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Parasitoid foraging and oviposition behavior in the field

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Abstract

Since parasitoids can be reared from their hosts and leave evidence of parasitism after they emerge from hosts, some general outlines of their foraging behavior can be inferred from field studies that do not involve direct observation. However, direct observations are often needed to uncover critical aspects of patch use, host finding, and host use. Studies of parasitoid foraging in the field utilizing direct observation were rare until relatively recently. However, a nascent literature on parasitoid foraging in the field can now be identified that is shedding some light on how parasitoids allocate their time in the field and what they do when they encounter hosts. These studies have been performed on a variety of parasitoids in natural as well as agricultural systems. They range from observations of host-species selection by *Drosophila* parasitoids foraging in fermenting fruits and sap fluxes in Dutch woodlands to investigations of the amount of time that parasitoids of stem-boring Lepidoptera will wait for their concealed hosts to emerge from within corn plants in the USA, and a number of other interesting studies. In this chapter we review studies of parasitoid behavior in the field, focusing primarily on the implications of these behaviors for density-dependent parasitism and optimal foraging.

3.1 Introduction

In this chapter we consider the foraging and oviposition behavior of adult parasitoids in the field. While the ease with which parasitoids can be studied in laboratory settings has made them superb subjects for testing some aspects of foraging and evolutionary theory, field studies have lagged behind laboratory studies. This has in some cases made it difficult to interpret the results of laboratory studies or to put them into a realistic context. One problem with relying primarily on laboratory data to test foraging theory is that parasitoid behavior is often context dependent. Indeed, laboratory studies are the primary means by which this context dependence has been demonstrated. A classical example is the body of work from the laboratory showing that female parasitoids allocate increasing fractions of sons to hosts as the foundress number increases under conditions of local mate competition (Hamilton 1967, Hardy 1994). We know very little about sex allocation decisions by females under field circumstances, including the underlying conditions thought to influence behavior.

A second problem with relying on laboratory studies is that such studies are much better at telling us what parasitoids can do rather than telling us what they actually do. For example, hundreds of elegant laboratory studies have demonstrated the extent to which parasitoids use olfactory cues to locate hosts and host habitats (Vet & Dicke 1992), but we are relatively ignorant of the extent to which olfactory or other cues are used by parasitoids foraging freely in the field (Sheehan & Shelton 1989, De Farias & Hopper 1997).

However, recognition of the paucity of field-based studies of parasitoid behavior has been growing (Hardy et al. 1995, Casas 2000) and the situation is improving. Thus, we are able to review a number of studies in this chapter that are improving our understanding of what parasitoids do in the field. Most of the advances that we review have come from an increasing willingness of researchers to conduct observations of parasitoids foraging in the field over the past two decades (Casas 2000). Advances in our understanding of parasitoid dispersal have also come from new developments in insect marking methodologies (Hagler & Jackson 2001, Lavandero et al. 2004, Wanner et al. 2006), but a review of parasitoid dispersal is outside the range of this review. Similarly, the adoption of biochemical tests that can be used to infer the feeding status of field-caught parasitoids has improved our understanding of sugar feeding by parasitoids in the field (Casas et al. 2003, Heimpel et al. 2004, Heimpel & Jervis 2005, Lavandero et al. 2005, Lee et al. 2006), which we also do not cover here (see also Chapter 7 by Bernstein and Jervis). Finally, we do not cover field studies of mating behavior (Crankshaw & Matthews 1981, Tagawa & Kitano 1981, Antolin & Strand 1992, Field & Keller 1993).

Rather, this chapter is organized around two topics that have received attention over the past few decades with respect to investigations of parasitoid oviposition and foraging behavior in field settings. The first of these is spatial density-dependent parasitism. Here we will discuss the role that field behavior studies have played in contributing to the long-standing quest to determine the mechanisms leading to density-dependent parasitism rates. In particular, we will discuss aggregation to patches of high host density and behaviors once patches are found. Second, we will focus on reproductive strategies, concentrating on behaviors that parasitoids engage in once hosts have been found. Much of the progress in this area has been centered on tests of state-dependent foraging models (see also Chapter 2 by van Baalen and Hemerik and also Chapter 15 by Roitberg and Bernhard). In addition though, females of some parasitoid species experience difficulty in identifying whether hosts are dead or alive in the field. We deal with this point in more detail in the chapter as well.

