are lower because the parasitoid does not re-visit previously searched areas with the same probability, e.g., when it always walks upwards along branches or when it marks areas already visited and avoids re-searching such areas.

The previous examples show that there are major pitfalls associated with using egg distributions to determine whether a parasitoid can discriminate between parasitised and unparasitised hosts. Other components of the behaviour of the parasitoid, or of the behaviour of the hosts, can influence egg distributions. Moreover, a regular egg distribution with a mean number of eggs much greater than one requires more than just an ability to discriminate between parasitised and unparasitised hosts. This has already been illustrated in the above-mentioned example of *A. tabida* where no regular egg distributions are found. The following example illustrates how, in *Leptopilina heterotoma*, different mechanisms are responsible for egg distributions tending to be regular even at a high mean number of eggs per host (Bakker et al., 1972). One explanation for this phenomenon is that *L. heterotoma* is able to discriminate between hosts containing different numbers of eggs. There is, however, a second possible interpretation: when the parasitoid is able to distinguish hosts containing an egg of her

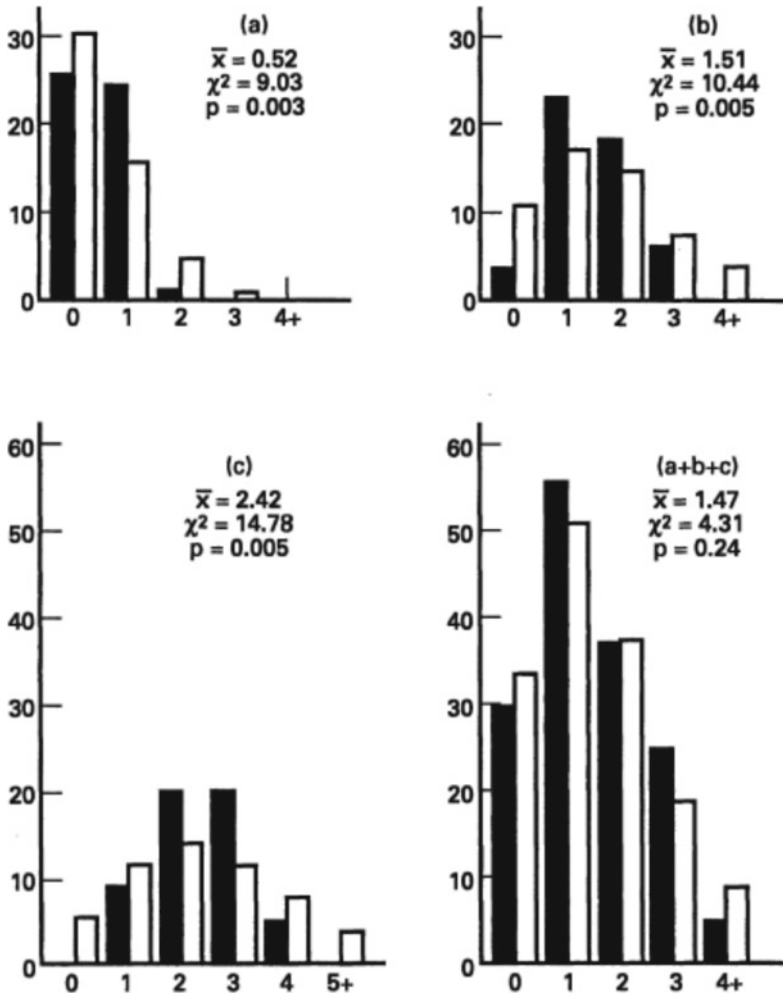


Fig. 1.16 Host discrimination by parasitoids: egg distributions for *Leptopilina heterotoma* (= *Pseudeucoila bochei*) parasitising *Drosophila melanogaster*. Three groups (a, b, c) of around 50 host larvae were presented to female wasps, and the hosts subsequently dissected and examined for wasp eggs. The mean number of eggs recovered per host larva (\bar{x}) was different in each case. Although in all three cases (a, b, c) superparasitism occurred, when the egg distribution (black bars) was compared (using χ^2 tests) with the distribution that would have been obtained had the wasps been ovipositing at

random (i.e., a Poisson distribution, white bars), the egg distribution was found to be more regular (underdispersed), indicating that the parasitoids discriminate. However, if data from all three distributions are pooled (a + b + c), a distribution is obtained that is indistinguishable from a Poisson distribution (lower right panel), a result that would lead to the erroneous conclusion that the parasitoid species studied cannot discriminate. Source van Lenteren et al. (1978), reproduced by permission of Blackwell Publishing

own from those containing eggs of conspecifics and avoids ovipositing in the former, regular egg distributions would result. Therefore, it is not possible to decide, based on egg distributions alone, whether a parasitoid is able to assess the number of eggs already present in a host.

Experiments therefore need to offer a parasitoid female a choice of hosts containing different numbers of eggs, all laid by other (conspecific) females. Bakker et al. (1990) offered hosts containing two eggs and hosts containing one egg of other females to individual

L. heterotoma. The wasps oviposited significantly more often in hosts containing a single egg, thus showing that *L. heterotoma* is indeed able to distinguish between hosts containing different egg numbers. Visser (1992) showed that *L. heterotoma* females are also able to recognise hosts containing their own eggs. Thus, both of the above mechanisms may have contributed to the regular egg distributions found by Bakker et al. (1972).

It is thus clear that, by comparing observed egg distributions with those predicted by a Poisson distribution, one can neither conclude that a parasitoid is able to discriminate between parasitised and unparasitised hosts, nor conclude that it lacks this ability. This does not mean a statistical analysis of egg distributions is useless; it is possible to construct models predicting distributions of eggs for parasitoids having different abilities to avoid superparasitism (e.g., discriminating between healthy hosts and parasitised hosts and counting, discriminating but not counting, discriminating between hosts parasitised by self and hosts parasitised by others), and to compare the theoretical egg distributions with distributions recorded in experiments. Bakker et al. (1972) and Meelis (1982) adopted this approach when investigating whether wasps are able to assess the number of eggs already laid in a host. These authors assumed that parasitoids search randomly, and that there exists a certain probability that the wasp will lay an egg when it encounters a larva. This probability is 1.0 at the first encounter but is lower at subsequent encounters. By keeping the probability of oviposition at the subsequent encounters constant, the model could be used to describe superparasitism by *A. tabida*.

1.9.3 Direct Observations of Behaviour

The other method of determining whether parasitoids are able to discriminate between parasitised and unparasitised hosts involves observing the insects, and recording and comparing encounters resulting in oviposition and

rejection of the different host categories. This method provides behavioural evidence that the parasitoid under study rejects parasitised hosts more often than unparasitised hosts. It is, however, wise to use other behavioural criteria in addition to acceptance/encounter ratios.

Because distributions of parasitoid eggs among hosts potentially have an important effect on parasitoid–host population dynamics, one requires a good statistical description of those distributions, for incorporation into population models. We prefer to use the observed behaviour as a basis for a model calculating egg distributions, instead of inferring the underlying behaviour from an analysis of the egg distributions.

More than three decades after host discrimination by hymenopteran parasitoids was discovered, evidence was found of host discrimination by dipteran parasitoids. The phenomenon was described for tachinid flies by Lopez et al. (1995). In field and laboratory experiments, these authors showed that *Myiopharus doryphorae* and *M. aberrans*, both parasitoids of Colorado beetle (*Leptinotarsa decemlineata*) larvae, almost always reject parasitised larvae, whereas they readily oviposit in unparasitised larvae. While little is known of the host discrimination ability of non-hymenopteran parasitoids, even less is understood of the situation where it is the parasitoid larva, rather than the ovipositing female, that actively seeks hosts. Larvae of the staphylinid parasitoid *Aleochara bilineata* locate and attack fly pupae. Royer et al. (1999) found that these larvae can distinguish hosts that were self-parasitised from those that were attacked by conspecifics, and that this was based on chemical cues. Superparasitism was more common when hosts were scarce, and if given a choice, *A. bilineata* larvae would preferentially attack hosts that contained the related species *A. bipustulata*, rather than conspecifics (Royer et al., 1999).

Edwards and Hopper (1999) took a novel approach to investigate levels of superparasitism by *Macrocentrus cingulum*, a braconid parasitoid of the European corn borer, *Ostrinia nubilalis*. Since *M. cingulum* is polyembryonic, the number of parasitoid larvae present per host does not reflect the number of females that have attacked

that host. By using random amplified polymorphic DNA (RAPD) markers (Chap. 3), the authors were able to identify the number of females that had oviposited.

1.9.4 Superparasitism

Many, if not all, parasitoids are able to discriminate between parasitised and unparasitised hosts, but superparasitism is a common feature in nature (van Alphen & Visser, 1990; Godfray, 1994; D'Auro et al., 2021), posing the question: why and when should parasitoids superparasitise?

Van Lenteren (1976) addressed this question from the standpoint of causation. He assumed that superparasitism was caused by a failure to discriminate. He found that females of *L. heterotoma* inexperienced with unparasitised hosts readily oviposited in already parasitised hosts but avoided ovipositing in parasitised hosts after they had been able to oviposit in unparasitised ones. He concluded from this that parasitoids superparasitise because they are unable to discriminate between parasitised and unparasitised hosts until they have experienced oviposition in unparasitised hosts. A similar conclusion was drawn by Klomp et al. (1980) for *Trichogramma embryophagum*.

A functional approach to the problem is to ask whether it is adaptive for a parasitoid always to avoid superparasitism. Van Alphen et al. (1987) re-analysed the data of van Lenteren (1976) and Klomp et al. (1980), starting with the hypothesis that superparasitism can be adaptive under certain conditions. They reasoned that host discrimination is an ability which the parasitoid can use to decide either to reject a parasitised host or to superparasitise it, depending on the circumstances, i.e., superparasitism is not the result of an inability to discriminate. Van Alphen et al. (1987) argued that an inexperienced female arriving on a patch containing only parasitised hosts should superparasitise, because the probability of finding a better patch elsewhere is low. In a similar vein, Sirot et al. (1997) showed through modelling that the tendency to

superparasitise should vary with egg load and life expectancy.

Van Lenteren's (1976) inexperienced wasps rejected hosts previously parasitised by themselves more often than unparasitised ones and encountered significantly fewer hosts in experiments involving patches containing only parasitised hosts compared with similar experiments involving patches containing the same density of unparasitised hosts. It was known that *Lepidopilina heterotoma* females search by stabbing with the ovipositor, twice per second, in the substrate, and it was possible to measure both the surface area of a host and that of the patches. It was possible therefore to calculate, from the numbers of encounters observed during a 30-min observation period, that inexperienced wasps spent on average 13.12 min searching and handling hosts when introduced on to a patch with parasitised hosts, whereas they spent on average 2.14 min when introduced on to patches with unparasitised hosts. Van Alphen et al. (1987) interpreted the differences in behaviour between inexperienced wasps and experienced wasps as evidence that inexperienced wasps do recognise parasitised hosts and thus concluded that host discrimination does not need to be learnt. Experiments by van Alphen et al. (1987), involving *L. heterotoma* and *Trichogramma evanescens*, confirmed that females inexperienced with unparasitised hosts are, like experienced wasps, already able to discriminate, although inexperienced females superparasitise more frequently. This example shows that alternative hypotheses can be overlooked if one asks only causal questions.

Static and dynamic optimality models as well as ESS models (Sect. 1.2.2) have shown that superparasitism is often adaptive (Iwasa et al., 1984; Parker & Courtney, 1984; Charnov & Skinner, 1985; Hubbard et al., 1987; van der Hoeven & Hemerik, 1990; Visser et al., 1990; Field & Keller, 1999; Hemerik et al., 2002;). The models predict that oviposition in already parasitised hosts, though resulting in fewer offspring than ovipositions in unparasitised hosts, may still be the better option when either there is

no time available to search for and locate unparasitised hosts or when unparasitised hosts are simply not available. By ovipositing into an already parasitised host under such conditions, a female may increase her fitness if there is a finite chance that her progeny will out-compete the other progeny (Sect. 2.10.2). Experimental tests of some of these models have shown that parasitoids behave in such a way that the models' predictions are at least met qualitatively (Hubbard et al., 1987; Visser et al., 1990; van Alphen et al., 1992). For example, Sirot et al. (1997) tested predictions that superparasitism by *Venturia canescens* would be less common if females were provided with food, reducing their risk of mortality. As predicted, superparasitism rates were correlated with egg load and previous access to (non-host) food.

Attacking previously parasitised hosts is evidently adaptive if females can kill parasitoid eggs or young larvae present in the host. *Encarsia formosa* can kill eggs present in hosts by grabbing them with her ovipositor (Netting & Hunter, 2000). A similar effect is seen with *Haplogonotopus atratus* (Dryinidae), where the female wasp kills parasitoid larvae present in the host before ovipositing (Yamada & Kitashiro, 2002). Similarly, ectoparasitoids may eat eggs already present on a host, or kill feeding larvae by pulling them from the host, before laying their own clutch (e.g., Goubault et al., 2007b).

Female parasitoids can often discriminate between hosts that have been self-parasitised from those that have been attacked by a conspecific. *Venturia canescens* females avoid superparasitising hosts that contain their own progeny, a behaviour mediated by the presence of a marking pheromone (Hubbard et al., 1987). Such ability to discriminate among hosts led to the suggestion that females would increase their inclusive fitness by avoiding hosts that contain kin (Fellowes, 1998), and indeed, female *V. canescens* avoid attacking hosts containing relatives (Marris et al., 1996). However, *V. canescens* is parthenogenetic, and this may be an example of extended self-recognition, rather than kin discrimination. Ueno (1994) studied the behaviour of *Itoplectis narayanae* and found that

whereas females would avoid parasitising hosts they had previously attacked, there was no difference in their likelihood of attacking hosts that contained kin or unrelated conspecifics.

While in the examples above the females recognise their own odour marks, others distinguish between self-parasitised hosts and those attacked by conspecifics by different means. Ueno and Tanaka (1996) found that *Pimpla nipponica* females do not deposit chemical markers, but instead use visual location cues to avoid self-superparasitising.

Avoidance of self-superparasitism may be one reason that patches are incompletely exploited (e.g., Outreman et al., 2001). With *Venturia canescens*, the likelihood of avoiding superparasitism increases in the 20 min after oviposition if the females have been provided with alternative hosts during the interval, but this does not occur if the female is deprived of other hosts. This suggests that the females can rapidly obtain information on the number of hosts in the patch, and this influences their decision to superparasitise (Hubbard et al., 1999). *Anaphes victus*, a mymarid parasitoid of curculionid beetle eggs, can learn to avoid marked hosts in 4 h, and are quicker to learn if the mark was made by a close relative (van Baaren & Boivin, 1998).

It is unclear where the oviposition deterrent marker originates, although it is usually suggested that it originates from the female's Dufour's gland. The pteromalid *Dinarmus basalis* avoids superparasitising hosts that have been attacked over 20 h previously. Gauthier and Monge (1999) found that the marker originated from the parasitoid egg and required contact between the egg and the host for at least 4 h before the deterrent effect became evident. However, with *Leptopilina boulardi* and *Asobara tabida*, parasitoids of drosophilids on fermenting substrates, the mark spreads within the host within about a minute (van Alphen & Nell, 1982).

