Host Location and Selection in the Field

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MOST of what is known about the behavior and ecology of parasitoids has been discovered in the laboratory (Godfray 1994; Quicke 1997), and behavioral field studies of parasitoid species are rare (Waage 1983; Thompson 1986; Casas 1989; Janssen 1989; Driessen and Hemerik 1992; Connor and Cargain 1994; Visser 1994; Völkl 1994; Völkl and Kranz 1995; Heimpel et al. 1996, 1997; Völkl and Kraus 1996; Ellers et al. 1998; Henneman 1998). The lack of knowledge about host searching and host location in the field leads to two legitimate questions about (1) the importance, in the field, of the mechanisms studied in the laboratory and (2) the rationale in the choice of parameters in individual based models of host-parasitoid interactions (see Bernstein, chapter 4).

Foraging behavior in the field can be inferred *indirectly* from capture-recapture data and sampling of host and parasitoid populations. The information available by using this approach is on a time scale ranging from one hour to a generation. The processes of host finding and host selection occur on a much shorter time scale, however, typically of the order of minutes, and requires the *direct* observation of the foraging behavior of females.

In this chapter, I will identify three foraging parameters whose importance have been identified by conducting direct observations of foraging females in the wild. These parameters have been neglected in laboratory and theoretical studies so far. They are (1) the abundance of hosts as perceived by the parasitoid, (2) imperfect foraging cues, and (3) the time available for foraging. My arguments are developed by exploring in detail the few case studies in which parasitoids have been tracked continuously and their behavior recorded. Information about searching behavior in the field as observed in other, less studied, host-parasitoid systems is included when possible. It is my opinion that a deeper understanding of the foraging behavior of parasitic wasps will emerge through a comparative analysis of detailed case studies.

Sampling Rules and Host Abundance

A scientist's sampling rules designed to obtain unbiased estimates of host density may be quite different from those used by foraging parasitoids. We know surprisingly little, except for the two examples described below, about the sampling rules used by parasitoids in the field, and how abundant hosts really are from the point of view of a parasitoid. In the first example, the parasitoid seems to have adopted a sampling strategy very well suited to the distribution of its host. In the second example, the low frequency of encounters with hosts leads to the acceptance of suboptimal hosts. Hence, both examples can be interpreted to show that perceived host abundance and distribution act as strong selection pressures on parasitoid traits related to host searching and host selection in the field. A third example shows how new knowledge about host density and host distribution in the field has changed our understanding of the patch leaving mechanisms of a parasitoid.

The moth *Greya subalba* (Lepidoptera: Incurvariidae) feeds within immature seeds of *Lomatium dissectum* (Umbelliferae) (Thompson 1987). The flowers are grouped into umbellets, commonly with five to fifteen flowers; these umbellets are, in turn, grouped into compound umbels of fifty to two hundred flowers. Until they mature, seeds are held together tightly in pairs, or a "schizocarps." *G. subalba* females lay one—or less frequently, two—eggs per schizocarp, and the larva feeds within the immature schizocarp. Females tend to distribute their eggs broadly among umbellets, so that most umbellets have some larvae and the great majority of plants are attacked to some degree (25%–40% of seeds per plant are attacked). The distribution of attacked schizocarps among umbellets is well fitted by a truncated geometric distribution. The geometric distribution is the discrete analogue of the exponential, and also possesses the Markovian property. This property implies for the parasitoid that finding an attacked schizocarp does not change the likelihood of finding another one. Hence, the moth is distributing its progeny in a way that minimizes the information available to the parasitoid.

Given these circumstances, how should its parasitoid, *Agathis* sp. (Hymenoptera: Braconidae), search for hosts? Searching females seem unable to distinguish seeds with larvae from those without larvae, as the following behaviors show (Thompson 1986). First, the distributions of time needed to check empty schizocarps and to oviposit are similar. Second, the parasitoids did not preferentially probe schizocarps with many hosts. Third, they preferentially probed large schizocarps, but large schizocarps were not more likely to contain larvae. Finally, females did not probe more schizocarps on umbellets in which many of the schizocarps had larvae. In conclusion, *Agathis* has to probe to detect host presence. The distribution of schizocarps probed by *Agathis* is also a truncated geometric distribution, with almost the same mean. This is the only case study in which the sampling strategy of the parasitoid has been studied in relation to its host distribution, and the similarity between the two distributions is striking. However, it remains unclear whether other sampling rules would be better and how the parasitoid perceives host abundance (abundance being defined here as the successful proportion of probes).