3.2 Density dependence

By regressing the parasitism rate against the host density found at various locations, we can determine whether parasitism is positively density dependent, inversely density dependent, or density independent in a spatial context. While the link between density dependence and population dynamics certainly provides a good reason to document patterns of density dependence for their own sake (Hassell 2000, Murdoch et al. 2003), we would also like to know how particular patterns of spatial density dependence are achieved in the field. For instance, positive density dependence can come about through aggregation of many parasitoids to sites of higher host density or through an increased per capita search rate in areas of higher host density. However, the examination of patterns of parasitism cannot help us to distinguish between these two explanations. Similarly, two explanations are available for inverse density dependence: handling time limitation and/or egg limitation at higher host densities. Examination of parasitism rates cannot distinguish between these two hypotheses either. Thus, while parasitoids offer great advantages for detecting patterns of density dependence, a more detailed understanding of behavior in the field is necessary to understand the determinants of density dependence.

In the following paragraphs we review case studies that employed direct observation of parasitoids foraging in the field to explore the determinants of density dependence. We deal specifically with three questions that are germane to this topic. First, we ask whether parasitoids aggregate to patches of higher host density. Second, we ask whether parasitoids endeavor to use as many hosts as possible in a patch once it is found or whether they tend to spread their reproductive effort over multiple host patches. Finally, we ask whether female parasitoids lay more eggs at higher host densities.

3.2.1 Do parasitoids aggregate to patches of higher host density?

A pioneering study in this area was done by Waage (1983) who used binoculars to census naturally occurring *Diadegma* spp. foraging on Brussels sprouts plants in the field that were artificially infested with various densities of diamondback moth larvae. Waage (1983) did document aggregation of *Diadegma* to plants with higher host densities, but the rate of parasitism was density independent, hovering around 70% for all host densities tested. These results were corroborated by a similar study done at the same site by Legaspi and Legaspi (2005). Waage (1983) posed two hypotheses to explain the lack of positively density-dependent parasitism despite aggregation. The first was higher rates of superparasitism at higher densities, a hypothesis he was able to reject using host dissections and the second was increased devotion to non-searching activities at higher host densities. These activities could include host handling time or mutual interference with conspecifics. Using both field and laboratory observations, Waage (1983) rejected the mutual interference hypothesis, but concluded that handling time could indeed have limited oviposition rates at the highest densities (Wang & Keller 2002). Increased handling time at higher densities typically leads to a type II functional response and so inverse density dependence (Hassell 2000), but the combination of handling time limitation at higher densities and aggregation could, in principle, lead to density-independent parasitism, as observed by Waage (1983).

A few other studies have recorded the density of adult parasitoids in patches of hosts that varied in density. Two behavioral studies of host finding in leafminer parasitoids conducted in the field found that parasitoids disproportionately visited leaves with higher miner densities (Casas 1989, Connor & Cargain 1994). However, in the case of *Closterocerus tricinctus*, the proportion of leafmines visited per leaf decreased with increasing miner density and the per-leaf parasitism rate was inversely density dependent (Connor & Beck 1993, Connor & Cargain 1994). This result was explained by the effects of mutual interference: increasingly more time was spent handling and rejecting previously parasitized hosts as the density increased. On the other hand, Thompson (1986) found that the attack rate of *Agathis* sp., a braconid parasitoid of a seed-mining moth, was not related to host density but, in this case, aggregation to patches of varying host density was not quantified. Umbanhowar et al. (2003) recorded females of the tachinid *Tachinomyia similis* foraging freely on patches of western tussock moth larvae feeding on lupine bushes in coastal California. These researchers found both aggregation to patches of higher host density and patterns of positively density-dependent parasitism. They also performed separate studies showing that the per-parasitoid attack rate decreased with host density, an effect that would, on its own, lead to inverse density dependence. Thus, it appears that, in this case, the aggregative response of the flies was strong enough to overcome a decelerating functional response to maintain an overall pattern of positive density dependence. The precise behavioral mechanism(s) leading to aggregation were not identified, however. For example, it is not known whether the observed aggregation was due to higher arrival rates, lower leaving rates at patches of higher host density, or both.