Experience is often important in determining whether a female superparasitises a potential host. Naïve *Cotesia flavipes* females readily attack hosts that contain a conspecific, yet experienced females will reject such hosts. This

discrimination is influenced by the presence of a patch-marking odour (Potting et al., 1997). Nufio and Papaj (2001) review patch-marking behaviour in parasitoids.

When parasitoids attack a host that already contains a developing conspecific, the likelihood is that the larvae within the host will fight to the death for ownership of the resource. While it may be expected that older larvae will have a competitive advantage, this does not appear to be the case with *Venturia canescens*, where first instar larvae are more likely to kill older larvae in the same host (Marris & Casperd, 1996). This result appears to explain why the level of superparasitism by *V. canescens* females is higher the longer the period of time that has elapsed since the host was first attacked.

While superparasitism is now typically seen as an adaptive aspect of parasitoid foraging behaviour (e.g., Visser, 1993; D'Auro et al., 2021), it may be greatly influenced by viral infection, with virus transmitted both vertically (mother–daughter) and horizontally (between immature parasitoids developing in the same host) and with infected individuals engaging in superparasitism. Superparasitism thus leads to the horizontal transmission of the virus, and may well increase the fitness of the virus at the expense of that of the wasp (Varaldi et al., 2003; Varaldi & Lepetit, 2018).

1.9.5 Multiparasitism

Multiparasitism (oviposition in a host attacked by heterospecifics) has been less studied than superparasitism. In general, it is thought that the ability to identify hosts attacked by other species is less frequent than discrimination against hosts attacked by conspecifics. There are two main situations where females should discriminate against hosts containing a heterospecific egg or larva. First, competitively inferior species should avoid attacking hosts where a superior competitor has already oviposited (Vyas et al., 2019; Sect. 2.10.2). Second, where the outcome of competition depends upon the time since the host was initially attacked (Sect. 2.10.2), the

multiparasitising female should be able to detect this factor and incorporate it when making the decision of whether to parasitise or not.

Ueno (1999c) tested this latter prediction, using *Pimpla nipponica* and *Itopectis naranyae*, two solitary parasitoids of moth larvae. When presented with *Galleria mellonella* larvae, both species preferred attacking previously unattacked hosts when the time since parasitism of the host by the heterospecific parasitoid was over 48 h. However, if less than 24 h had passed since the initial attack, then no such preference was shown. How the parasitoids can distinguish the time since the initial parasitism is not known. Bokonon-Ganta et al. (1996) found that competitively inferior species do not always avoid ovipositing in hosts previously attacked by a competitor. *Gyranusoidea tebygi*, a parasitoid of the mango mealybug, *Rastrococcus invadens*, readily accepts hosts that have previously been attacked by *Anagyrus mangicola*, although their offspring generally fail to survive. Conversely, competitively superior species may prefer hosts parasitised by an inferior competitor (Aguirre et al., 2021).

1.9.6 Cannibalism

In many ways, cannibalism by predators can be considered analogous to superparasitism. Cannibalism is a common feature of the behaviour of many predatory insects and is probably a consequence of polyphagy (New, 1991; Dostalkova et al., 2002). Consuming unrelated conspecifics will have two main benefits (Polis, 1981; Elgar & Crespi, 1992; Anthony, 2003). First, when resources are scarce, the added nourishment gained will increase the survival chances of the cannibal (e.g., the green lacewing *Chrysoperla carnea*, Duelli, 1981). Second, potential competitors are removed from the patch. When alternative resources are common, then it is unlikely that consuming relatives will be beneficial, but when resources are limiting it may be better to eat kin so that some individuals survive, rather than sacrificing all (Fellowes, 1998).

Cannibalism has been most intensively studied in the Coccinellidae, where some species can

complete their larval development on conspecific eggs (Dimitry, 1974). *Adalia bipunctata* will frequently consume conspecifics (Hodek & Honěk, 1996), although adult females and young larvae will avoid their own and sibling eggs, respectively (Agarwala & Dixon, 1993). Males that fathered the eggs do not show any such discrimination. In many non-social insects, such avoidance would be explained by environmental cues, rather than through direct genetic cues (Fellowes, 1998). Joseph et al. (1999) investigated these cues using the ladybird *Harmonia axyridis*. Third-instar *H. axyridis* larvae avoid cannibalising kin, and when they do cannibalise them, they take longer to attack kin than non-kin. These results suggest that environmental cues are unimportant, with discrimination linked to genetic differences among the individuals (Joseph et al., 1999).

Given that there will be heterogeneity in habitat quality, it is perhaps unsurprising that there is heritable variation in cannibalistic behaviour in *H. axyridis* (Wagner et al., 1999). When conditions are favourable, cannibalism is maladaptive given that foraging larvae are more likely to encounter kin. However, in unfavourable patches, increased propensity to cannibalism will increase the development rate and survivorship of the cannibal (Wagner et al., 1999).

1.9.7 Intraguild Predation

If we consider that cannibalism is analogous to superparasitism, then it is reasonable to compare intraguild predation to multiparasitism. Intraguild predation, IGP, is a combination of predation and competition, and occurs when two predators share a common prey species, but one (or both) of the predators will also attack the other (Polis et al., 1989; Arim & Marquet, 2004), resulting in a 'trophic loop'. The study of IGP thus connects research on foraging behaviour to research on the structure and function of ecological communities, in particular the properties of trophic webs (Marques et al., 2018; Blue Pahl et al., 2020; Aguirre et al., 2021; Chap. 6). IGP interactions are likely to be common, with many adult

predators attacking the eggs and the larval stages of other species, as well as their own (Rosenheim et al., 1995). The effects on the suppression of hosts achieved by biological pest control are predicted to be negative or neutral, but there is little empirical evidence for the predicted negative effect (Jansen et al., 2006; Aguirre et al., 2021). Here we briefly review several examples of IGP interactions between predators, between parasitoids and also between predators and parasitoids.

The anthocorid bug *Orius laevigatus* is frequently used to control the thrips *Frankliniella occidentalis*, a pest of many greenhouse crops. Phytoseiid mites, such as *Neoseiulus cucumeris*, are also used in thrips control. Wittmann and Leather (1997) found that, due to intraguild predation by *O. laevigatus* on *N. cucumeris*, the use of both predatory agents together was unlikely to increase the degree of control. However, *O. laevigatus* does not prey upon another predatory mite (*Iphiseius degenerans*), making a pairing much more suitable for *F. occidentalis* control (Wittmann & Leather, 1997). Similarly, Tsuchida et al. (2022) found that IGP between two species of predatory mites could lead to reduced control of pest mite populations. In another mite system, Marques et al. (2018) found that the adults of two co-occurring predatory species, *Iphiseiodes zuluagai* and *Euseius concordis*, feed on juveniles of the other species, whether or not their shared feeding resource is present, and that adult *I. zuluagai* also attack adult *E. concordis* individuals. These IGP interactions result in *E. concordis* populations failing to persist unless the environment has a sufficiently complex spatial structure. However, under some conditions it is the populations of *I. zuluagai* that tend not to persist. The fact that the outcome of IGP interactions is conditional on the physical environment illustrates the challenges of assessing their importance in natural and agroecosystems, as experiential observations might not be relevant to field conditions.

IGP between parasitoids typically involves facultative hyperparasitism (the offspring of one parasitoid developing on another parasitoid) or predation (one parasitoid feeding as a predator of the other) but may also be intertwined with

aspects of resource competition (determining which parasitoid feeds on the host). These classes of interactions may be termed ‘intrinsic competition’ when occurring between parasitoid larvae in the same host and ‘extrinsic competition’ when occurring between foraging adult females (Cusumano et al., 2022a, 2022b).

The role of competition and IGP between two endoparasitoids, *Anagyrus cachamai* and *A. lapachosus* (Encyrtidae), candidates for biocontrol of the Puerto Rican cactus pest mealybug, *Hypogeococcus* sp. (Pseudococcidae), was studied by Aguirre et al. (2021), using Bayesian model selection for statistical analysis to infer difficult-to-observe parasitoid–parasitoid intrinsic competition interactions. They found that the species differed in their ability to compete, and in multiparasitism decisions (Sect. 1.9.5) and functional responses (Sect. 1.14), indirectly indicating IGP of *A. lapachosus* on *A. cachamai* (most likely by acting as a predator rather than as a hyperparasitoid), and also that a multiple release strategy for both the parasitoids would produce better suppression of *Hypogeococcus* sp. than a single species release. In another studied endoparasitoid–endoparasitoid interaction, *Ooencyrtus telenomicida* (Encyrtidae) and *Trisolcus basalis* (Platygastridae) attacking the pentatomid bug, *Nezara viridula*, differed in their intrinsic and extrinsic competitive abilities, such that coexistence is promoted and biocontrol may not be disrupted, even though *O. telenomicida* is a facultative hyperparasitoid of *T. basalis* (Cusumano et al., 2013, 2022). However, facultative hyperparasitism by one of several ectoparasitoids attacking the coffee berry borer (*Hypothenemus hampei*), alongside readily observable extrinsic competitive interspecific interactions, is likely to be disruptive to biological control (Pérez-Lachaud et al., 2004; Batchelor et al., 2005, 2006; Sect. 1.13).

IGP by the anthocorid bug *Cardiastethus exiguus* on the larvae of two parasitoids of *Opisina arenosella*, a pest of coconut, *Bracon brevicornis* (Braconidae) and *Goniozus nephantidis* (Bethyliidae) has been reported (Nasser & Abdurahiman, 1990) through competitive interactions between the two parasitoids themselves

(Hardy & Blackburn, 1991). When, in laboratory studies, adult *G. nephantidis* females encounter foraging *C. exiguus* in the presence of a host/prey larva, the parasitoid attacks the predator, sometimes killing it, but predators are not aggressive towards parasitoids. Despite parasitoid aggression, surviving predators sometimes manage to consume the parasitoid’s eggs that had been laid onto the host. Such IGP interactions may reduce the overall suppression of the pest (Velasco-Hernandez et al., 2021).

1.10 Clutch Size

Since a host represents a limited amount of resource, and parasitoid offspring have the potential to compete for that resource (Sects. 2.9 and 2.10), gregarious parasitoids must make an additional decision after accepting a host for oviposition: how many eggs to lay in (or on) a host. Many studies have addressed this question (e.g., Skinner, 1985; Waage & Godfray, 1985; Waage, 1986; Godfray, 1987a, 1987b; Hardy et al., 1992b; Vet et al., 1994; Visser, 1996a, 1996b; Zaviezo & Mills, 2000; Bell et al., 2005; Goubault et al., 2007a; Hasan & Ansari, 2010; Villacañas de Castro & Thiel, 2017; Samková et al., 2022). Here we are mainly concerned with variation in the size of clutches allocated to hosts of a fixed size, although we shall also consider host size variation.

Given that the amount of resource a developing parasitoid obtains will determine its fitness, a fitness function $f(c)$ can be used to describe the fitness of each offspring in a clutch of size c allocated to hosts of a certain size. The fitness gain to the mother per host attacked is therefore the product of clutch size and the *per capita* fitness function, i.e., $cf(c)$. The value of c where $cf(c)$ is maximised is the parental optimum clutch size, known as the ‘Lack clutch size’, after Lack (1947) who studied clutch size in birds. Predicted and observed fitness functions for three parasitoid species are shown in Fig. 1.17. In each case, the probability of survival to the adult stage is used as the measure of fitness.

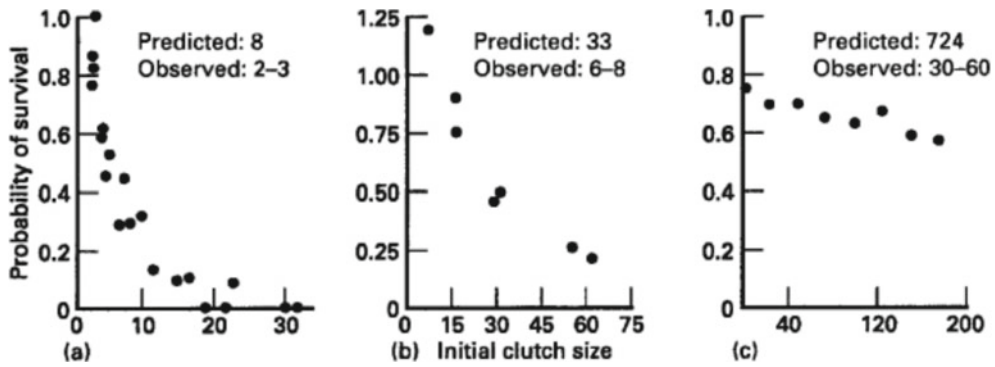


Fig. 1.17 Optimal progeny allocation in gregarious parasitoids—clutch size: *per capita* fitness of offspring as a function of clutch size, estimated by the probability of survival in initial clutches of different sizes (Observed = observed clutch size; Predicted = predicted by calculation of $cf(c)$; see text). **a** *Trichogramma evanescens* in eggs of the cabbage moth, *Mamestra brassicae*; **b** *Telenomus farai* in eggs of the bug *Triatoma phyllosoma pallidipennis* (the overestimate of survival [>1.0] in this case is attributable to sampling error); **c** *Dahlbominus fuliginosus* on pupae of the sawfly *Neodiprion lecontei*. Source Waage and Godfray (1985) and Waage (1986), who used data from Pallewatta (1986),

Escalante and Rabinovich (1979) and Wilkes (1963). In all three cases, there is a continuous decline in *per capita* fitness with increasing clutch size. For some other gregarious parasitoid species there is evidence of an Allee effect, i.e., an initial rise then a fall in fitness. Such a dome-shaped fitness relationship may prove to be common among gregarious endoparasitoids, because in such parasitoids small larval broods often perish entirely due to their inability either to overcome host physiological defences or to consume all the host tissues (a prerequisite in some species for successful pupation and emergence). Reproduced by permission of Blackwell Publishing and Elsevier Science

Fitness function curves can be constructed as follows:

1. By exposing hosts to individual parasitoids and examining/dissecting some of these hosts immediately after oviposition to determine clutch size, and rearing parasitoids from the remainder to determine offspring survival (Fig. 1.17a, b). If larval mortality arising from resource competition occurs late in development, and dead larvae are not consumed by surviving larvae, one may simply record the numbers of emerged and unemerged offspring (Fig. 1.17c).
2. By manipulating parasitoid clutch sizes. This is relatively easy in the case of ectoparasitoids, as different clutch sizes can be obtained simply by adding or removing eggs, manually, from clutches present on the host's body surface (Hardy et al., 1992b; Zaviezo & Mills, 2000; Milonas, 2005; Villacañas de Castro & Thiel, 2017). With this technique, however, there is a risk of damaging eggs during manipulation. It may be possible to deal with this problem by using the number of

larvae that successfully hatch from the manipulated eggs as a proxy for clutch size, rather than the manipulated clutch size itself. With endoparasitoids, clutch sizes can be manipulated by interrupting oviposition, by allowing superparasitism to occur, or by exchanging the host for one of a different size after the wasp has examined it but immediately before it has the opportunity to begin ovipositing in it (Klomp & Teerink, 1962). However, a problem with at least the latter technique is that the parasitoid may alter its sex allocation behaviour and the sex ratio of the clutch of eggs may influence progeny fitness and thus also the optimum clutch size (Waage & Ng, 1984).

