REVIEW

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Foraging behaviour in aphid parasitoids: Spatial scale and resource assessment

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Abstract. This review examines recent research on the foraging behaviour of aphid parasitoids and highlights current knowledge on host location, searching mechanisms and variation in parasitoid performance. In addition, the theoretical relationships between host spatial distribution and parasitoid behaviour are explored. Predictions from this theoretical framework are compared with results from recent experimental studies on foraging behaviour.

INTRODUCTION

In order to be successful, aphid parasitoids need to locate, recognise and attack suitable hosts. This selection process has been viewed as a sequence of behavioural responses to environmental or habitat cues which bring the adult parasitoid into an appropriate habitat and thence into contact with the host. This host selection sequence can be divided into a number of steps: host habitat selection, host location and host acceptance (Doutt, 1964; Vinson, 1976). The foraging behaviour of parasitoids includes all of these steps and thus foraging takes place on a range of spatial scales. As Li et al. (1992) point out, foraging behaviour takes place between patches and within patches; where a patch is defined as a spatial unit of the environment within which resources are aggregated (Hassell & Southwood, 1978; Bell, 1991). So to understand the foraging behaviour of a particular parasitoid species, we need to study: 1) the ways in which the species uses information to localise and assess resources, 2) the mechanisms used in searching and 3) those factors that act as sources of variability (Bell, 1991).

The foraging behaviour of aphid parasitoids has a major effect on the population dynamics of both the parasitoids and the hosts. The patchiness of host populations and the behaviour of the parasitoids should influence the way the patches are exploited. This mini-review examines recent research on the foraging behaviour of aphid parasitoids and highlights current knowledge on host location, searching mechanisms and variation in parasitoid performance. In addition, I explore the theoretical relationships between host spatial distribution and parasitoid behaviour, and examine how the experimental outcomes from current behavioural studies relate to predictions arising from this theoretical framework.

LOCATING RESOURCES

Infochemicals from hosts and their host plants often play a critical role in the foraging behaviour of parasitoids (Vet & Dicke, 1992) and it is clear that some aphid parasitoids respond to volatile chemicals from the food-plants of their aphid hosts (Powell & Zhang,

1983). Powell & Wright (1992) suggest that, in some cases, these plant allelochemicals can play a part in host habitat location and host recognition. They examined the behaviour of four aphidiine species which varied in the extent of their host ranges. In a series of laboratory experiments, these authors showed that the leaves of aphid host plants influenced the attack behaviour of relatively specialised species (*Aphidius ervi* and *Aphidius rhopalosiphi*) but not that of more generalist species (*Aphidius picipes* and *Ephedrus plagiator*). This suggests that host recognition in generalist parasitoid species does not involve allelochemical cues from specific host plants during the examination phase of host selection, whereas host recognition by specialists may include these cues. However, these generalists respond to plant semiochemical cues in olfactometer tests; suggesting that they can be significant in host habitat and host location.

SEARCHING MECHANISMS

Aphidophagous insects search along veins on the lower surfaces and at the edges of leaves where aphids are most likely to be found. Honeydew from these aphid colonies often accumulates on the upper surfaces of leaves below them, as well as in the colonies. These accumulations of honeydew are attractive to parasitoids and can determine the pattern of within-plant foraging (Starý, 1970; Ayal, 1987). In these cases, honeydew acts as a kairomone for parasitoids (Bouchard & Cloutier, 1984; Budenberg, 1990). Responses to honeydew can be very general; for example, Budenberg (1990) showed that *Aphidius rhopalosiphi* responded to the honeydew of a range of aphid species and Bouchard & Cloutier (1984) demonstrated that *Aphidius nigripes* responded to the honeydew from its host and two other species. In the field, these responses may be significant in host habitat location. Gardner & Dixon (1985) showed that *Aphidius rhopalosiphi* searched longer on the leaves and ears of wheat plants contaminated with honeydew compared with non-contaminated plants. While in the species *Ephedrus cerasicola*, individuals were found to accumulate on contaminated plants rather than fresh ones (Hågvar & Hofsvang, 1989).