The question of arrival versus leaving rates was broached by Sheehan and Shelton (1989), who observed the aphid parasitoid *Diaeretiella rapae* on seven artificially prepared patches of cabbages near a cabbage field. These included one patch of 40 plants, one of 20 plants, one of 10 plants, and four patches of five plants. All of the patches with the exception of two of the five-plant patches included one cabbage aphid-infested plant for every four aphid-free plants. The sample size in this study was clearly small, so the results have to be viewed with caution, but the authors found no evidence for aggregation to either high-density patches of plants or to plant patches that included aphid-infested plants or not. In contrast, *D. rapae* tended to stay longer on plants with higher aphid densities and also in patches with more rather than fewer plants. These observations, although best considered preliminary because of the limited sample size, are consistent with random host finding followed by density-dependent host-patch leaving tendencies. Unfortunately, no estimates of density-dependent parasitism were made in this study.

Using direct hourly observations of *Aphytis melinus* in the field over the entire foraging period on 23 citrus leaves containing various densities of California red scale insects, Casas (2000) noted that the number of parasitoids aggregating on leaves was not related to the number of hosts on leaves nor to the number of eggs laid on single leaves. There was also no correlation between the number of hosts and the number of eggs laid. In fact, only five eggs were laid during the observations and they were all laid on the same leaf, which was itself not the most highly-visited leaf. These observations are consistent with previous findings of density-independent parasitism by *A. melinus* at the scale of the leaf, fruit twig, and whole tree (Reeve & Murdoch 1985, Reeve 1987). Field entomologists know all too well that certain spots in the wild will be highly attractive to butterflies and other insects over many years and generations. The mechanisms responsible for such fined-tuned behavioral preference represent a novel field of study beyond parasitoids. In addition to biotic factors such as resource abundance, a complex mix of abiotic factors such as the color of light in the immediate surroundings and the presence of particular architectural features of the physical environment, among others, may be at play as well.

White and Andow (2005) used a creative approach to manipulate host densities. They planted conventional (non-Bt) corn plants into a Bt-corn field in patches of different sizes. Since the Bt corn is toxic to the European corn borer *Ostrinia nubilalis*, while the non-Bt corn is non-toxic, the non-Bt patches could be expected to have higher host densities than the surrounding Bt corn (Orr & Landis 1997). To make sure, White and Andow (2005) also out-planted corn borers onto these plants. Using this method, they created replicated patches of 2, 8, and 32 plants that had much higher per-plant corn borer densities than the surrounding corn plants. Into this field they released about 10,000 laboratory-reared *Macrocentrus grandii* (Hymenoptera: Braconidae), a specialist parasitoid of the European corn borer. Surveys of *M. grandii* foraging on the patches of three sizes were made and these observational data were compared to parasitism rates. In this case, no aggregation to high densities was detected, yet parasitism rates were positively density dependent and the number of *M. grandii* found foraging in a plot was not a good predictor of the parasitism level in that plot. The authors concluded that the survey observations were an insensitive measure of parasitoid aggregation since survey times were relatively short. The determinants of the density-dependent parasitism found in this study therefore remain unknown.