Other models predict that the best strategy for a parasitoid is to maximise fitness per unit time rather than per host attacked. If there is a cost in time to laying an egg, it may benefit a female to cease adding more eggs to a host and to allocate the time saved to locating a new host. The fitness gain from leaving hosts and searching for new

ones will increase as the travel time between oviposition sites decreases, i.e., as host availability increases. As hosts become more abundant, females should leave each host sooner, i.e., produce smaller clutch sizes. Thus, with the maximisation of fitness per unit time models, females maximise fitness per host attacked (i.e., produce Lack clutch sizes) only when hosts are scarce (Godfray, 1994). *Trichogramma minutum* appears to be a species whose strategy is to maximise fitness per unit time. Schmidt and Smith (1987a) presented females with nine host eggs attached by glue to a cardboard base and employed various egg spacing treatments: the eggs were situated with their centres either 2, 3, 4 or 5 mm apart on a grid. Clutch size was found to decrease with increased crowding of eggs, i.e., increasing host density per unit area.

There are also models that take into account egg-limitation constraints, i.e., they assume that the parasitoid has a limited number of eggs to lay at any one time. Such a parasitoid is always in a position where available eggs are fewer than potential clutch sites. If eggs are severely limiting, i.e., egg load is much smaller than the number of hosts available (this could be due to the fact that the female has laid most of her eggs, e.g., Heimpel et al., 1998), a female should spread out her eggs between hosts so that the fitness gain per egg, rather than per clutch, is maximised. When *per capita* fitness of offspring decreases monotonically (as in Figure 1.17), the optimal clutch size under severe egg limitation is always one (see Zaviezo & Mills, 2000, for the effects of female life expectancy on optimal clutch size).

What if data and model predictions do not match? As can be seen from Fig. 1.17, clutch sizes predicted by optimality models tend to differ from the ones recorded in experiments. This discrepancy may occur for one or several reasons:

1. The wrong fitness currency has been used. For example, the parasitoid's strategy may be that of maximising fitness per unit time rather than per host attacked, or a classic (static or dynamic) optimality model has been used

rather than a game-theoretic model (see below).

2. The model does not take account of stochastic variability in certain parameters (Godfray & Ives, 1988).
3. The measure of fitness (e.g., offspring survival to adulthood) used may be inappropriate or incomplete (e.g., Visser, 1994).
4. The measure of fitness is appropriate but difficult to quantify (e.g., laboratory estimates do not accurately reflect field estimates, e.g., Visser, 1994; West et al., 1996).

If the fitness measure, such as juvenile survival, is inappropriate, measures such as adult fecundity or longevity, both influencing foraging performance, may be more important. Calculating fitness as total offspring fecundity may lead to a closer fit between model and data (Waage & Ng, 1984; Waage & Godfray, 1985). Measuring offspring fecundity is likely to prove very time-consuming, so an alternative procedure is to measure offspring body size or weight; both of these factors are usually good predictors of fecundity in parasitoids (Sect. 2.7.3). Le Masurier (1991) used a combined measure of fitness: the product of progeny survival and the calculated mean egg load at emergence (a measure of lifetime fecundity) of the surviving female progeny. The egg load for each emerging wasp was determined indirectly, from a regression equation relating egg load to head width. Le Masurier (1991) found that the fitness function curve constructed for a British population of *Cotesia glomerata* in larvae of *Pieris brassicae* showed no density-dependent effect of clutch size on fitness, and this therefore prevented him from calculating the optimum clutch size for that host: all that could be predicted was that females should lay at least the maximum number of eggs recorded in a host.

Release-recapture experiments with different size classes of parasitoids in the field may provide useful information on size–fitness relationships, although ideally these relationships should be directly measured (Visser, 1994; West et al., 1996; Ellers et al., 1998).

It has become increasingly apparent that measurements of size–fitness relationships are strongly influenced by environmental variation (Rivero & West, 2002). In addition, laboratory studies tend to underestimate the disadvantages of small body size in parasitoid wasps (Hardy et al., 1992b; Visser, 1994; West et al., 1996). Therefore, any assumption that there is a general size–fitness correlation in parasitoids needs to be treated with caution. Furthermore, the fitness of an individual with a given body size may be dependent on the sizes of other individuals in the population. This occurs, for instance, when foraging females compete directly, via agonistic interactions, for access to hosts (Sect. 1.13) and the probability of gaining or retaining access is higher for relatively large competitors. If such competition occurs frequently, mothers are expected to produce smaller clutches that generate fewer but larger offspring, in response to the sizes of clutches (and offspring) being produced on other hosts by other mothers. The optimal clutch size in these circumstances is an ESS (Sect. 1.2.2), found by game theory, rather than a prediction of the classical optimality approach (Petersen & Hardy, 1996; Mesterton-Gibbons & Hardy, 2004; Goubault et al., 2007a).

A further factor to consider is variation in host size. If a gregarious parasitoid's strategy is that of maximising fitness per host attacked, then the optimal clutch size ought to increase with increasing host size. Gregarious parasitoids do tend to lay larger clutches in or on larger hosts, both within and across species (e.g., Hardy et al., 1992b; Mayhew & Hardy, 1998; Shameer et al., 2002; Wang et al., 2008; Kapranas et al., 2011; Malesios & Prophetou-Athanasiadou, 2014; Tang et al., 2014; Villacañas de Castro & Thiel, 2017). How do gregarious (and solitary) parasitoids measure host size? Schmidt and Smith (1985) studied host size measurement in *Trichogramma minutum*. Females allocated fewer progeny to host eggs that were partially embedded in the substratum than into host eggs that were fully exposed. Since the eggs were of identical diameter and surface chemistry, it was concluded that the mechanism of host size determination is neither chemosensory nor visual,

but is essentially mechanosensory, based on accessible surface area. Schmidt and Smith (1987b) subsequently observed the behaviour of individual *T. minutum*, during the host examination phase, on spherical host eggs of a set size, and recorded: (1) the frequency of and intervals between contacts with the substratum bearing the eggs, and turns made by the wasps, and (2) the number of eggs laid per host. In analysing the data, seven variables were considered: the total number of substratum contacts, the mean interval between such contacts, the interval between the last contact and oviposition, the longest and shortest interval between contacts, the total interval between the first three contacts, and the interval between the first contact with the host and the first contact with the substratum (initial transit). Of these, only the duration of the initial transit across the host surface showed a significant positive linear relationship with the number of eggs deposited. By interrupting the path of wasps during their initial transit, and thereby reducing their initial transit time, Schmidt and Smith (1987b) succeeded in reducing the number of progeny laid by a female. Schmidt and Smith (1987b) concluded that wasps are able to alter progeny allocation by measuring short time intervals. Interestingly, the duration of initial transit was found to be the same for both large and small wasps (Schmidt & Smith, 1987b, 1989).

Large-bodied gregarious parasitoids (and solitary parasitoids) are likely to measure host size in other ways, for example by determining whether the tips of the antennae reach certain points on the host's body. Such stimuli are thought to be tactile (e.g., King, 1998). Alternately, simple visual examination of the whole host may provide the correct cues.

Finally, using the isofemale line method, Wajnberg et al. (1989) demonstrated a significant intra-population genetic variation in the clutch size laid by *Trichogramma maidis* (= *T. brassicae*) females and the distribution of eggs within *Ephesttia kuehniella* host eggs. This demonstrates that the trait can be the target of natural selection, leading to optimal clutch sizes in different environmental situations.

In this section we have focused on clutch size as an optimality problem for foraging natural enemies. We note that observed clutch sizes of parasitoids and predatory insects may be influenced by a wider suite of constraints and considerations than are covered here, such as phylogeny, anatomy and even geometry (e.g., Mayhew & Hardy, 1998; Abram et al., 2023).

1.11 Sex Allocation

1.11.1 Introduction

Haplodiploidy (the production of haploid males from unfertilised eggs and diploid females from fertilised eggs; also known as arrhenotokous parthenogenesis, Sect. 3.3.2) allows female wasps to determine the sex of their offspring. Such control of sex allocation has made the parasitoid Hymenoptera a favoured subject for behavioural ecologists studying adaptive sex allocation (Godfray, 1994; Godfray & Shimada, 1999; Ode & Hunter, 2002; Ode & Hardy, 2008; West, 2009; Hardy & Boulton, 2019; Abe et al., 2021). There is much more to this topic than can be covered in any detail here: Chaps. 3, 4 and 5 also contain discussions of sex allocation and closely associated topics.

Natural selection will normally favour equal investment in the sexes in an outbreeding (panmictic) population (Fisher, 1930; Gardner, 2023) (Fig. 1.18). Many hymenopterans, however, frequently exhibit sex ratios that are strongly divergent from equality: explaining these differences has resulted in a robust and intricate set of models that are well, and reciprocally, supported by empirical investigations (Godfray, 1994; West, 2009; Gardner & Hardy, 2020; Abe et al., 2021; Lehtonen et al., 2023). In general, patterns of sex allocation are influenced by two main factors: the population's mating structure and the environmental conditions experienced (Hardy & Boulton, 2019). While both can select for the ability to maximise fitness through manipulation of offspring sex ratio, the patterns of sex allocation they influence are quite different.

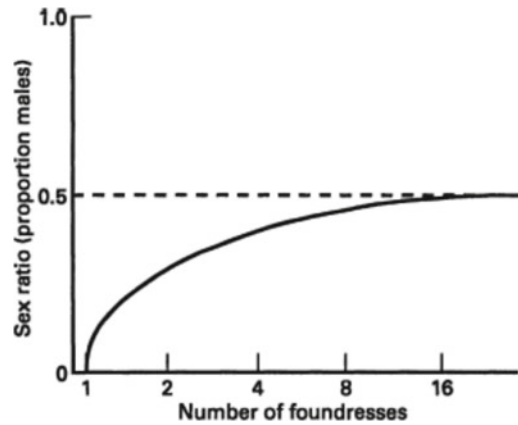


Fig. 1.18 Sex allocation theory for panmictic and for locally mating species. The optimal primary sex ratio (proportion of offspring that are males) in relation to the number of foundress females (mothers) exploiting a patch. The dashed line represents the ‘Fisherian’ scenario of population-wide mating among maturing offspring (panmixis) leading to selection for equal investment in sons and daughters by mothers: even sex ratios maintained by frequency-dependent selection (Fisher, 1930; Gardner, 2023). The solid line represents the ‘Hamiltonian’ scenario of strict local mating (LMC) by offspring within their natal patch followed by the dispersal of mated daughters only (Hamilton, 1967): the optimal sex ratio for individual mothers (termed foundresses) depends on sex allocation decisions by other mothers on the patch and the unbeatable solution for them all to adopt (the ESS) is given by $(n - 1)/2n$, where n is the number of females colonising the patch. For the single-mother case, the prediction of a sex ratio of zero is taken to mean ‘just sufficient males to mate with all daughters in the patch’. The LMC prediction shown is for diplo-diploid genetics; the prediction for haplo-diploid genetics is that sex ratios are slightly more biased. The models summarised here form much of the core of sex allocation theory (consisting of many empirically justified modifications), which has become a very successful area within evolutionary biology

1.11.2 Local Mate Competition

The first broad pattern that needs to be explained is a cross-species one: sex ratios (usually expressed as the proportion of the progeny that are male) can vary from highly female biased to equality, or much more rarely, become male-biased. For example, Bernal et al. (1998) reported that mated female *Coccophagus semicircularis* produce strongly female-biased sex ratios; the *Drosophila* parasitoid *Leptopilina*

heterotoma has a sex ratio near equality, whereas the closely related species *L. bouhardi* has a male-biased sex ratio (Fauvergue et al., 1999).

This variation has been explained by the theory of local mate competition (Hamilton, 1967; Godray, 1994; West, 2009). Under conditions of Local Mate Competition (LMC) ovipositing females are predicted to lay an increasingly female-biased offspring sex ratio as the likelihood of sib-mating increases. Imagine a patch where only one female oviposits and lays a given number of eggs and then, on maturity, her sons mate with her daughters, before the sons die and the daughters disperse to find new patches to lay their eggs on. With an unbiased sex ratio, the males in the maturing brood will compete with each other for matings with their sisters. The ovipositing female can increase her fitness by changing the proportions of male and female offspring in her brood, increasing allocation to females to the point where there are only enough males present to ensure that all females in the brood are mated. Biasing the sex ratio in this manner means that competition between sons for access to mates will be lower, the number of available mates for each male will be increased, and the overall production of mated daughters from the brood will be maximised (Antolin, 1993; Ode et al., 1998; West, 2009).

Conditions suitable for LMC are most likely to be met when patches are discrete (the classic example is that of the pollinating fig wasps where only one female will oviposit within each fig fruit; Hamilton, 1979; see Greeff & Kjellberg, 2022, for a review of pollinator wasp sex ratios), when patches are defended by females from attack by other searching females (Sect. 1.13), or when the density of females is low and offspring tend to mate near the emergence site (Hardy, 1994; Chap. 5). With increased numbers of females ovipositing in a patch, the males of different mothers are able to mate with a focal mother's daughter and the focal mother's sons can also mate with the daughters of other mothers. Sex allocation decisions by individual mothers within groups can be seen as a game-theoretic problem, and the ESS (Sect. 1.2.2) is that each female should increase the proportion

of males in her brood compared to what she would do if reproducing alone (Hamilton, 1967). When large numbers of females produce offspring on a patch, the optimal sex ratio becomes essentially the same as under population-wide mating systems (panmixis): an equal allocation to male and female offspring. Hamilton (1967) showed that the predicted ESS (which he termed the 'unbeatable' sex ratio) is $(n - 1)/2n$, where n is the number of females colonising a patch of resource, on which their offspring mate at random (Fig. 1.18). This applies to organisms with diplo-diploid genetics; for haplidioids the equation becomes $(n - 1)(2n - 1)/n(4n - 1)$, giving a very slightly more female-biased sex ratio than the diploid model when multiple mothers colonise a patch (Hamilton, 1979; Taylor & Bulmer, 1980; West, 2009).