In contrast to the previous example, host abundance is best approximated for *Drosophila* parasitoids as the frequency of encounters with hosts per unit time. The density of *Drosophila* on fermenting fruits and sap fluxes in temperate woodlands is low (A. Janssen, pers. comm.). The rate of host finding by the parasitoids *Asobara tabida* Nees (Hymenoptera: Braconidae) and *Leptopilina heterotoma* Thompson (Hymenoptera: Eucoliidae) is normally between one and five hosts per hour, with a maximum of ten hosts per hour. Oviposition does not take much time (about one minute) and the majority of these parasitoids seldom run out of eggs (Driessen and Hemerik 1992; Ellers et al. 1998). Observed females searched most of the time (A. Janssen, pers. comm.), so resting did not affect potential foraging time. Once they find a host, *A. tabida* females accept it readily, almost irrespective of the survival chances of their offspring (Janssen 1989). Hence, the near-total acceptance of hosts can be explained only by the fact that the rate of encounters is so low that there is a marginal fitness gain from an oviposition in a suboptimal host.

These two studies strongly suggest that host abundance, whether perceived or real, exerts a strong selection pressure on traits related to host finding and host selection. The third example shows how knowledge about field situations can make the difference between alternative theories based on laboratory experiments.

Dissection of wild fruits containing the moth *Ectomyelois ceratoniae* (Lepidoptera: Pyralidae), a host of the *Venturia caenescens* (Hymenoptera: Ichneumonidae), revealed that fallen fruits harbor only one, and seldom two, hosts (Driessen et al. 1995; Driessen and Bernstein 1999). A large portion of fruits have no host. Under such conditions, *Venturia* would be best served by increasing its tendency to leave after each oviposition—a "decremental" rule. This result is in contradiction with the incremental model developed for the same species by Waage (1979). This model, which found its way into many textbooks (Krebs and Davies 1984; Bell 1991; Godfray 1994; Begon et al. 1996a), was based on highly unnatural petri dish experiments with host densities several times higher than those encountered in the known field situations.

Imperfect Foraging Cues

Parasitoids use a set of cues associated with their hosts. Examples are semiochemicals from host feces, attacked plants, and visual cues such as galls or mines (Godfray 1994). These cues have been widely studied, the assumption being that a parasitoid using them is at a reproductive advantage compared to a parasitoid searching at random. This assumption is best met when host density is low; metaphorically, any clue is welcome when it leads to a needle in a haystack. High host density may drastically reduce the efficiency of the searching parasitoid due to the distraction caused by unsuitable hosts. Also, unsuitable hosts often produce or trigger the same cues that were so effective at low host densities. However, searching for metallic objects is not really helpful in a haystack full of screws and nails. While the reliability and detectability of different cues have been the focus of much recent work (see Vet et al. 1995 for a review), the constancy in time and space of these cues in the field remains largely unstudied.

The following two field studies identify the declining reliability of cues as a handicap for the foraging parasitoid. In the first case, the decline is due to parasitism itself, introducing a negative feedback effect. In the second case, the necessity to use easily detectable cues for finding hosts at low density actually *inhibits* host-finding at high density, because the parasitoid is constantly arrested by low-quality, unsuitable hosts.

Tentiform leaf miners (*Phyllonorycter* sp., Lepidoptera: Gracillariidae) make very conspicuous spotted mines, which are searched for visually by eulophid parasitoids attacking later larval and pupal stages (Casas 1989; Connor and Cargain 1994). A field observational study showed that *Sympiesis sericeicornis* (Hymenoptera: Eulophidae) is unable to assess the quality of the inhabitant from a distance. It is only after the parasitoid has landed that the time spent and the sequence of behaviors on the mine become functions of the content of the mine. Unsuitable mines may be empty, or contain dead or already parasitized hosts. The percentage of unsuitable hosts increases over time; this is a real problem for those *Sympiesis* that continue to find unsuitable hosts. The problem is exacerbated because the probability of being found is not uniformly distributed over the host population. Hence, while some hosts escape parasitism, others are frequently rediscovered. In the light of the problems faced by *Sympiesis* foraging under those conditions, it is not so surprising that it is able to recognize and reject a dead host in about four seconds, 10% of the time needed for oviposition. Broadly, the same pattern seems to emerge for *Cameria hamadryadella* (Lepidoptera: Gracillariidae), a leaf miner on oak in North America, and its parasitoid *Closerocerus tricintus* (Hymenoptera: Eulophidae) (Connor and Cargain 1994; E. Connor pers. comm.).