We conclude this section by reviewing a set of studies that investigated the relationship between parasitoid aggregation and density-dependent parasitism involving cleptoparasitoids of solitary ground-nesting sphecid wasps. The parasitoids considered in these studies include chrysidid wasps and sarcophagid flies and the studies were done in the spirit of the classical observations of hunting wasps done by comparative ethologists dating back to the work of J-H. Fabre and N. Tinbergen (for general reviews of this body of work, see Tinbergen 1958, Crompton 1987, Evans & O'Neill 1988). The most complete studies of this kind were those of the chrysidid *Argochrysis armilla*, a cleptoparasitoid of *Ammophila* ground-nesting hunting wasps. Parasitoids foraging freely for nests of *Ammophila* to oviposit into were observed in natural settings by Rosenheim (1987a,b, 1988, 1989, Rosenheim et al. 1989) and manipulative field experiments showed that *Argochrysis* oriented to *Ammophila* nests using visual cues and also that they used landmarks to locate the nests (Rosenheim 1987a). Rosenheim (1989) also found that, while *Argochrysis* consistently aggregated to sites of local *Ammophila* nest density, patterns of parasitism showed density dependence in only one of 2 years where this was investigated. To investigate aggregating foraging more thoroughly, Rosenheim et al. (1989) regressed the abundance of foraging *Argochrysis* females onto *Ammophila* nest abundance at 13 spatial scales and were able to determine that the parasitoids aggregated to patches of higher host density at the spatial scale of 3–50 m^2. Strohm et al. (2001) obtained a similar result by using field observations of a chrysidid parasitoid of beewolves. They found positive density-dependent foraging at a spatial scale of 16 m^2, but not at 4 m^2. In their study, parasitism was positively density dependent when measured at a site different from the site at which wasp behavior was monitored, but evaluations of both factors at the same site were not possible. For parasitoids of ground-nesting wasps, density-dependent foraging can occur in conjunction with positively density-dependent, inversely density-dependent, and density-independent patterns of parasitism (Wcislo 1984, Rosenheim 1990, Strohm et al. 2001). Thus, this microcosm of field behavioral studies on host–parasitoid interactions confirms the theoretical expectation that behavior cannot be inferred from patterns of parasitism (Hassell 1982, Morrison 1986) and that aggregation to patches of high host density does not necessarily lead to positive density dependence (see also Chapter 13 by Bonsall and Bernstein).

3.2.2 Do parasitoids exploit all hosts in a patch?

Host patch use should be related to density dependence (see also Chapter 13 by Bonsall and Bernstein). Increased residence and oviposition times in larger patches have the potential to lead to positive density dependence, while inverse density dependence is a likely outcome when parasitoids provide equal time and/or eggs to host patches regardless of their size. Host patch use as a determinant of density-dependent parasitism has been studied using field observations or similar techniques for a number of host–parasitoid systems, as reviewed in the following paragraphs.

A study of the relationship between the reproduction of the mymarid parasitoid *Anagrus delicatus* (= *Anagrus sophiae*) in the field and the size of host patches revealed an initially puzzling pattern: individual females oviposited into a small fraction of the hosts in each patch encountered, leaving many apparently high-quality hosts unparasitized and spreading their eggs over a series of host patches (Cronin & Strong 1993). Similar patterns were seen for the congener *Anagrus columbi* (Cronin 2003). Per capita field oviposition rates in this study were not estimated based upon direct observation, but by capturing parasitoids as they were entering host patches and comparing these catches to the numbers of parasitoid eggs found per patch to arrive at an estimate of the per capita eggs laid. Cronin and Strong (1993) called this pattern of host use 'substantially submaximal oviposition' and argued that it contributes to the general pattern of density-independent parasitism found by *A. delicatus* in the field (Stiling & Strong 1982, Strong 1989, Cronin & Strong 1990). This observation of submaximal oviposition by *Anagrus* in the field has led to interesting discussion and insights. Cronin and Strong (1993) originally interpreted the pattern as an example of risk spreading (or 'bet hedging'), where the strategy of spreading eggs over multiple patches is favored as a response to a high rate of catastrophic patch failure. They documented that 20–30% of the host-plant leaves senesced in the field, leading to the death of all host eggs and any parasitoids developing in them. The argument then was that the high variability in such patch failure selected for a strategy (risk spreading) that decreased the variance of fitness at the cost of a lower arithmetic mean per-female fitness. Their field and laboratory experiments were able to exclude a number of other potential factors that could explain submaximal oviposition, including egg limitation, long handling times, host refuges, variation in host quality, and parasitoid density.