In a comparative study of the sex ratios of non-pollinating fig wasps (which are primarily inquilines or parasitoids), Fellowes et al. (1999) used the wing morphology of males to distinguish between species that naturally vary in the levels of LMC experienced. Species with wingless males have to mate within the fig fruit, and hence are likely to experience high levels of local, often sibling, mating. In contrast, species with winged males will mate outside the fig, often after dispersal, resulting in near-random mating throughout the population. In some species of non-pollinating fig wasps an intermediate proportion of males are winged; these species should experience an intermediate level of local mating (termed partial LMC, Hardy, 1994). Theory predicts that sex ratios should follow the rank order of winged males > dimorphic males > wingless males, and a phylogenetically controlled analysis (Sect. 1.2.3) confirmed this pattern. Further comparative studies of sex allocation under LMC are provided by Griffiths and Godfray (1988), Hardy and Mayhew (1998) and Smart and Mayhew (2009); see also Mayhew and Pen (2002).

Within species, similar patterns are also found. Indeed, Salt (1936) noted that the proportion of male *Trichogramma evanescens* offspring emerging from hosts increased when more females oviposited in a patch. This observation

was confirmed and developed further by Waage and Lane (1984), who found that while sex ratio did increase with the number of ovipositing females, the sex ratio was more male-biased than expected. They explained this by proposing that females were less likely to survive superparasitism. More recent examples of parasitoid sex ratio responses to the numbers of females reproducing on a patch can be found in, for example, Burton-Chellew et al. (2008), Ode and Hardy (2008), West (2009), Abdi et al. (2020a) and Abe et al. (2021).

1.11.3 Conditional Sex Allocation

The second pattern of sex allocation behaviour that needs to be explained is the preferential oviposition of one-offspring sex (usually female) in better-quality hosts. This was explained by the theory of Conditional Sex Allocation (Charnov, 1979; Charnov et al., 1981; King, 1993; Godfray, 1994; Hardy & Boulton, 2019; West, 2009). The size of parasitoids (especially idiobionts) is often determined by host size. As there is often a positive correlation between parasitoid body size and fitness (Sect. 1.10), larger hosts should be preferred. However, if the size–fitness relationship is stronger for female parasitoids than for males, an ovipositing female will maximise her fitness by placing female eggs in better-quality hosts and males in poor-quality hosts (e.g., King & King, 1994; King & Lee, 1994; Morris & Fellowes, 2002; Ode & Hardy, 2008; Hardy & Boulton, 2019). The relative fitness benefits of larger male and female size are, however, challenging to assess, especially in the field (Karsai et al., 2006; King & Napoleon, 2006; Sect. 2.7.3).

Aphelinus abdominalis is a common parasitoid of several aphid species. In a detailed study, Honěk et al. (1998) investigated the sex allocation behaviour of this parasitoid when presented with several potential host species. In all four aphid species (*Macrosiphum euphorbiae*, *Metapolophium dirhodum*, *Sitobion avenae* and *Rhopalosiphum padi*), females preferentially placed male offspring in smaller hosts. If females were provided with small hosts only, then over

time the sex ratio became less male-biased. Interestingly, virgin females (i.e., those constrained to produce male progeny only) initially favoured small hosts, but over time preferentially attacked larger hosts when provided with a choice. Further examples of parasitoid sex allocation responses to host size are reviewed in, for example, Godfray (1994), Ode and Hardy (2008) and West (2009).

1.11.4 Sex Allocation and Mass Rearing

Female-biased sex ratios are clearly the preferable outcome of parasitoid mass rearing for biocontrol programmes, as only female parasitoids attack hosts in the field. In a survey of the sex ratios of parasitoids and predators mass reared for biological control purposes, Heimpel and Lundgren (2000; see also Lundgren & Heimpel, 2003) found that while predators all had an unbiased sex ratio, a large proportion of the parasitoids had a more male-biased sex ratio than expected. Such work suggests that the producers of biocontrol agents may be able to improve the quality of their product with changed rearing techniques. Thus, the study of sex allocation in insect parasitoids is an important area of study not only for those interested in evolutionary ecology but also for practitioners of biological control (Hardy & Ode, 2007; Luck, 1990; Ode & Hardy, 2008), and such considerations have underpinned several studies of parasitoid sex allocation behaviour.

Sagarra and Vincent (1999) suggested that *Anagyrus kamali*, a parasitoid of the hibiscus mealybug, should be reared on larger hosts to maximise the production of female progeny. However, one point that can be missed in such studies is that conditional sex allocation is usually a relative behaviour. Female offspring will be placed in larger hosts, but if only large hosts are presented then the sex ratio will approach equality. Thus, a mother may lay a son in a medium-sized host that is encountered among a batch of large hosts but would lay a daughter in a medium-sized host found among small-sized

hosts. Females are expected to update their estimations of the distributions of host sizes as they encounter a succession of hosts during their lives. Several studies, on *Catolaccus grandis* (Hymenoptera: Pteromalidae) a parasitoid of boll weevils, and *Diglyphus isaea* (Hymenoptera: Eulophidae), which attacks agromyzid leafminers, have shown that increasing the size of hosts presented to females over several days leads to a greater production of female offspring than does presenting similar host sizes each day, and presenting smaller and smaller hosts leads to male-biased sex ratios. The technique works not just with females held in isolation (which would be labour intensive in a mass-rearing facility) but also when hosts are presented to groups of parasitoids. Under simulated mass-rearing conditions the production costs of females can be cut by as much as a half (Ode & Heinz, 2002; Chow & Heinz, 2005, 2006; Ode & Hardy, 2008).

Similarly, attempts have been made to use LMC theory to improve mass-rearing efficiency. Since a major prediction is that sex ratios will be more female biased when fewer females contribute offspring to a patch, rearing programmes can be set up such that females encounter hosts in isolation rather than in the presence of other females. Experiments by Irvin and Hoddle (2006) on three species of Mymarids, parasitoids in the genus *Gonatocerus*, indicated that mass-rearing efficiency can be substantially improved by minimising contact between females presented with hosts.

1.11.5 Density-Dependent Shifts in Sex Ratio

In a population of wasps adjusting sex allocation as predicted by Hamilton's (1967) model, the proportion of male offspring produced per female will be higher at high wasp densities than at low densities. Thus, individual optimisation does not go hand in hand with maximal female production in a population. This is one reason why the mass rearing of parasitoids often does not result in desired female-biased sex ratios (Sect. 1.11.4).

Models like Hamilton's (1967), which predict adaptive shifts in sex allocation in response to the presence of other females, raise the question of how these shifts can be achieved. Waage (1982) was the first to show that simple fixed mechanisms, such as always laying one or more male eggs first (Fig. 1.19), can lead to variable sex ratios under different conditions, close to those predicted by the functional models (Waage & Lane, 1984; Waage & Ng, 1984). Rather than counting the number of hosts in a patch and calculating what fraction of her offspring should be sons, the female can lay a son, then lay the number of daughters he can fertilise, then lay another son, and so on (reviewed in Hardy, 1992, see also Greeff & Kjellberg, 2022). This has been theoretically demonstrated by Wajnberg (1994). Other mechanisms are also known where the stimulus to change the sequence of sex allocation comes from contacts with marks of conspecifics or with parasitised hosts (Viktorov, 1968; Viktorov & Kochetova, 1971).

To show that females adjust sex ratio in response to the presence of other females, offer patches containing equal numbers of standardised hosts to different densities of parasitoid females (as in a mutual interference experiment, Sect. 1.15.3). Primary sex ratio can be determined as described below (Sect. 1.11.6). If females use a simple 'males-first' rule, a shift in sex ratio can be found with this setup. Alternatively, one could offer a fixed number of standardised hosts per female in experiments with different numbers of females. In such an experiment, the number of hosts increases with the number of wasps. Where females use a 'males-first' rule, no sex ratio adjustment should be found unless, that is, females react to parasitoid odour or marks.

Strand (1988) adopted a quite different approach in studying density-dependent shifts in sex ratio in *Telenomus heliothidis*. He kept groups of around 200 females together, without hosts, for variable periods of time shortly after emergence and mating, then allowed subsequently isolated females to oviposit in unparasitised hosts (Strand, 1988, also tested for the effects of subsequent isolation by varying the

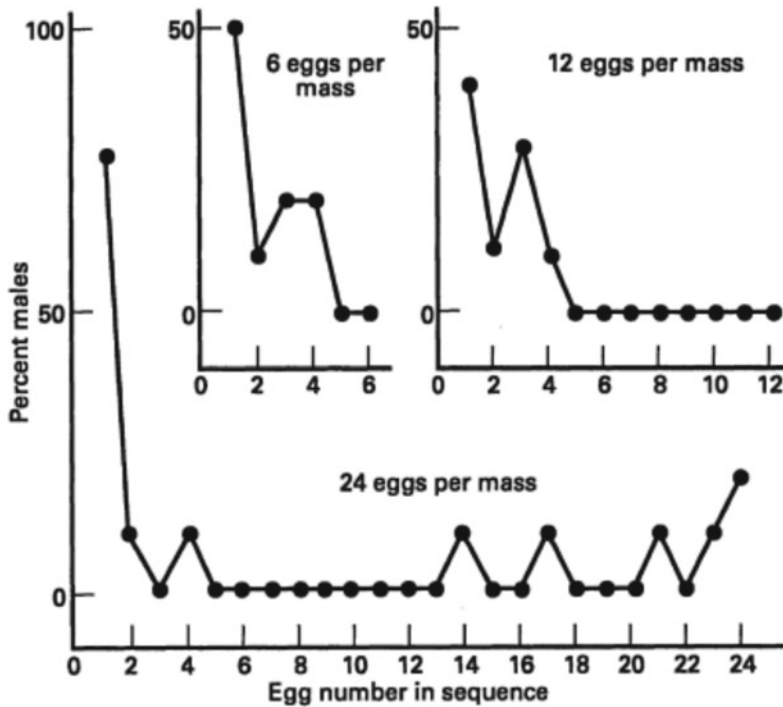


Fig. 1.19 Sex allocation by parasitoids: the sequence in which the solitary scelionid parasitoid *Gryon pennsylvanicum* (= *atriscapus*) lays male and female eggs in host egg masses of 6, 12 and 24 eggs. Data are based on observations of mated females and subsequent dissection of host eggs at the time of adult emergence. In all egg masses, males (usually one per mass) are placed in the first few host eggs. By this strategy, every host egg mass, independent of size, is ensured a male wasp offspring. In very large egg masses, e.g., of 24 eggs, a second male is

sometimes produced towards the end of the sequence, suggesting that females measure the ratio of males to females and keep it constant for a particular size of egg mass. The males-first strategy alone will also produce an adaptive increase in sex ratio with increased female crowding, since each wasp will lay fewer eggs per egg mass and therefore allocate proportionately more males. *Source* Waage (1982), reproduced by permission of Blackwell Publishing

isolation period). With this method, one can rule out the possibility that females alter sex ratio in response to encounters with already parasitised hosts. Strand (1988) concluded that the observed effects were directly due to crowding.

Simple mechanisms such as 'males first' can easily be studied in solitary parasitoids by collecting a sequence of hosts parasitised by an individual female and rearing each of the hosts in separate containers. Investigating such behaviour in gregarious parasitoids is more difficult, but by interrupting oviposition at various points during the laying of egg clutches and rearing the parasitoids, information on the sequence of male and female eggs can be obtained. Sometimes the

sequence of male and female eggs can be inferred from the behaviour of the female during the oviposition bout (Sect. 1.11.6).

1.11.6 Measuring Primary Sex Ratios

Theories of sex allocation deal with the oviposition decisions of female wasps. Tests of these theories may require accurate measurement of the sex ratio of the oviposited eggs, i.e., the allocated or primary sex ratio. Often, however, due to differential mortality of male and female immatures, the sex ratio of emerging parasitoids, the so-called secondary sex ratio, does not

always reflect the primary sex ratio, and even if mortality is not different between the sexes, mortality can affect the sexual composition of broods and obscure sex allocation strategies (van Baaren et al., 1999; Khidr et al., 2013; Wilkinson et al., 2016; Liu et al., 2023). It is possible, especially when working on ectoparasitoids where egg-to-adult mortality is readily observable, to use a subset of broods in which there was no mortality as an indicator of the primary sex ratio. Although this may serve a useful purpose in some cases (e.g., Werren, 1980), this method is, strictly speaking, flawed because the subset of broods without mortality are a self-selected subset, with sex ratios biased towards the sex with the lowest mortality (Krackow & Neuhäuser, 2008; Khidr et al., 2013, see also Wellings et al., 1986). To take account of this problem, the following empirical methods can be used to obtain unbiased estimates of primary sex ratios:

1. Behavioural indicators: Cole (1981), Suzuki et al. (1984) and Strand (1989) discovered for some species that one can determine, on the basis of differences in the insect's abdominal movements during oviposition, whether or not a female parasitoid fertilises an egg. A feature common to these species is a pause during oviposition of a fertilised (female) egg.
2. Positional indicators: Flanders (1950) and Luck et al. (1982) used a non-destructive method for *Aphytis* that involves determining the sex of an egg from the position in the host in which it is laid: wasps lay male and female eggs on the host's dorsal surface and ventral surface, respectively.
3. Chromosomal counts: cytological techniques for counting chromosomes of haplo-diploid parasitoids can be used to establish the sex of freshly laid eggs (Dijkstra, 1986; van Dijken, 1991): further details are given in Sect. 3.4.1.
4. Molecular genetics: between-strain polymorphisms in microsatellite markers can be used in crosses between males and females from stain carrying different alleles and then eggs in which only one allele is detected (hemizygous) are identified as male and those containing both alleles (heterozygous

diploids) are identified as female (Khidr et al., 2013; Liu et al., 2023; Sect. 3.4.1). De Menten et al. (2003) used fluorescence *in-situ* hybridisation (FISH) to sex ant eggs. This approach has been applied to parasitoid wasps (Carabajal Paladino et al., 2013) but not yet to assess primary sex ratios.

1.12 Switching Behaviour

Species and host stage preference by natural enemies has been discussed in Sect. 1.6.7. Preference (parameter c in Eq. 1.1) may not be constant but may vary with the relative abundance of two prey or host types, in which case if the predator or parasitoid eats or oviposits in disproportionately more of the more abundant type (c increases as N_1/N_2 increases) it is said to display a switching behaviour (Murdoch, 1969) or an apostatic selection (Clarke, 1962), the latter term being used by geneticists. Where disproportionately more of the rarer type is accepted (c increases as N_1/N_2 decreases) negative switching is said to occur (Chesson, 1984). Positive switching behaviour has aroused the interest of students of population dynamics because it is associated with a Type 3 functional response (to prey type N_1) (Sect. 1.14) (Murdoch, 1969; Lawton et al., 1974).

Switching behaviour in parasitoids has been observed by Cornell and Pimentel (1978) in *Nasonia vitripennis*, van Alphen and Vet (1986) in *Asobara tabida*, Chow and Mackauer (1991) in *Aphidius ervi* and *Praon pequodorum*, and probably by Lill (1999), while switching in insect predators has been observed by Lawton et al. (1974) in the waterboatman *Notonecta glauca* and the damselfly *Ischnura*. Other examples are given in Sherratt and Harvey (1993) who provide a comprehensive review of switching and frequency-dependent selection in general.