Most parasitoids respond to honeydew, even if it is from an aphid species outside the normal host range (Table 1). However, the effects of honeydew on individuals are complex. Studies on *Aphidius rhopalosiphi* show that the searching time of females increases with the concentration of honeydew and that searching times are of a similar duration if the source of the honeydew is from aphids feeding on either plants or artificial diets. This suggests that honeydew acts as a within patch searching stimulant (Budenberg, 1990). On the other hand, parasitoid searching time decreases after confinement in environments containing honeydew; indicating that individuals can habituate to these cues (Budenberg, 1990).

TABLE 1. Estimates of mean searching time (seconds) spent by female parasitoids of various species of different origins on filter paper treated with the honeydew of the cereal aphid, *Sitobion avenae*, and on control papers (based on data in Budenberg, 1990).

Species	Honeydew	Control
Aphidius rhopalosiphi	80	8
Aphidius picipes	26	9
Aphidius ervi	26	7
Praon volucre	32	8

Recent studies have investigated the effects of honeydew on parasitoid aggregation. The responses of *Ephedrus cerasicola* were greatest when presented with aphids plus honeydew, compared with honeydew alone or uninfested plants. Budenberg et al. (1992) suggest that this could be attributable to the increased attraction of plants with honeydew to flying parasitoids and increased searching times in these environments. Experiments on *Diaeretiella rapae* show that this species: 1) leaves small plant patches more rapidly than large patches, 2) leaves patches where aphids were absent or rare more rapidly than when they were abundant, and 3) the arrival rate is not dependent on host numbers (Sheehan & Shelton, 1989). Their data show that the departure rate from host patches is important in determining aggregation patterns in aphid parasitoids.

VARIATION IN FORAGING STRATEGIES

Within a species, there may be considerable variation in the foraging behaviour of parasitoids depending on the genetic structure of the population and environmental experience of individuals. In insects, the physiological status of females is a major source of variability in foraging and oviposition behaviour, and part of this variation is driven by egg load (Minkenberg et al., 1992). In the aphid parasitoid, *Monoctonus pseudoplatani*, egg load has been shown to influence the time spent searching, the speed of search, host acceptance and oviposition rate (Collins & Dixon, 1986). More recently, Chow & Mackauer (1992) show that foraging decisions may be influenced by both current and previous experience with hosts.

Non-host factors may also be sources of variation in the performance of individual parasitoids. For example, adults of some species exploit flowers and nutrients derived from these non-host foods may be important in parasitoid foraging (Jervis et al., 1993). Other research has shown that foraging success in aphidophagous insects may depend on plant architecture (e.g. Gardner & Dixon, 1985; Grevstad & Klepetka, 1992). The main factors influencing foraging behaviour are plant structures and leaf surface texture.

INDIVIDUALS AND POPULATIONS

The behaviour exhibited by parasitoids in locating and exploiting hosts has a major effect on the population dynamics of both the parasitoids and the hosts (Hassell & May, 1985; Hanski, 1991). The patchiness of host populations and the behavioural factors influencing the way these patches are exploited determine the rate of immigration and emigration between patches and the birth rates of parasitoid populations. These, in turn, influence the death rates of the host population. Behavioural models, describing the allocation of foraging time in patches of different host densities, incorporate a variety of simple decision making rules. These include foraging by expectation, foraging for a fixed time in each patch, fixed searching time in each patch and encounter rate mechanisms (Waage, 1979; Hassell, 1980).

Host populations are non-randomly distributed throughout habitats, and models describing the dynamics of host/parasitoid populations suggest that aggregation of host populations has a powerful influence on stabilising these interactions (May et al., 1981). It is possible to incorporate simple behavioural models of time allocation to patches of different host density into population models, and to examine the consequences to the host

population of the different generalised behaviour patterns of individual parasitoids foraging for aggregated hosts (Wellings, 1991). The predicted consequences of various time allocation models are broadly similar: parasitism rates should increase with increasing mean host population densities and increasing levels of aggregation. The behavioural models differ in terms of resource use and adaptive significance. However, the different behaviours should have qualitatively similar influences on host population dynamics.