Cronin and Strong's (1993) risk spreading theory proved to be controversial, however. Godfray (1994) doubted that risk spreading alone could account for *A. delicatus* behavior because the risk in this system would purportedly be spread out spatially and not temporally, as is the case in classical models of risk spreading (Hopper 1999, Hopper et al. 2003). Some other researchers have also proposed possible reasons for submaximal oviposition in this species. Rosenheim and Mangel (1994) noted that *A. delicatus* was reportedly unable to discriminate between parasitized and unparasitized hosts and they constructed an optimality model showing that the risk of self-superparasitism alone could explain the oviposition patterns documented by Cronin and Strong (1993) (see also Chapter 8 by van Alphen and Bernstein for details on the discrimination abilities of parasitoids). In addition, Bouskila et al. (1995) concentrated on the fact that a fair number of hosts were probed and then rejected by *A. delicatus*, leading to the suggestion that differences in host quality did exist and could explain at least some of the submaximal oviposition rates. Other possibilities that have been hypothesized to lead to submaximal patch utilization by parasitoids include avoidance of density-dependent hyperparasitism or predation (Ayal & Green 1993, Mackauer & Völkl 1993) and reducing the risk of inbreeding among offspring.

Further studies by Cronin and Strong (1999) showed that *A. delicatus* parasitize more hosts per patch after bouts of long-distance dispersal than the more typical dispersal bouts of 10 cm or less. These authors found that *A. delicatus* depleted their entire egg load on a single host patch if it was more than 250 m from other hosts. Similarly, *A. columbi* depleted 60% of their egg load on a single patch when arriving at patches located at least 25 m from a source of parasitoids and hosts versus 30% in the source itself (Cronin 2003). Thus, it appears that the parasitoids perceive the lower opportunities for future reproduction on these far-flung patches and adjust their oviposition strategy accordingly. The inevitable outcome will be some level of self-superparasitism given the inability of these parasitoids to discriminate between previously-parasitized hosts but, as Rosenheim and Mangel's (1994) model suggested, this cost should be accepted under conditions of time-limitation.

A second example of what could be termed under-exploitation of host patches comes from aphid parasitoids. Völkl (1994) conducted field observations of *Aphidius rosae* that were manually released onto patches of rose aphids that varied in size from 19 to 42 individuals. He found that *A. rosae* females were more likely to alight on parts of the rose bushes that had aphid colonies on them and spent more time on shoots and bushes with aphids rather than without aphids. However, the parasitoids laid, on average, only 2.8 eggs per colony and the number of eggs laid, residence time in the colony, and the oviposition rate were all unrelated to colony size. This lack of a relationship was found at the spatial scales both of single shoots and whole rose bushes and led to an inversely density-dependent pattern of parasitism at both spatial scales. Völkl (1994) explained this by noting that the inter-patch travel times were very short in this case, leading to an expectation of low patch utilization (Weisser et al. 1994). Similar patterns were observed for another aphid parasitoid attacking the grey pine aphid, *Schizolachnus pineti*, in the field (Völkl & Kraus 1996).

Another interesting case of what could be considered early patch leaving was uncovered by van Nouhuys and Ehrnsten (2004) for the specialist ichneumonid *Hyposoter horticola* attacking eggs of the Glanville fritillary butterfly *Mellitaea cinxia* throughout an archipelago of dozens of small islands in southern Finland. Laboratory studies showed that host eggs are only susceptible to parasitism by *H. horticola* when within a few hours of hatching. In the field, host eggs are laid in large batches of 100–200 and mature slowly and asynchronously so that, at any given moment, only a small fraction of eggs are susceptible to parasitism. van Nouhuys and Ehrnsten (2004) conducted field observations and other experiments suggesting that *H. horticola* females monitored host egg masses as they matured and returned to masses once they had eggs that were susceptible to parasitism. They suspected that *H. horticola* uses spatial learning of the kind documented in hunting wasps and the parasitoid *A. sarmilla* (Rosenheim 1987a) to locate host patches. This behavior, along with generally high mobility by *H. horticola* females (van Nouhuys & Hanski 2002, van Nouhuys & Ehrnsten 2004) is the likely explanation for a relatively constant rate of parasitism of *M. cinxia* by *H. horticola* over both time and space, a pattern that is not typical for a specialist parasitoid.