Switching can be tested for by offering parasitoids combinations of different host species in single-patch experiments. The combined density of the two host species should be kept constant,

but the relative abundance of the two species should vary among treatments. If the mechanism causing the switching is to be determined, full records of parasitoid (and host) behaviour ought to be made. As in other host selection experiments (Sect. 1.6.7) females should be observed continuously and the number of acceptances and ovipositions scored, to show whether females accept more or fewer individuals of a host type than they successfully parasitise (this possibility is usually ignored by authors).

One can either conduct fixed-time experiments, in which depletion of the hosts is prevented by replacing each parasitised host by an unparasitised one of the same species, or terminate experiments when the parasitoid leaves the patch that it is allowed to deplete. Switching, like many other aspects of parasitoid and predator behaviour, is likely to be affected by previous experience of the natural enemy (see below).

The resulting data can be analysed using Murdoch's (1969) null or no-switch model:

$$P_1 = cF_1 / (1 - F_1 + [cF_1]) \quad (1.2)$$

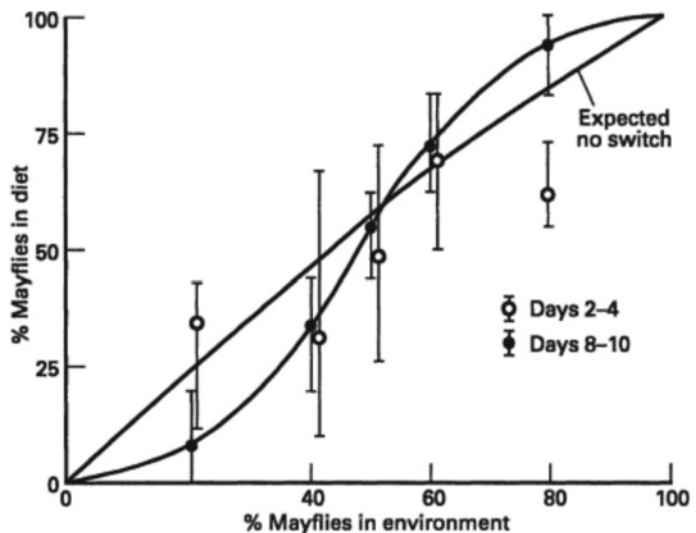
where F_1 is the proportion of host species 1 in the environment, P_1 is the proportion of species 1 among all the hosts oviposited in, and c (a parameter we have already mentioned in Sect. 1.6.7) corresponds to the one used in Eq. (1.1) (Sect. 1.6.7). In the absence of

switching behaviour, c is a constant that can be estimated in various ways, although it is convenient to estimate it when $N_1 = N_2$. The value of P_1 for any level of availability of species 1 can be estimated by substituting the estimated value of c in Eq. (1.2), and an expected no-switch curve plotted (Fig. 1.20). If the parasitoid or predator species' preference is not constant but alters with changing host or prey availability (or encounter rate) the observed proportion of host/prey species 1 among all the accepted hosts or prey will be higher than expected when species 1 is abundant and lower than expected when species 1 is rare.

Elton and Greenwood (1970, 1987) and Greenwood and Elton (1979; see also Sherratt & Harvey, 1993) provide a model which can be used for the detection of switching and other forms of frequency-dependent selection, and which includes a measure of the deviation from constant preference as one of the parameters. Another model developed by Manly et al. (1972), and Manly (1972, 1973, 1974; see Sherratt & Harvey, 1993, for a discussion) takes account of prey depletion (this model requires modification before it can be used to take account of depletion of unattacked hosts or prey). The latter model can also be easily generalised for more than one host/prey or host type.

Tinbergen (1960) suggested, as a mechanism for switching, that predators form a search image

Fig. 1.20 Switching in insect natural enemies: the percentage of mayfly larvae in the diet of *Notonecta glauca* L. (Hemiptera: Heteroptera) was a function of their relative abundance in the habitat. The almost straight line is the 'no-switch' curve. Source Lawton et al. (1974)



of the most abundant prey species, i.e., they experience a perceptual change in the ability to detect a cryptic prey type, and this change does not occur when that type is rare (Lawrence & Allen, 1983; Guilford & Dawkins, 1987, discuss evidence for search image formation). However, switching could well result from other behaviour such as active rejection of the less preferred host species as the preferred hosts become more abundant, a prediction of optimal prey selection models (Sect. 1.6.7). Note that Murdoch's (1969) definition of switching is couched in terms of relative prey density, whereas optimal foraging models refer to absolute densities or encounter rates with prey.

Lawton et al. (1974) investigated whether experience with a particular prey species may be a contributory mechanism in the switching behaviour of *Notonecta glauca* presented with *Asellus* and *Cloeon*. In this case, negative switching was recorded over days 2–4 of the experiment and positive switching over days 8–10 (Fig. 1.20). In a separate experiment, the authors measured the proportion of successful attacks on *Asellus* prey in relation to the proportion of this prey available in the environment during the previous seven days. They found that the more *Asellus* the predator was exposed to, the greater was the proportion of successful attacks recorded. While this strongly suggests that experience with *Asellus* affects the predator's prey capture efficiency, it does not prove conclusively that it does so, since no information was obtained on the encounter rates, and therefore on the experience of the insects, during the pre-experimental period. The development of a search image could be ruled out as a mechanism for switching in this predator/prey system since: (1) in the switching test *N. glauca* took different prey species in a random sequence instead of attacking prey in 'runs' (Lawton et al., 1974), and (2) the prey were unlikely to have been cryptic in the experimental tanks used.

Switching behaviour may not necessarily be adaptive. Chow and Mackauer (1991) found that *A. ervi* and *P. pequodorum* switched to the alfalfa aphid when pea aphids and alfalfa aphids were

offered to wasps in a 1:3 ratio. However, the authors hypothesised that since alfalfa aphids are more likely than pea aphids to escape from an attacking wasp, a foraging wasp incurs a potentially higher cost in lost 'opportunity time' (Sect. 1.6.7) when attacking alfalfa aphids. Furthermore, since it is possible that alfalfa aphids are poorer-quality hosts in terms of offspring growth and development, wasps may not derive a fitness gain from switching to alfalfa aphids.

1.13 Patch Defence Behaviour

When a predatory insect finds a resource, there is a trade-off between allocating time to consuming it or defending it against competitors (Field & Calbert, 1998). However, the resources utilised by parasitoids are relatively long-lived and thus potential hosts in a patch may not yet be suitable for attack, or any offspring that have already been invested in are vulnerable to attack themselves. As a result, some female parasitoids defend hosts, or patches of hosts, against conspecific and heterospecific intruders (Hardy et al., 2013; Couchoux & van Nouhuys, 2014; Mathiron et al., 2018; Goubault et al., 2019), occasionally leading to the death of one of the protagonists (Pérez-Lachaud et al., 2002; Velasco-Hernandez et al., 2021; Guo et al., 2023, see also Dunn et al., 2015). This patch defence behaviour consists of two components, resource defence (where competing females are prevented from gaining access to potential hosts; Waage, 1982) and maternal care (where previously parasitised hosts are protected from superparasitism or hyperparasitism; van Alphen & Visser, 1990), and the relative importance of both factors will influence patch defence behaviour (Field & Calbert, 1998; Guerra-Grenier et al., 2020). Thus, patch defence can be an alternative competitive strategy to one of allowing conspecifics on the same patch and competing with them through superparasitism (Sect. 1.9.4).

Patch defence is only advantageous under a limited set of conditions. The following factors favour defence of patches:

1. Synchronous development of the hosts in the patch.
2. Rapid development of the host to a stage which can no longer be attacked by the parasitoids, or rapid development of the parasitoid offspring to a stage at which they have a competitive advantage in cases of superparasitism (after which continued defence may no longer be necessary; Goubault et al., 2007b).
3. Short travel times between patches. When travel times are long, intruders are likely to be 'reluctant' to lose the contest for the patch. This would prolong fighting and increase the cost of defence.
4. A low probability of finding more than one host or host patch during adult life. This factor selects for foragers to spend long periods guarding those resources that they do find (host- and brood-guarding; Hardy & Blackburn, 1991).
5. Patches should be of a defensible size; larger patches are harder to defend.

Patch defence was first described for scelionid egg parasitoids (Waage, 1982), which defend small and intermediate-sized host egg masses. However, it is also found in braconids (e.g., *Asobara citri*), ichneumonids (e.g., *Rhyssa persuasoria*, *Venturia canescens*, *Hyposoter horticola*), and bethylids (e.g., *Goniozus nephantidis* and *G. legneri*).

In some parasitoids, such as the aforementioned scelionid egg parasitoids, patch defence appears to be a fixed response to an intruder (but see below). However, in other species such as the braconid *Asobara citri*, patch defence and fighting behaviour decrease in frequency with increasing patch size and increasing numbers of intruders, and wasps may switch to competition through superparasitism. Patch defence can have a pronounced effect on the distribution of adult parasitoids over host patches. It can lead to a regular distribution of parasitoids (de Jong et al., 2011), and is thus one of the factors reducing aggregation (Sect. 1.15).

Whether patch defence or competition by superparasitism is the better strategy depends on species-specific traits such as the encounter rate with hosts and the handling time. Thus, it is possible that one species attacking a certain host defends hosts or patches against intruders, while another parasitoid species attacking the same host does not.

One of the better-studied systems involves the scelionid wasp *Trissolcus basalis*, a parasitoid of the egg masses of pentatomid bugs (Field, 1998; Field et al., 1997, 1998; Field & Calbert, 1998, 1999; Sujii et al., 2002; Wajnberg et al., 2004; Cusumano et al., 2011; Mesterton-Gibbons et al., 2021; see also Guerra-Grenier et al., 2020). Here, if a female finds a patch, she will initially search for, and oviposit in, suitable hosts. Later, she will patrol the patch, still ovipositing until the patch is depleted. Once this occurs, the female will remain on the patch for about 5 h, before departing, although the length of time spent guarding will depend on patch quality. If two females find a patch, then at first both will exploit it without aggression. However, after a period of time, fighting will be initiated and the females take the roles of 'intruder' or 'resident', with the resident usually being the female that first arrived. The likelihood of a female *T. basalis* initiating conflict will depend on several factors: the number of potential hosts in the patch and the encounter rate with them, the asymmetry in arrival time and the number of conspecifics encountered, and the number of eggs invested in the patch. The resident will guard the patch because if the intruder attacks within the first 3 h after oviposition by the resident, the intruder's developing offspring will compete with those of the resident. During this period, the female will be exposed to a trade-off between exploiting new hosts and guarding the patch. The intruder will regularly attempt to cryptically invade the patch, and eventually will succeed once the resident has left. Finally, Wajnberg et al. (2004) found a significant intrapopulation genetic variation in the behavioural mechanisms involved in the patch defence strategy adopted by *T. basalis* females.

Patch defence should preferably be studied in multi-patch experiments. In single-patch experiments, one could easily underestimate the significance of defence behaviour. A classic example of this is the fighting and chasing which occurs when two females of *Venturia canescens* meet whilst searching the same patch. This aggressive behaviour is an important component of mutual interference in laboratory experiments with *V. canescens* (Hassell, 1978; Sect. 1.15.3). The function of the fighting and chasing is not easily understood from such experiments because the behaviour leads, on large patches, to a decrease in attack rate for both wasps but not to the permanent exclusion of the intruding wasp. However, field observations of *V. canescens* searching for *Ephestia (Anagasta) kuehniella* larvae feeding on fallen figs suggest that a fig containing a host larva can be successfully defended against intruding competitors, with the latter moving on to nearby figs following an aggressive encounter (Driessen et al., 1995). Field or semi-field condition observations are, of course, extremely valuable but often difficult to achieve and sample sizes may be in consequence relatively low (e.g., Couchoux & van Nouhuys, 2014).

1.14 Functional Responses

Understanding how predators and parasitoids respond to changes in prey and host density is critical to gaining a grasp of the interactions between natural enemies and their victims. Solomon (1949) coined the term functional response when describing the response shown by individual natural enemies to varying host (prey) density. With increasing host or prey availability, each natural enemy will attack more host or prey individuals, but several types of functional response are possible (Fig. 1.21, Chap. 7; Hassell, 2000b, provides a detailed review). Four types, called Type 1, 2, 3 and 4, have been observed:

Type 1: where there is a rectilinear rise to a maximum (N_x) in the number of prey eaten per

predator as prey density increases. The response is described by the following equation:

$$N_a = a'TN \quad (1.3)$$

where N_a is the number of hosts parasitised or prey eaten, n is the number of hosts or prey provided, T is the total time available for search, and a' is an acceleration constant, the instantaneous attack rate (Eq. 1.3 applies only when $N < N_x$).

The Type 1 response is likely to be found when handling times (see below) are negligible and eggs are in limited supply.

Type 2: where the response rises at a constantly decreasing rate towards a maximum value, i.e., the response is curvilinear, in contrast with the Type 1 response. Holling (1959a, 1959b) predicted such a response, reasoning that the acts of quelling, killing, eating and digesting prey are time-consuming activities (collectively called the handling time) and that these will reduce the time available for further search. Following from this, as prey density increases, a predator will spend a decreasing proportion of its (total available) time on searching:

$$T_s = T - T_h N_a \quad (1.4)$$

where T_s is the actual time spent searching, and T_h is the handling time. The Type 2 functional response is probably the most commonly reported in parasitoids (Fernández-Arhex & Corley, 2003).

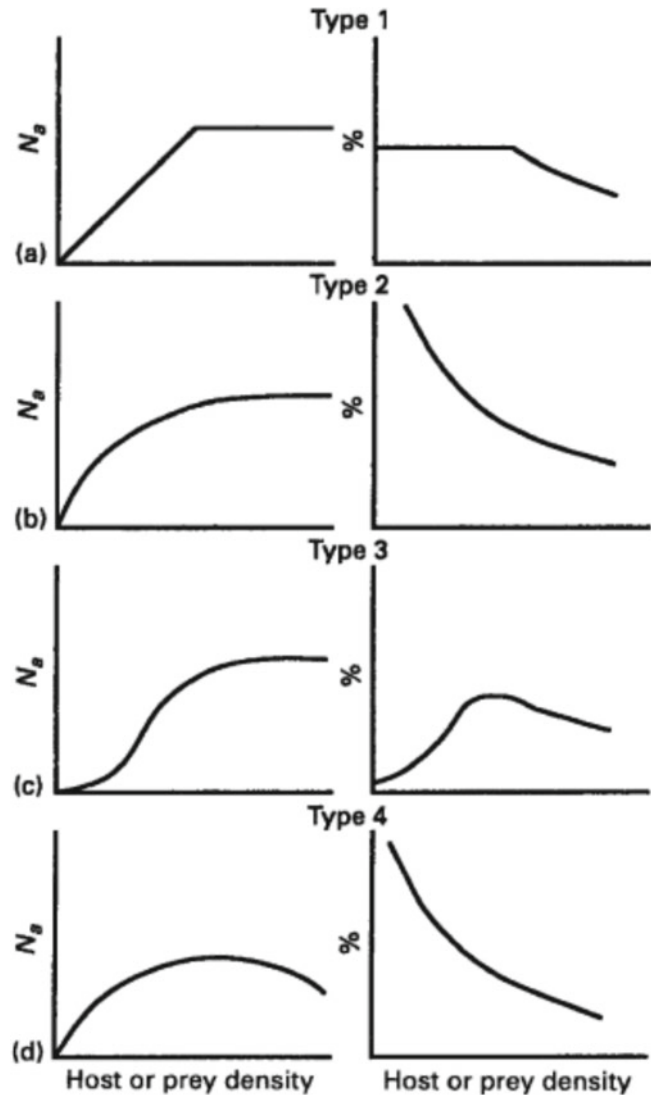
Type 3: where the response resembles the Type 2 response except that at lower prey densities it accelerates. The response is thus sigmoid.