Aphytis melinus (Hymenoptera: Aphelinidae), the highly successful biological agent of the California red scale, *Aonidiella aurantii* (Murdoch 1994), forages in two strikingly different habitats within a given tree (pers. obs.). In the outer canopy, host density is very low and the analogy of the needle in a haystack seems appropriate. While foraging on bark, *A. melinus* is literally surrounded by hosts: There are enough suitable hosts within a few square centimeters for *A. melinus* to lay all its daily egg complement in a fraction of the time available for foraging (one oviposition lasts around six minutes; pers. obs.). Given these considerations, *Aphytis* seems surprisingly inefficient, having a mean oviposition rate of 0.6 eggs per hour (Casas et al. 2000).

Part of the explanation of this low realized parasitism rate is that suitable hosts make up a tiny fraction of the total scale population; as much as 90% of the scale are, in fact, dead! Adding the amount of time spent dealing with dead hosts to the time spent searching increases the fraction of the total time spent in searching by only 20%, from 40% to 60%. Thus, handling dead scale is not a major factor determining the oviposition rate. The most likely hypothesis for the inefficiency of *Aphytis* is that the presence of so much dead scale and debris on the bark makes it difficult for *Aphytis* to discover or recognize desirable hosts. The description is valid not only for this species, but also for *Aphytis aonidiae*, a parasitoid of San Jose scale on almond trees. About 21% of scale examined by the parasitoid for more than sixty seconds were dead, and the percentage was much higher for shorter encounters (Heimpel et al. 1996; G. E. Heimpel, pers. comm.). Laboratory studies on *Aphytis* have demonstrated host-size discrimination in the context of host selection, sex allocation, superparasitism and host feeding (Luck and Podoler 1985; Opp and Luck 1986; Walde et al. 1989; van Lenteren 1994; Collier 1995; Morgan and Hare 1997; Morgan and Hare 1998). All of these fine-tuned behaviors become blunted in the field under circumstances such as those described, where finding a suitable host is simply difficult. However, it is a fact that many parasitoid species do make fine-tuned choices in specific situations. Since these choices have consequences in terms of fitness, appropriate behaviors in these situations, even if they are rarely encountered in the field, do matter. The unique contribution of behavioral studies in the field is an estimation of the frequency with which parasitoids encounter these situations. The relationship between field and lab studies will be dealt with again at the end of this chapter.

Other Sources of Foraging Variability

Both the industry of near perfect petri dish experiments and decade-long bivariate host-population dynamics have left the misleading impression that host-parasitoid systems are tightly coupled pairwise interactions occurring in a vacuum. Experience in the field tells quite another story. Parasitoids encounter a range of situations unlike those in laboratory studies: for example, incredibly complex spatial structures of the foraging environment, and microclimatic conditions varying severalfold over very short distances. It is a truism that the foraging behavior of parasitoids is under the influence of many factors. More discomforting is the fact that parasitoid behavior may be sometimes totally unrelated to host and parasitoid population densities, as the next preliminary results show.

In order to explore the relationship between aggregation of searching parasitoids, host density, and parasitism rate in the field ("spatial aggregation of parasitism"; for a review, see Hassell and Wilson 1997, and Bernstein, chapter 4), twenty-three leaves at the interior of a single grapefruit tree were tagged and the number of *Aphytis* spotted on the leaves counted every hour during one day from the onset to the end of activity. There was no relationship between the total number of visits per day on a leaf and the number of unparasitized hosts, the number of live scale of all stages and the total number of scale (live, parasitized, and dead scale). Only five *Aphytis* eggs were recovered. Three were laid on the same leaf, which was not among the highly visited ones. Given the lack of relationship between *Aphytis* behavior (visits and ovipositions) and host population size on the different leaves, one may tentatively conclude that leaves were chosen at random. However, a statistical analysis showed that visits to the different leaves were not at random, but slightly aggregated (data from the first day $CV = 1.28$, mean $= 2.4$, $S.E. = 0.64$, $n = 23$). An extension of the experiment over two days for six of the original leaves rejected the hypothesis of random visits. The ranking of visits between leaves over the two days was very similar (table 2.1).