Experimental studies on the effects of host spatial distribution on the patterns of parasitism have rarely been reported (e.g. Jones & Turner, 1987). Table 2 summarises results from one laboratory study on *Aphidius ervi* attacking populations of the blue-green lucerne aphid, *Acyrthosiphon kondoi* (Wellings, unpublished). Individual experienced female parasitoids were released into arenas containing nine stems of lucerne, some of which were infested with aphids. The number of aphids placed in each arena was either 18 or 36 (giving mean host densities per stem of 2 or 4) and these aphids were distributed between stems to conform with one of five spatial distributions, based on the coefficient k from the negative binomial distribution. Variation in the coefficient k was used to describe aggregation: when k is small, populations are aggregated and, when k is large, populations tend towards random distributions. Each host density x spatial distribution combination was replicated five times. All aphids were either second or third instars and were thus suitable hosts.

TABLE 2. The proportion of *Acyrthosiphon kondoi* attacked by *Aphidius ervi* and the mean number of eggs oviposited per female *A. ervi* over a 24 h period (10 h dark : 14 h light).

Spatial distribution	Proportion of hosts attacked		Mean number of eggs/female	
k	2*	4*	2*	4*
0.5	0.26	0.12	14.2	9.4
1.0	0.26	0.18	9.0	13.0
2.0	0.20	0.37	6.0	24.2
4.0	0.08	0.17	3.8	11.6
8.0	0.23	0.41	9.2	15.4
Overall mean	0.20	0.23	8.4	14.7

* Mean host density per patch

The data summarised in Table 2 suggest that there are no systematic trends in parasitism rates relative to variations in the spatial distribution of the hosts. Between a quarter and a fifth of the aphids were parasitised during the exposure period. However, the data in Table 2 show that the mean number of eggs oviposited per female was 8.4 and 14.7 for host densities of 2 and 4, respectively. In other words many of the parasitised aphids in this experiment contained more than one egg or larva. Again, the data show that there were no systematic trends relative to spatial distribution.

The lack of response to variation in host spatial distribution suggests that, for *Aphidius ervi*, host distribution per se may not be a major factor in determining foraging activity. However, experiments of this kind also identify some major problems in designing adequate multi-patch experiments. Generalised experiments can not 1) account for the range of factors that might cause variation in parasitoid performance, 2) determine whether the "experimental patch" is equivalent to a foraging unit for the parasitoid and 3) easily

establish host populations along with appropriate chemical cues. This latter factor is the main weakness of the experiment described here. Aphids were placed on uninfested lucerne cuttings about 8 h prior to the release of the parasitoid. Thus levels of honeydew associated with each patch may have been very low. On the basis of the results of studies described in earlier sections, resource location, assessment and the searching behaviour of aphid parasitoids may be heavily dependent on these cues rather than merely the distribution of aphids.

In addition, the high levels of superparasitism observed in this experiment contrast with field observations on the oviposition behaviour of *Aphidius ervi*, where parasitised hosts containing more than one host are rarely observed. Micha et al. (1992) showed that recently parasitised *Acyrthosiphon kondoi* can remain susceptible to attack by *Aphidius ervi*. Previously parasitised hosts are avoided by female parasitoids about six hours after the first egg is oviposited but until then appear to be acceptable hosts. The experiment outlined here was conducted over a short period and most hosts would have remained susceptible to superparasitism during this period. In the field, local variations in host population age structure and micro habitat differences may act to reduce superparasitism rates. Other laboratory studies have recorded high levels of superparasitism in aphidiine parasitoids (e.g. Cloutier, 1984).

CONCLUSIONS

Most of the studies described in this paper are laboratory experiments dealing with individual level processes. Research on searching mechanisms in aphid parasitoids is well developed and provides a framework for a general model of within-patch foraging. Investigations on locating resources have been conducted less frequently and further work is needed on factors influencing host habitat location. More problematic is the scattered nature of research on factors causing variation in foraging strategies. Here, the literature is fragmented and composed of single studies that have not been followed up. Detailed studies are needed to provide estimates of the variance in parasitoid performance and the sensitivity of host populations to variation in parasitoid performance.

The links between individual level processes that shape foraging behaviour and the predicted population processes are very weak. It seems unlikely that host spatial distribution per se is significant in determining foraging activity. Future studies need to be based on experiments that include the behavioural cues derived from aggregations of hosts. These studies need to incorporate variations in spatial scale and patch history. This poses considerable difficulties but adequate experiments are essential in order to build realistic models of functional responses.

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