Type 4: where the response resembles the Type 2 response except that at higher densities it declines, producing a dome-shape curve.

Sabelis (1992) also recognised a fifth type of response, which is intermediate between the Type 1 and the Type 2. This response appears to be shown by some predatory mites and will not be discussed further here.

The functional response of a predator or parasitoid species is usually measured as follows: individual insects are confined in an arena (e.g.,

Fig. 1.21 The four types of functional response: **a** Type 1; **b** Type 2; **c** Type 3; **d** Type 4. N_a = number of hosts parasitised or number of prey eaten; % = percentage of hosts parasitised or eaten



cage), with different numbers of prey or hosts, for a fixed period of time (Fig. 1.22). At the end of the experiment, the natural enemies are removed and either the number of prey killed or the number of hosts parasitised (or both, in the case of some host-feeding parasitoids, see below) is counted. Hosts are either dissected or reared until emergence of the parasitoids. From the counts made, a graph can then be plotted relating the number of prey or hosts attacked to the number offered. The plots are then fitted to mathematical models (Holling, 1959a, 1959b, 1966; Rogers, Royama, 1971, 1972; Mills, 1982; Arditi, 1983;

Casas et al., 1993; Casas & Hulliger, 1994; Dannon et al., 2010; Bodino et al., 2019; D'Auro et al., 2021; Wang et al., 2020; Aguirre et al., 2021).

Determining the type of functional response is an important step that needs to be taken by the investigator before attempting to obtain parameter estimates from functional response models. Incorrect estimates may be obtained if a model for a Type 2 response is used to estimate parameters from what is in reality a Type 3 response, and *vice versa*. For advice on how to determine the functional response, and for

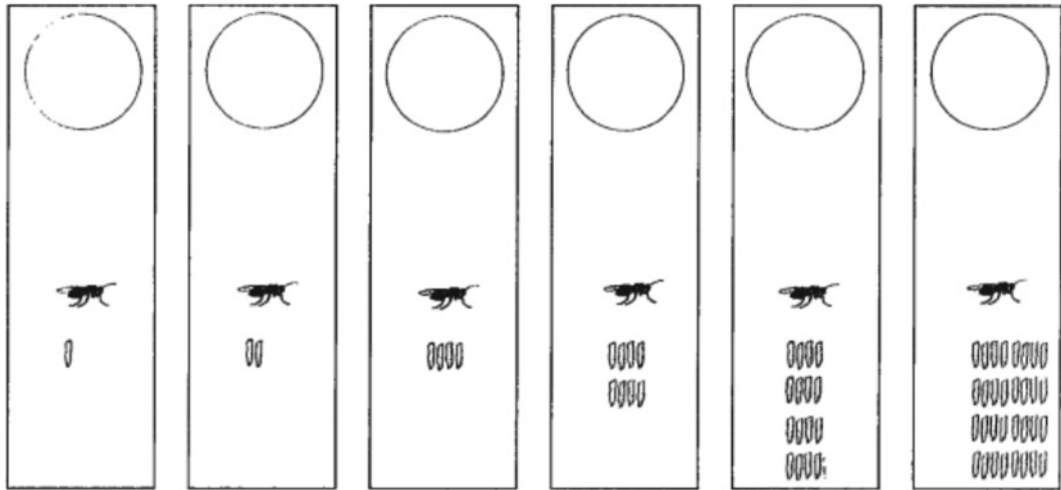


Fig. 1.22 Functional responses of parasitoids and predators: schematic representation of traditional design of a functional response experiment. Circles denote the

experimental host patch, and rectangles the experimental arena. See text for discussion

information on curve-fitting routines, see Trexler et al. (1988), Casas and Hulliger (1994), Juliano (2001) and Schenk and Bacher (2002). There are R packages that can fit functional responses to experimental data using correct statistical methods (e.g., `frair`, Pritchard et al., 2017). An alternative to measuring functional responses is to undertake an integrated analysis of all factors affecting patch time allocation in parasitoids (Sect. 1.5).

With predators, the functional responses of the different larval instars, as well as those of the adults, can be measured. With both predators and parasitoids, functional responses in relation to prey and hosts of different sizes can be measured.

There are two likely reasons why a Type 3 response may be recorded using the aforementioned experimental setup:

1. As host density decreases at the lower range of host densities, the parasitoid spends an increasing proportion of the total time available in non-searching activities. For example, at lower host densities, *Venturia canescens* spends a greater proportion of its time performing activities such as walking and resting on the sides of the experimental cage. Similar behaviour is probably responsible for the Type 3 response observed in parasitoids and predators that are offered unpreferred prey

species: in *Aphidius uzbekistanicus*, *Coccinella septempunctata* and *Notonecta glauca*, a Type 3 response was recorded when the unpreferred host and prey species was provided, compared with a Type 2 when the preferred species was provided (Hassell et al., 1977; Dransfield, 1979). The parasitoid under investigation may be a host feeder, mainly feeding upon hosts rather than ovipositing, at low host densities (Sect. 1.8) (in host-feeding parasitoids that feed and oviposit on different host individuals, we may distinguish between the following functional responses: that for parasitism alone, that for host feeding alone, and that for parasitism and feeding combined; i.e., the ‘total’ functional response; Kidd & Jervis, 1989). If, as is likely, the handling time for feeding encounters is longer than for oviposition encounters, a Type 3 response for parasitism may result (Collins et al., 1981).

2. Handling times may be shorter at higher host densities. In solitary parasitoids, this is an unlikely cause of a sigmoid functional response, but gregarious parasitoids may decrease clutch size at higher host densities (Sect. 1.10), and so decrease handling time per host. Predators may ingest less food from each

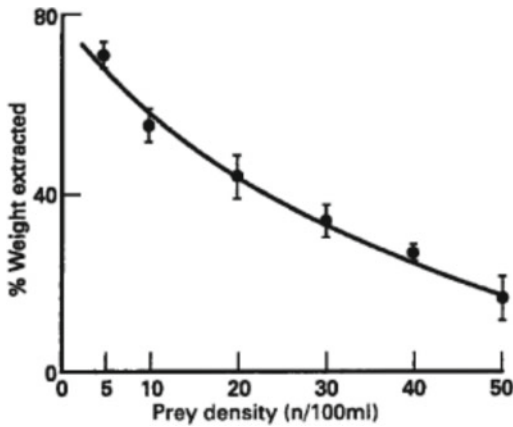


Fig. 1.23 The relationship between prey availability and the percentage of the mass of each prey individual consumed by the belostomatid bug *Diplonychus rusticum*: The bug is more 'wasteful', eating proportionately less of each prey (*Chironomus plumosus*) as prey density increases. This effect is predicted by optimal foraging (i.e., functional) and gut-filling (i.e., causal) models and is shown by a wide variety of predators. Values given are means \pm SE. Source Dudgeon (1990)

prey item at higher prey densities (Fig. 1.23) and so reduce handling times. When extracting food from a prey item becomes increasingly difficult with the time spent feeding on it, predators may optimise the overall rate of food intake by consuming less of each individual prey item when the rate of encounters with prey is high (Charnov, 1976; Cook & Cockrell, 1978). Optimal foraging models predict this behaviour, while a similar prediction can be made based on a causal model relating the amount of food in the gut to the amount eaten from each prey. Some authors have argued that the optimal foraging model can be refuted because there is a causal explanation for the observed behaviour. However, causal and functional explanations are not mutually exclusive; indeed, they complement each other (Sect. 1.2). When predictions of a causal and a functional model are quantitatively similar, this can be taken as evidence that the mechanism does not constrain optimisation of a behavioural trait.

A Type 4 functional response will occur if: (1) when dealing with prey individuals, other prey individuals interfere with the predator and cause it to abort the attack more frequently at high prey densities than at low densities; and/or (2) the prey have a well-developed group defence reaction that is more effective at high prey densities than at low ones.

The classical functional response experiment assumes there is a homogeneous environment, or at least it does not consider the spatial distribution of prey and hosts. However, most insects are patchily distributed and the spatial distribution of hosts or prey within an experimental arena is likely to vary significantly with the density of the insects. Predators and parasitoids respond to differences in prey and host densities between patches by adjusting the amount of time spent in each patch (Sect. 1.5). By allowing the parasitoid, rather than the experimenter, to determine the amount of time it spends in an experimental patch (in a so-called variable-time experiment), a different type of functional response may be obtained compared to experiments where the time spent is fixed by the experimenter (so-called fixed-time experiments; Collins et al., 1981; van Alphen & Galis, 1983; Hertlein & Thorarinnsson, 1987). Van Lenteren and Bakker (1978) suggest that in fixed-time experiments, some parasitoids are likely to show a Type 2 response, rather than a Type 3, because parasitoids are caused to revisit low-density patches they would otherwise leave. Thus, a Type 2 response may be an artefact of the fixed-time experimental design.

Designing an experiment for estimating functional responses from experimental data is usually considered a difficult task since the goal is to estimate the number of hosts or prey attacked as a function of the density of hosts or prey available. Such a density must remain constant (i.e., undepletable patches). Hence, any host or prey attacked should ideally be replaced immediately by a new one. Okuyama (2013) points at several methodological problems like this one.

Since the type of functional response found in an experiment depends very much on the experimental design adopted, one should first clearly define what sort of question one wishes to address before measuring a functional response. Often, a functional response is measured to provide insights into the suitability of a parasitoid as a biological control agent. The problem is then how one can use the information generated by the experiments to predict the performance of the parasitoid in the field. The context in which the data will be used is one of population dynamics (D'Auro et al., 2021; Aguirre et al., 2021; Chap. 7), and thus relates to the response of the parasitoid population to host density. The spatial structure of natural host populations, and the interactions between individual parasitoids in the population, make it hard to relate the results of experiments on individuals in single-patch, single-parasitoid experiments to processes occurring at the population level.

If single-patch experiments are, nevertheless, to be carried out, the minimum requirements for experimental design should be as follows: the foraging insect should be observed continuously (in many functional response experiments, parasitoid and predator behaviour have not been examined directly) and a record made of how the parasitoid spends its time in the experimental arena. Parasitoids should be allowed to leave the arena when they decide to leave, so the experiment should be a variable-time one. It may prove difficult for the observer to decide when an experiment should be terminated. A parasitoid may leave the experimental patch for a short period, but then return and continue searching for hosts. Experiments may need to be terminated after the insect has spent an arbitrary period of time outside the patch (Waage, 1979; van Alphen & Galis, 1983), but of course the choice of the period is subjective and it acts as a censor in the data (a censor is a factor, other than a decision by the foraging insect, that terminates an experiment, e.g., a decision by the experimenter or an external disturbance, see Haccou et al., 1991; Sect. 2.8.2). A solution to the problem of when to

terminate an experiment is to use an arena containing two patches. Once the insect has left the first patch and arrived in the second one, the experiment can be terminated.

However, there is a drawback to conducting such experiments under artificial conditions in the laboratory. The searching efficiency of the natural enemy will be influenced by the spatial structure of the patch (e.g., variation in plant architecture) and in the age structure of the victims (Wang et al., 2020). As an illustration of this, consider the parasitoid *Aphidius ervi* that preferentially attacks second- and third-instar pea aphids within a given patch. Among patches it exhibits variation in foraging efficiency resulting from variation in plant architecture. Ives et al. (1999) found that when aphid numbers were low *A. ervi*, a species that would normally be considered to exhibit a strong Type 2 functional response, shows a Type 1 response. Foraging experiments should therefore be conducted under a range of scenarios, of which at least some would reflect more natural foraging conditions.

Ideally, functional response experiments should measure encounter rates with concurrently available patches containing different densities of hosts. To do this, a multi-patch experiment needs to be carried out. Such an experiment might show that high-density patches are found more easily by the parasitoid, since such patches produce greater quantities of volatile attractants than low-density patches (Sect. 1.6.3).

Functional response experiments have typically not taken into account the possibility that the response of a parasitoid to patches of different densities depends on whether patches are scarce or common in the habitat. In 'poor' habitats when distances between patches are large and high-density patches are scarce, parasitoids should, when exploiting low-density patches, stay longer and parasitise more hosts. Finally, functional response experiments need to take account of the reaction of a parasitoid to the presence of conspecifics or other competitors (Aguirre et al., 2021).

1.15 Distribution of Parasitoids Over a Host Population

1.15.1 Introduction

The distribution of parasitoids over a spatially structured (i.e., heterogeneous) host population has attracted considerable attention from theoretical ecologists. Hassell and May (1973) and Murdoch and Oaten (1975), among others, have shown that this is one of the key features affecting stability of parasitoid–host population models (Chap. 7).

1.15.2 Aggregation

The term aggregation is usually used to refer to the host-searching behaviour of parasitoids. Parasitoids may be more attracted to patches of high host density than to patches of low host density or they may show a stronger degree of arrestment in patches of high host density (Sect. 1.6.3). Insect ecologists refer to an aggregative response of parasitoids and predators, because the aforementioned patch response behaviour leads to the concentration of parasitoids and predators in high-density patches (e.g., Vanbergen et al., 2007; Couchoux & van Nouhuys, 2014). Latterly, the term aggregation has also been applied to the concentration of parasitoids on patches of low host density or on certain patches irrespective of the number of hosts they contain; this can occur if parasitoids are attracted to some patches in response to stimuli that are either negatively correlated with, or independent of, host density. In studies of population dynamics, the term aggregation has also been used in a statistical sense, in terms of both the variance in parasitoid distribution and the covariance between the distributions of host and parasitoid (Godfray & Pacala, 1992).

Aggregation of adult parasitoids is the result of two different processes:

1. Differences among patches in the probability of discovery by parasitoids. In a

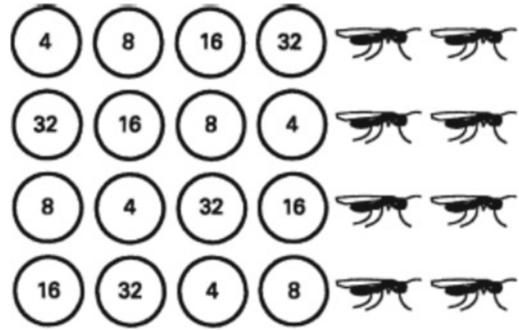


Fig. 1.24 Aggregative responses of parasitoids and predators: Schematic representation of the design for an experiment used for detecting and measuring the aggregative response, and which takes account of the effects on interactions between foragers. Numbers within circles indicate the number of hosts present in each patch

heterogeneous environment, it is likely that not every patch has the same probability of being detected, even if all patches are otherwise similar. Patches may also differ in the probability of detection by parasitoids because of differences in host density or other aspects of quality of the patch.