The sum, over the six leaves, of the absolute differences between the daily visits is a good measure of constancy of attractiveness of leaves over two days. The smallest possible sum of differences is four, as we observed ten visits the first day, and fourteen visits on the second day. The observed sum of differences is six. There is a single permutation able to produce a sum of differences of four (permuting the visits of leaves four and five on the second day). The other 718 permutations of the number of visits on the second day produce larger sums. The probability of observing a sum of differences smaller than or equal to six by randomly assigning visits to leaves is 0.003. While a lack of dependence of parasitoid aggregation and parasitism rate on host density is rather frequent ("host-density-independent heterogeneity"; see Hassell and Wilson 1997 for a review, and Smith and Maezler 1986 for similar results on the same system), these field observations show that para-

TABLE 2.1
Number of Visits by *Aphytis melinus* to Six Leaves over Two Consecutive Days

Leaf Number	*1*	*2*	*3*	*4*	*5*	*6*	*Total*
Day 1	6	1	0	2	0	1	10
Day 2	7	1	0	1	4	1	14

sitoids visit specific host patches preferentially and repeatedly, for reasons apparently independent of host density.

Time Available for Foraging

Climatic conditions, such as temperature, wind, and rain, strongly determine the foraging window available to parasitoids. Daily activity of parasitoids in the field has hardly been studied (but see Völkl and Kranz 1995), despite its obvious importance for behavioral ecology and population dynamics of host-parasitoid systems. The mean and variance in the extent of the foraging window determine the rate of oviposition and, thereby, the parasitism rate. This was demonstrated in a recent study by Weisser and colleagues (1997). They first studied the impact of climatic conditions on the length of foraging activity of *Aphidius rosae* (Hymenoptera: Aphidiidae), an aphid parasitoid, in the laboratory. Using weather data from Bavaria and a set of assumptions, they then estimated the realized fecundity of this species in the field. Although some individuals could reach their full potential, which is more than nine hundred hosts parasitized, most were predicted to perform poorly. The average could be as low as eighty to one hundred if unfavorable weather is included in the model.

Given that the quantification of the daily foraging window of parasitoids based on behavioral observations in the field is exceedingly rare, the following preliminary results are worth presenting. In a study on *Aphytis melinus* attacking red scale, I scanned the bark of the lower portion of a tree visually for *Aphytis* for six minutes every hour from the onset of activity on two separate days. *Aphytis* forages at the interior of trees (bark and a few twigs) for only a few hours per day (figure 2.1). Somewhat more time is spent in the outer canopy, but the exact extent of the increase is unknown. The reasons for such a restricted use of total available time to a few hours are unclear, but could be related to lower light intensities in interior portions of trees and to lower temperatures. When females forage for six hours, models of egg load dynamics based on field experiments predict that between one-third and one-half of the population of *Aphytis* run out of eggs at least once during the foraging period (Casas et al. 2000; see also van Baalen, chapter 8). Restricting the foraging window to four hours reduces the egg-limited proportion of the population to one-quarter. In contrast, more than half of the population experiences egg limitation when the foraging period is extended to eight hours (pers. obs.). Given the current debate about the dichotomy of time and egg limitation strategies (Collier 1995; Getz and Mills 1996; Rosenheim 1996; Heimpel et al. 1996; Heimpel et al. 1998; Mangel and Heimpel 1998; Ellers et al. 1998; Rosenheim 1999; Sevenster et al. 1998;

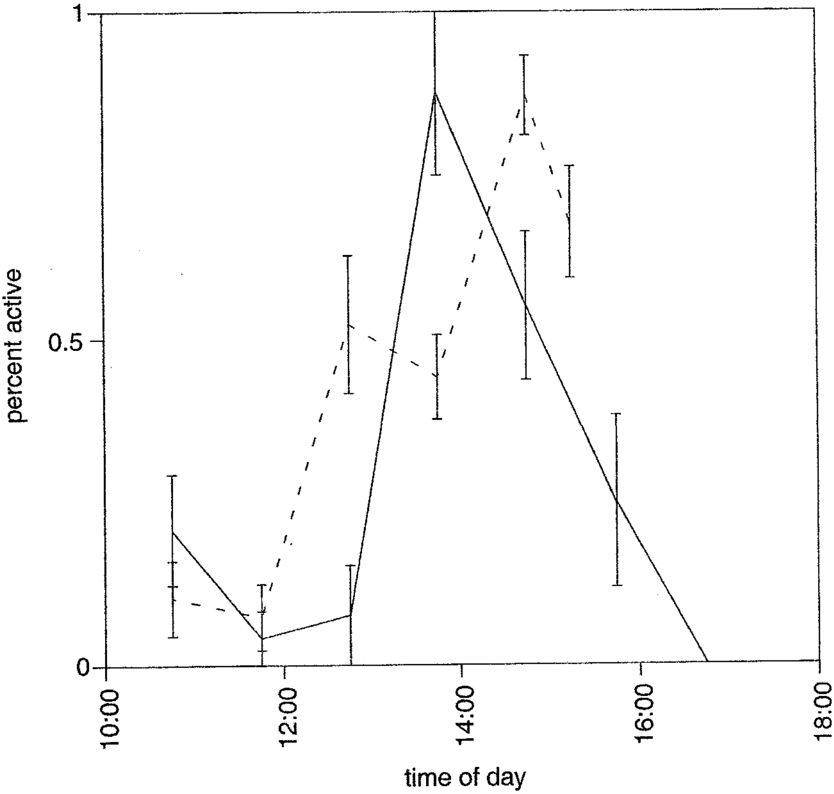

Figure 2.1. Percentage of foraging *Aphytis melinus* on bark on each of two sampling days (*solid line*, October 23, 1994; *dashed line*, October 30, 1994).

see also van Baalen, chapter 8), hard data such as these are urgently needed to keep theoretical arguments rooted in reality.

Field versus Laboratory Experiments

In this chapter, I have argued that field observations provide a unique understanding of host searching and host selection in four ways: (1) by identifying new and important processes and parameters we ought to study in the laboratory and include in our theoretical models; (2) by confirming and reconsidering the role and importance of widely established processes; (3) by distinguishing between alternative theories developed in the laboratory or through theory; and (4) by producing a priority list of all the parameters and processes that require our attention.

Given the obvious benefits of field behavioral studies, one may wonder how laboratory experiments fare compared to them. In the context of behavioral studies conducted in an evolutionary mindset, laboratory experiments are ideally suited to explore how effective parasitoids are at solving particular problems and the way in which they solve them. Care has to be taken in the interpretation phase, in particular when referring to "the natural conditions" under which a particular trait may have evolved. I regard a combination of field and laboratory experiments as the most promising approach.

It is fair to recognize that field studies have their own set of limitations. Small sample size is an obvious one. The insidious consequence is that one requires situations (e.g., patches, time of the year) characterized by high densities of hosts and parasitoids in order to obtain a reasonable sampling size. This, in turn, may lead to a biased view of the conditions usually encountered by a foraging parasitoid. Studying rare species and species occurring at low densities is a daunting task, even though the great majority of host-parasitoid associations probably are of these types.

Conclusions and Future Directions

The future for field studies is bright because technology continues to provide better experimental apparatuses, and because there is ample room for originality in how this technology is employed.

Among the battery of new technologies available for field studies, I see miniature chemical and physical sensors able to characterize the environment in which parasitoids forage in real time, I see ever-smaller tracking devices, and I see long-distance microscopes enabling the observation of a foraging parasitoid at a distance of several meters. Some of these tools do already exist: insects as small as tachinid flies (yes, parasitoids) can be tracked using harmonic radar (Roland et al. 1996), a miniature accelerometer as light as 0.08 grams can be placed on large leaves without perturbing the field of vibrations, the body temperature of a parasitic wasp can be measured at a distance of three meters (by combining an infrared CCD to a Questar long-distance microscope resolving 12 microns at three meters), and portable electroantennograms, which are about one hundred times more sensitive than gas chromatograph measurements (Metcalf 1998) are now being commercialized (van der Pers and Minks 1998).

At an even more challenging level, there is plenty of opportunity for original contributions linking field studies and laboratory work. After a long, unfinished, but necessary period of observational studies in the field, it is encouraging to see manipulative studies now being conducted (Waage's 1983 pioneer study was partly manipulative). The reverse can (and should) also be done: catching wild foraging females and conducting pseudo-laboratory experiments on the spot, employing well-defined, controlled protocols.

Despite these exciting perspectives, I do not see the number of field observational/manipulative studies increasing dramatically over the next several years. The highly unbalanced ratio of field studies to laboratory and theoretical studies will remain constant. The main reason for this is that field studies are particularly difficult and time-consuming. The optimistic conclusion is that studies on the behavioral ecology of parasitic wasps in the wild will continue to be a rewarding field of investigation for the scientist inspired by challenging tasks; indeed, we need much more fieldwork to make our understanding of host-parasitoid interactions approach reality.

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