2. The period of time that each parasitoid stays in a patch after discovering it. The number of parasitoids visiting a patch and the period of time they stay there determine the amount of ‘search effort’ devoted to a patch.

Aggregation can be measured in two main ways:

1. Individual parasitoids can be presented with several patches of different host density, as in studies of patch time allocation.
2. Several parasitoids at one time can be presented with several patches of different host density (Fig. 1.24).

When measuring aggregation using the second of these experimental designs, one should ideally monitor the behaviour of all parasitoids in all patches and record the time each parasitoid spends in each patch. In laboratory experiments with a modest number of host patches and with the insects continuously observed with video-recording equipment, this is possible, but in field experiments such observations are very labour

intensive and often impossible to make. Published field studies on aggregation have therefore relied on periodic observations of the patches (e.g., Waage, 1983; Cronin, 2003a).

One problem associated with studying aggregation in the field is deciding upon the spatial scale at which aggregation should be measured. Clumped distributions of hosts may occur at different levels of host distribution, and so may aggregation by parasitoids (e.g., Doak, 2000). It is often possible, for practical purposes, to define what a patch is. For example, when studying the distribution of parasitoids of the cassava mealybug within a cassava field, cassava plant tips infested with mealybugs are the most relevant foraging units, whereas if one wants to compare biological control between different fields, whole cassava fields can be considered as patches.

The dispersal behaviour of the predator or parasitoid itself may also influence the aggregation pattern of aggregation seen. The likelihood of the minute fairyfly (Mymaridae) egg parasitoid *Anagrus sophiae* laying all of its eggs is correlated with dispersal distance among patches. Females that have dispersed over 250 m from their natal patch will oviposit all their eggs in that patch (Cronin & Strong, 1999).

Such patterns may also be environment-dependent. Cronin (2003b) found that parasitism of the planthopper *Prokelisia crocea* by the egg parasitoid *Anagrus columbi* depended on the location of the planthopper's host plant, prairie cordgrass. When plant patches were surrounded by other grass species, parasitism rates were lower on the periphery of the patch, whereas if the host plants were surrounded by mudflat, attack rates were even throughout the patch. The dispersal behaviour of the parasitoid also varied with cordgrass patches surrounded by non-host grasses having a higher likelihood of colonisation by the egg parasitoid. It is evident that, ideally, studies of parasitoid aggregations should combine knowledge of host, and host-plant, distributions with an understanding of parasitoid dispersal and foraging behaviour (Vanbergen et al., 2007).

1.15.3 Interference

Before we describe interference, we need to stress that mutual interference, pseudo-interference and indirect mutual interference are concepts that can only be properly understood with reference to mathematical models, in particular those of searching efficiency (Chap. 7). The reader is therefore recommended to explore literature dealing with host–parasitoid population dynamics (e.g., Hassell, 2000a, 2000b).

The tendency for some parasitoids and predators to cease searching and to leave the immediate vicinity after an encounter with a conspecific would account for the results of laboratory experiments designed to measure emigration rates in relation to parasitoid density. In these experiments, the proportion of female parasitoids leaving a single, fixed-density host patch increased significantly with increasing numbers of parasitoids (see Fig. 1.25 for experimental design). It has also been observed that when females encounter either an already parasitised host or a parasitoid mark on the substratum, they move away from the area where the encounter occurred. Any of these behavioural interactions are likely to cause the searching efficiency of a natural enemy in the single-patch experiment to be reduced, a phenomenon known as mutual interference (Hassell & Varley, 1969; Visser & Driessen, 1991; Lynch, 1998; Kristoffersen et al., 2001; Elliott, 2003; Couchoux & van Nouhuys, 2014; Yazdani & Keller, 2015; Sreenivas & Hardy, 2016).

The study of mutual interference began with Hassell and Varley (1969) who noted a negative relationship between parasitoid searching efficiency and the density of searching parasitoids:

$$\log a' = \log a - m \log P \quad (1.5)$$

where P is the density of searching parasitoids; a' is the effective attack rate or area of discovery per generation, $a'P = \log$ [initial number of hosts/number of hosts surviving parasitism]; a is the attack rate in the absence of interference. The

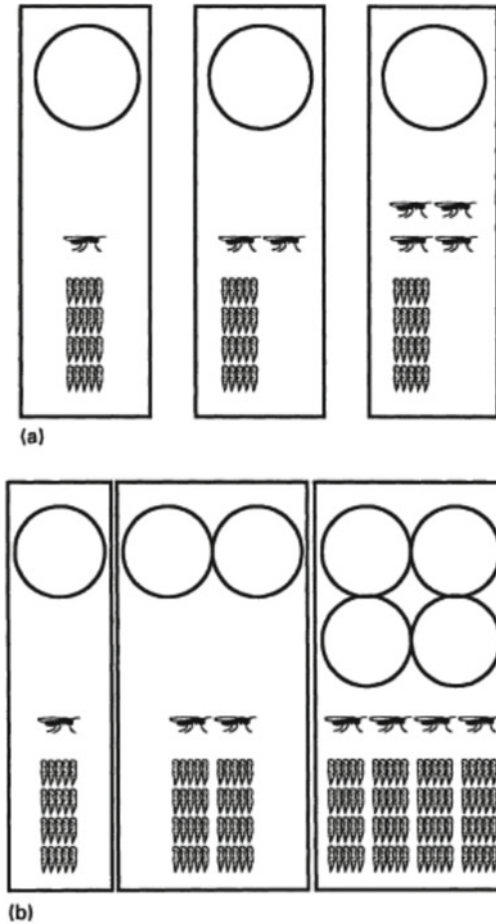


Fig. 1.25 Mutual interference and pseudo-interference: Schematic representation of the design of two types of experiment for studying interference: **a** the design normally adopted for measuring interference, with a single host patch (denoted by a circle); **b** the design used by Visser et al. (1990): either a single parasitoid female searches a single unit patch containing 20 hosts, or two females search a double unit patch containing 40 hosts, or four females search a quadruple unit patch containing 80 hosts. Hassell (1971a, 1971b) used a design similar to that given in Fig. 1.22, although the number of foraging parasitoids was also varied. Both Visser et al. (1990) and Hassell (1971a, 1971b) designs take account of the multi-patch context in which interference occurs

parameter m is the measure of the extent of mutual interference. Such a relationship is to be expected because, as parasitoid density increases, individual parasitoids will waste an increasing proportion of their searching time in encounters with other conspecifics. Similar patterns are to be found with insect predators, and even among

closely related species the importance of mutual interference will vary (Elliott, 2003).

Free et al. (1977) argued, using deductive models, that marked parasitoid aggregation (e.g., resulting from a strong tendency of parasitoid individuals to spend longer periods of time in higher host-density patches, and the consequent differential exploitation of patches) can lead to apparent interference, termed pseudo-interference, even if behavioural interference is lacking. As a consequence of parasitoids aggregating in high-density regions (because these are initially the most profitable), a higher proportion of the hosts in the whole area (i.e., experimental cage) is parasitised than would be obtained with random search. If parasitoids do not respond (i.e., by dispersal) rapidly to the declining profitability of the high host density (i.e., more heavily exploited patches), then overall searching efficiency will be lower at high parasitoid densities. Thus, pseudo-interference results from ‘over-aggregation’ by the parasitoids (Hassell, 1982). In a population of optimally foraging parasitoids capable of responding rapidly to exploitation, overall searching efficiency would, at high parasitoid densities, be the same as for random search.

A third form of interference has been identified (Visser & Dreissen, 1991; Visser et al., 1999). Indirect mutual interference was first found in the parasitoid *Leptopilina heterotoma*, a generalist parasitoid of drosophilids. Mutual interference is not found in this species, but as a result of superparasitism, searching efficiency is reduced at the population level, but not at the level of the patch (Visser & Dreissen, 1991).

These different forms of interference can lead to the stabilisation of consumer–victim population interactions, and as a result have proved important in studies linking individual behaviour and population dynamics. Visser et al. (1999) used data collected by Jones (1986), studying *Trybliographa rapae* attacking *Delia radicum*, to explore how the three different forms of interference may influence host–parasitoid population dynamics. In this case, the effect of interference depended on host distribution and the parasitoid’s arrival and departure rules. Mutual interference did not appear to be important, but

both indirect mutual interference and pseudo-interference reduced parasitoid search rate, their relative importance depending upon host distribution.

Traditionally, parasitoid attack rates (number of hosts parasitised per unit time) are used when considering interference relationships. However, if one is concerned with optimal behaviour, encounter rates should be considered. Visser et al. (1990) and van Dijken and van Alphen (1991) went further and calculated the mean number of realised offspring per female parasitoid per unit of patch time as a measure of individual efficiency. ESS models developed by Visser et al. (1992a) predict that the presence of other females on a patch reduces this efficiency, even when the number of hosts per female is held constant. This interference is not caused by behavioural encounters that decrease the encounter rate with hosts but results from the parasitoids staying for longer on patches and superparasitising.

It needs to be stressed that when investigating interference phenomena, the parasitoid densities used and the host spatial distribution pattern should typically reflect those found in the field. As pointed out by Free et al. (1977), few experimenters take account of this requirement. Nonetheless, deliberately exposing parasitoids to unusual densities can elicit behaviours and aspects of reproductive performance that generate useful insights (e.g., Venkatesan et al., 2009; Sreenivas & Hardy, 2016; Abdi et al., 2020a; Malabusini et al., 2022).

Another factor to consider is the size of the experimental arena. Jones and Hassell (1988) found *per capita* searching efficiencies to be lower in field cages than in laboratory cages and interference to be more marked in the latter, the volume of which was relatively small. Jones and Hassell (1988) attributed the interference to an unnaturally high frequency of encounters between searching parasitoids (*Trybliographa rapae*). The much lower searching efficiency in the field cages was presumably due to the greater opportunities for parasitoids to spend time performing behaviour other than searching in close proximity to hosts.

It should also be noted that not all interactions between foraging parasitoids are necessarily negative. For example, if parasitoids respond to the presence of others by reducing handling time or by avoiding areas previously searched by conspecifics (through patch marking), then ‘positive interference’ may occur (Visser et al., 1999); indeed some parasitoids may even cooperate in host attack (Abdi et al., 2020b, 2020c; Liu et al., 2021).

1.16 Life-History Traits and Foraging Behaviour

1.16.1 Introduction

Insect parasitoids display an enormous diversity of life-histories (Blackburn, 1991a, 1991b; Godfray, 1994; Quicke, 1997; Mayhew & Blackburn, 1999; Jervis et al., 2001, 2003; Traynor & Mayhew, 2005; Jervis & Ferns, 2011; Iwabuchi, 2019; Poelman et al., 2022; Hardy & Godfray, 2023; Chap. 2). Some species have very short development times, can live for only a few days as adults, and emerge with all their eggs ready to be laid, in contrast to other species which develop slowly, can live for several months as adults, and produce new eggs throughout adult life. Some species produce a large number of small eggs, whereas others produce a small number of large eggs. These different life-history traits are associated with differences in searching and host selection behaviour. When designing experiments on parasitoid behaviour, it is important to be aware that this is so. We discuss this in relation to egg production strategy.

1.16.2 Egg Limitation Versus Time Limitation

Given that eggs are costly to produce and allocation to reproductive function will trade off with longevity (Segoli & Wajnberg, 2020, but see Segoli et al., 2018), natural selection can be expected to lead to reproductive strategies that

approach a quantitative match between egg supply and the availability of suitable hosts. An evolved match may become a mismatch if, for instance, host populations gradually decline over ecological time (Couchoux & van Nouhuys, 2014) or mismatches may be due to within-season variation in host availability (Phillips & Kean, 2017). More generally, aspects of environmental variability will typically prevent exact matches, leading to females either running out of eggs before death (egg limitation) or dying with eggs unlaidd (time limitation). Whether egg limitation or time limitation is predominant has been extensively debated. The consensus is that either may occur, depending on the details of the environmental variability (Rosenheim, 2011; Phillips & Kean, 2017).

Parasitoids can be divided into pro-ovigenic and synovigenic species (Sect. 2.3.4). Pro-ovigenic parasitoids emerge with their full potential lifetime complement of mature eggs, whereas synovigenic parasitoids emerge with at most only part of their complement, this fraction varying considerably among synovigenic species (ranging from very nearly one down to zero) (Boivin & Ellers, 2016; Jervis et al., 2001). These different patterns of egg production can be understood as adaptations to differences in the spatial and temporal distribution patterns of hosts (Jervis et al., 2001; Ellers & Jervis, 2003). Pro-ovigenic species are expected to behave in laboratory experiments in a time-limited manner, because even when large numbers of hosts are offered, these numbers do not exceed the number of mature eggs carried by the parasitoid. Conversely, synovigenic species are expected to behave in an egg-limited manner, often exhausting their daily egg supply in a few hours when the number of hosts offered to them exceeds the number of mature eggs in their ovaries (this oversimplifies the difference between pro- and synovigeny; see Ellers et al., 2000, for further details).

Theoretical studies considering stochasticity in host availability have shown it to be a major influence on optimal egg loads, and that the patchy distribution of hosts is a key source of stochasticity (Rosenheim, 1996; Ellers et al.,

1998, 2000; Ellers & Jervis, 2004; 2011), as is temporal stochasticity in reproductive opportunities (Rosenheim, 2011; Phillips & Kean, 2017). If stochasticity is high, investment is shifted away from lifespan to eggs, i.e., towards an optimal egg load that is higher than the expected number of hosts found, and thus a lower incidence of egg limitation. The ability of synovigenic parasitoids to mature eggs throughout life further reduces the incidence of egg limitation and it also reduces the degree to which individuals are time limited (i.e., they have a surplus of eggs but not too many) (Ellers et al., 2000). However, synovigenic females will still experience transient levels of egg limitation (Heimpel & Rosenheim, 1998; Heimpel et al., 1998; Casas et al., 2000; Rosenheim et al., 2000). Further, egg limitation may be ecologically important even when not prevalent, and the population dynamics of the hosts are also likely to influence selection for egg investment strategies (Phillips & Kean, 2017).

From a literature survey of fifteen species, Heimpel and Rosenheim (1998) concluded that egg limitation is common in the field. The results of empirical field studies, however, suggest that only some females experience egg limitation (Weisser et al., 1997; Ellers et al., 1998; Heimpel et al., 1998; Casas et al., 2000; Phillips & Kean, 2017; Segoli & Rosenheim, 2013b). Thus, it appears that parasitoids have evolved strategies that reduce the risk of egg limitation. However, concomitant with these would be an increased risk of time limitation, the risk being heightened by any lifespan cost, of egg production (Ellers et al., 2000). Indeed, West and Rivero (2000), using a sex ratio-based method to measure the relative importance of egg and time limitation among eight parasitoid species, concluded that on average, most species are at an intermediate position along the egg/time limitation continuum, with a bias towards time limitation.

The question of whether time and egg limitation, when observed in the laboratory, reflect the field situation or whether it is an artefact of unnaturally high host densities can be addressed by obtaining some measure of oviposition rate under field conditions, and comparing this with

the average rate of egg production in parasitoids. The outcome of experiments on aspects of parasitoid biology as diverse as patch time allocation, functional responses, host selection, sex allocation, superparasitism or encounter rates, will all depend critically on whether the experimental conditions place the parasitoid under the constraint of time or egg limitation. Either experiments can be run under conditions representing both of these constraints, or an experimental design can be chosen that is relevant to the particular question one is asking. For example, when asking about the performance of a parasitoid immediately following field release, present females in experiments with a superabundance of hosts so that they are egg limited, but when asking about the performance of the parasitoid after the host population has been suppressed below a damage threshold, present females with low densities of hosts so that the parasitoids are time limited. If one is asking evolutionary questions, it is advisable to choose a situation (e.g., range of host densities, host spatial distribution pattern) closest to what the wasps experience most often in nature.

1.17 The Cost of Reproduction

In many studies of time allocation, recognition time and handling time are taken to be the only time costs involved in oviposition. However, as discussed in Chap. 2, a trade-off can exist between reproductive effort and survival (e.g., Thorne et al., 2006). In at least one case, it appears that egg deposition, as opposed to egg production, incurs a survival cost (Sect. 2.8.3).

1.18 Age-Dependent Foraging Decisions

Although parasitoids may have a longer life expectancy when they lay fewer eggs, they do not live forever. The older they become, the less likely they are to survive to another day (e.g., Hardy et al., 1992b; Amante et al., 2017; Jucker et al., 2020). In addition, young adult parasitoids

may be more fecund than older females (De Vis et al., 2002; Riddick, 2003). Because of the diminishing probability of survival with increasing age, parasitoids should become less selective and accept more host types for oviposition (Iwasa et al., 1984). For example, young *Lysiphlebus cardui* preferentially attack second- and third-instar *Aphis fabae*, whereas older wasps show no preference (Weisser, 1994). All other things being equal, older wasps will superparasitise and accept less suitable hosts more readily than younger ones, a prediction that is supported empirically (Roitberg et al., 1992, 1993). One can try to make use of this alteration in behaviour with age in experiments that require parasitoids to oviposit in non-preferred hosts, e.g., parasitised individuals and unpreferred species, or to explore how the subjective value of hosts affects patch defence behaviour (Humphries et al., 2006; Stockermans & Hardy, 2013; Sect. 1.13).

1.19 Foraging Behaviour and Taxonomy

Taxonomists work primarily with preserved specimens and until recently relied heavily on morphological characters to describe species (Gauld & Bolton, 1988; Quicke, 1993). This is in most cases a satisfactory state of affairs, because differences in morphology can often be found, even between closely related species. Sometimes, however, morphologically identical specimens can be collected from populations found in ecologically different situations, e.g., attacking a different host species, occurring on different host plants or in different geographical regions. The question then is whether these populations belong to one species or not: an important question, not only in deciding whether a parasitoid is a specific natural enemy of a target pest, but also because the scientific name of an organism is used in publications.

By comparing the host habitat-finding behaviour and host selection behaviour of different populations, one can establish whether important ecological differences exist between them. Differences in host habitat finding and/or host

species selection can theoretically result in reproductive isolation between the two populations, which occupy different niches by virtue of the differences in their searching behaviour. When interpopulation differences in foraging behaviour are found, one should then determine whether cross-matings are possible. If such matings do not occur either in the laboratory or in the field, it is reasonable to conclude that the populations are separate species.

Vet et al. (1984) discovered *Asobara rufescens* by studying microhabitat location of wasps initially believed to be *A. tabida*. *Asobara rufescens* had until then gone unrecognised and its populations had been considered conspecific with *A. tabida*. Similarly, van Alphen (1980) discovered a new species of *Tetrastichus*, which attacks the twelve-spotted asparagus beetle, *Crioceris duodecimpunctatum*, by showing that it rejected the eggs of *Crioceris asparagi*, the host of *Tetrastichus coeruleus*. Information about the foraging behaviour of insect natural enemies may therefore prove useful in taxonomy and systematics, although this is complicated by behavioural plasticity (Japyassu & Viera, 2002).

1.20 Foraging Behaviour and Host Resistance

1.20.1 Introduction

Not all prey or host individuals are equally worth attacking. It has become increasingly clear that the success rate of natural enemy attack can vary due to host or prey defence. Such resistance may take many forms, but this can be conveniently divided into physiological and behavioural defences.

1.20.2 Physiological Host Resistance

Physiological defences to endoparasitoid attack centre on the innate immune response of insects, which typically involves the parasitoid egg being isolated in a melanised capsule (Sect. 2.10.2); a counter-strategy by parasitoids may be to lay

multiple eggs into the host such that they cannot all be encapsulated (van Alphen & Visser, 1990; Luna et al., 2016; D'Auro et al., 2021). The immune response is not, however, the only means by which hosts avoid the detrimental actions of parasitoids: many herbivorous insects sequester plant secondary chemicals that can be deployed as a means of defence against their natural enemies. *Utetheisa ornatrix*, an arctiid moth, feeds on legumes from which it sequesters pyrrolizidine alkaloids (Eisner et al., 2000). These alkaloids are passed onto the eggs, and this acts as a deterrent against the predatory lacewing, *Ceraeochrysa cubana*. However, the amount of alkaloid passed down to the eggs varies, depending on the host plant the parents have been feeding on. The moth's eggs are laid in batches of about twenty, and the lacewing will sample two or three before deciding to accept or reject the batch of eggs. Since the variation in noxious chemicals within a batch is low, sampling from a small number will provide a reliable indicator of prey quality. If there is considerable variation among batches in alkaloid concentration, sampling from all batches is worthwhile (Eisner et al., 2000).

It has been suggested that such secondary chemicals are more likely to be sequestered by specialist herbivores than by generalists. This leads to the prediction that generalists should be subject to greater levels of attack by natural enemies, and that levels of attack should reflect the presence of the secondary chemicals in the community. In an elegant experiment, Camara (1997) tested the latter hypothesis under natural conditions. Buckeye butterfly larvae, *Junonia coenia*, were reared on plants that contained iridoid glycosides (*Kickxia elatine* and *Plantago lanceolata*) or an artificial medium lacking the defensive chemicals. In the sites where many plants contained iridoid glycosides, fewer larvae that had been fed on the plants were consumed by predators, whereas no differences in predation were found in sites with lower proportions of the glycoside-containing plants (Camara, 1997). As well as individuals varying in the amount of secondary chemicals acquired from host plants, substantial variation among populations is also likely.

1.20.3 Behavioural Defences

Perhaps the classic example of a behavioural defence against predator attack is provided by aphid dropping behaviour (Losey & Denno, 1998a, 1998b, 1998c). Here, aphids drop from the plant in response to predator cues, although this may not always be to the benefit of the aphid, as ground predators will often successfully attack the escapees (Losey & Denno, 1998c). Pea aphids (*Acyrtosiphon pisum*) show genetic variation in dropping behaviour, and this behaviour is influenced by ambient temperature (Stacey & Fellowes, 2002). Aphids can also escape predation by the production of winged morphs in response to the presence of predators (Weisser et al., 1999).

For aposematic prey species, i.e., those with colouration or markings that repel or warn predators of their unsuitability as prey, both physiological and behavioural defences may be intertwined. Tullberg et al. (2000) showed that while two species of lygaeid bugs (*Lygaeus equestris* and *Tropidothorax leucopterus*) are unpalatable to birds, the likelihood of being preyed upon was in part determined by the degree of aggregation of the larvae. Fewer attacks occurred when the larvae were in groups, compared to individual larvae.

Some hosts are similarly able to resist parasitoids by dropping from the host plant (aphids) or jumping away (leafhoppers and planthoppers) and others may aggressively defend themselves (reviewed by Gross, 1993). Dipteran, lepidopteran and coleopteran larvae may wriggle, or otherwise defend themselves. Mealybugs may ‘flip’ the posterior end of their body or throw droplets of honeydew onto parasitoids attempting to parasitise them. Females in the ectoparasitoid genus *Sclerodermus* attack the larvae of wood-boring cerambycid beetles and face a mortality risk of around 20% when attacking small hosts and considerably higher risks when hosts are larger (Liu et al., 2011; Wei et al., 2014; Abdi et al., 2020b, 2020c). Host larvae react violently when attacked and have well-developed mandibles, and often the attacking wasp is bitten in two before it is able to subdue the host with an

injection of venom (Abdi et al., 2020b, 2020c; Liu et al., 2021). The dangers involved in attempting to subdue such hosts are expected to influence the degree of cooperation and competition exhibited by *Sclerodermus* females which, if hosts are successfully suppressed, will go on to produce a communal brood (Tang et al., 2014; Mesterton-Gibbons & Hardy, 2021; Liu et al., 2021).

Irrespective of the means of avoiding or resting attack, it is clear that not all hosts are equal in value to a foraging predator or parasitoid. They vary not only in quality as a resource, but also in terms of the likelihood of their being successfully attacked, and this will vary among individuals, populations and species. Additionally, although much less studied, it is clear that there will also be variation at a similar series of scales in natural enemy ‘virulence’.

1.21 Insect Natural Enemy Foraging Behaviour and Community Ecology

The role of insect natural enemy foraging behaviour in determining community interactions has been implicitly rather than explicitly implicated in many aspects of community ecology. These issues are well illustrated by the work of Müller et al. (1999), who studied an aphid-natural enemy (primarily parasitoids) system in Rush Meadow, an abandoned field in southwestern England. By producing a quantitative food web of the interacting species, Müller et al. (1999) were able to use the web to predict the strength of both direct and indirect interactions within the community. Such webs are immensely time-consuming to obtain but the return, measured in terms of detailed knowledge of the system, is potentially enormous (e.g., Schönrogge & Crawley, 2000; Lewis et al., 2002; Sect. 6.3.12). This web can be used to convincingly demonstrate the concept of apparent competition, where two species that do not directly compete for resources indirectly compete because of shared natural enemies (Holt, 1977; Sect. 7.3.7). Müller and Godfray (1997) tested for apparent

competition between the grass aphid, *Rhopalosiphum padi*, and the nettle aphid, *Microlophium carnosum*, mediated by shared natural enemies. They found that foraging ladybirds were attracted in increased numbers to the experimental site, mainly by the presence of grass aphids. However, the increased numbers of coccinellids preferentially attacked the nettle aphids, providing a clear example of apparent competition (Müller & Godfray, 1997).

Such food webs not only illustrate the importance of indirect effects within a community, but also point to the direct influence of insect natural enemies on community structure. Müller and Godfray (1999) studied why two species of aphids (*Aphis jacobaeae* and *Brachycaudus cardui*), common in surrounding areas, were uncommon in Rush Meadow. By excluding predators from artificially inoculated aphid colonies, they found that the aphids were able to colonise the field but were prevented from doing so by the presence of predators and parasitoids.

Clearly, the foraging decisions and abilities of insect natural enemies will have a significant influence on the community dynamics of any terrestrial ecosystem. Foraging success will often be influenced by the host plant a potential prey or host is attacking. For example, in *Encarsia formosa* (a parasitoid of whitefly), foraging success is greater on glabrous (smooth-leaved) varieties of cucumber (Hulspas-Jordaan & van Lenteren, 1978). In a different field system, recent field studies showed that the sizes and architectures of two plant species fed on by a single host species affects the species of parasitoid that attacks it, such that resource partitioning, parasitoid coexistence, and thus a more complex web, are likely promoted (Xi et al., 2017, 2020). Indirect effects of plants will also be common, as host species reared on poor-quality plants will have reduced population growth rates, and parasitoids emerging from such hosts may be smaller and less fecund (Stadler & Mackauer, 1996), while predators may consume more prey individuals for the same return.

Quantitative food webs also illustrate another important facet of insect natural enemy community ecology. While many predators and

parasitoids are thought to have an extremely wide host range (the fundamental niche), these ignore the effects of host preference or competition, which results in a much narrower range of regularly attacked victims (the realised niche).

From the above examples, it is readily apparent that the foraging behaviour of insect natural enemies is often (within bounds) context-specific, and the range of species attacked will depend on both direct and indirect effects within the community. Moreover, the strength of these interactions may be influenced by the herbivore's host plants. Without an understanding of the natural history of the species of choice, designing laboratory-based systems to assay behaviour is fraught with difficulty. The importance of the community context in trying to understand the foraging behaviour of an insect predator or parasitoid should not be underestimated.

1.22 Concluding Remarks

The study of the foraging behaviour of insect predators and, especially, parasitoids has provided a model system for ecologists for many years. Applied ecologists use such systems in the hope that information obtained from them will inform biological control measures (Wajnberg et al., 2016; Heimpel & Mills, 2017) and link to population dynamics (Godfray & Shimada, 1999; Hassell, 2000b; Segoli et al., 2023; Chap. 7).

Recent decades have seen rapid advances in the study of insect natural enemies, particularly as regards parasitoid behaviour. These developments have mainly been in response to advances in ecological theory. The availability of a whole suite of models of parasitoid–host population dynamics that incorporate important behavioural characteristics of parasitoids, combined with the rapid progress in behavioural ecology, has led to the formulation of more precise and quantitative hypotheses. In addition, tools for the analysis of complex time-series of behaviour have become available, allowing us to address problems that previously could not be analysed properly.

Behavioural studies of parasitoids have been conducted along two main lines: the functional

analysis of behaviour, which has been guided by largely model-based theories on the evolution of animal behaviour, and the causal analysis of behaviour, which has been guided much less by models (Chap. 4). Developments in causal and functional analyses of behaviour have been, for a large part, independent. As we hope to have indicated in this chapter, research can benefit from an increased integration of the study of mechanisms and the study of the function of behaviour.

There is a productive, and indeed synergistic, two-way interaction between theory and empirical research: behavioural and population models can guide us in the design of experiments, while the results of experiments stimulate new theory. Theories of population dynamics and behavioural ecology are now often concerned with the behaviour of parasitoids and predators in spatially heterogeneous environments, with patchily distributed resources. For reasons of convenience, behavioural studies on natural enemies have often been conducted in single-patch environments. Results from experimental studies on the behaviour of natural enemies in multi-patch environments, preferably in natural settings (Heimpel & Casas, 2008), can provide the information needed both to test current theories and to develop new ones.

Along with this call for a meshing of empirical and theoretical ecology is the continuing need for researchers to have a firm grasp of the natural history of the species they are working with. Natural history is difficult, if not impossible, to learn in the lecture theatre or the laboratory, and there is no better way of beginning to understand the ecology of any system than spending time with it in the field. Becoming thoroughly acquainted with one's study organisms must be a prerequisite for any successful research programme.

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