3.2.3 Are more eggs laid at higher host densities?

For the last topic of this section, we focus on a system in which an attempt was made to determine the relationship between oviposition behavior and host density. Adults of the thelytokous *Aphytis aonidiae* were collected in the field while foraging on almond trees infested with San Jose scale, the primary host of *A. aonidiae*. The parasitoids were put on ice in the field and brought to the laboratory for egg load dissections and the per-tree San Jose scale density was estimated (Heimpel & Rosenheim 1998). Observations of behavior were also made and these will be discussed below, but in this section we focus on the relationship between egg load and host density. Since the oviposition rate is expected to be higher at high host densities, it is predicted that egg loads will decline with host density (Rosenheim 1996). Contrary to this expectation, however, host density had no effect on the egg load of *A. aonidiae*. One hypothesis to explain this result involves a previous observation that these parasitoids (and other *Aphytis* species) are more choosy with respect to hosts that they use for oviposition in the field and laboratory as their egg load (number of mature eggs) declined (Rosenheim & Rosen 1991, 1992, Collier et al. 1994, Rosenheim & Heimpel 1994, Heimpel & Rosenheim 1995, Heimpel et al. 1996, Casas et al. 2004). Thus, it was hypothesized that lower oviposition rates at lower egg loads could weaken or even eliminate the relationship between the egg load and host density. This hypothesis was tested using a dynamic state variable model, which confirmed that egg loads should drop with increased host encounter rates and that increased choosiness at low egg loads (dynamic behavior) could weaken but not eliminate this relationship (Mangel & Heimpel 1998). So it is still not clear why no relationship was found between the egg load and host density in *A. aonidiae*. Remaining hypotheses include the possibility that the host density was measured at an inappropriate scale to detect density dependence of the egg load, mutual interference of parasitoids at high host densities, and the possibility that egg maturation rates are higher at higher host densities (Rivero-Lynch & Godfray 1997, Wu & Heimpel, 2007).

3.3 Reproductive strategies

Individual host-based patterns of parasitism, such as brood size and offspring sex ratio, can be discerned simply by collecting parasitized hosts in the field and either dissecting them or rearing them out in the laboratory. This can give clues to the reproductive strategies that parasitoids are employing, but the per capita behavior may remain unknown since we do not know how many female parasitoids visited the hosts that have been collected. Thus, it will not be clear whether a given number of offspring per host reflects clutch size or superparasitism decisions (even in solitary parasitoids) (Rosenheim & Hongkham 1996) although, under conditions of low parasitism rates, superparasitism can in some cases be considered unlikely (Bezemer & Mills 2003). Similarly, the number of foundresses contributing to the overall sex ratio produced by a collected host is unknown. Exceptions to this are cases where genetic methods can be employed to differentiate between the offspring of different females within a host. For example, Edwards and Hopper (1999) used molecular markers to show that more than a single female of the polyembryonic parasitoid *Macrocentrus cingulum* (= *M. grandii*) routinely contributed to single hosts. The high levels of superparasitism that they uncovered, along with the relatively low overall parasitism rates, supported the hypothesis that the hosts of *M. cingulum* (larvae of the European corn borer) were only available for short portions of their life cycle and invulnerable to parasitism for a large fraction of their larval life. Unfortunately, the use of genetic analyses for assessing parasitoid reproductive strategies in the field is not well developed.

In this section, we will review a number of studies that have used direct observations to uncover parasitoid oviposition strategies. We first discuss host species selection, then the complications that can arise when numerous dead hosts occur alongside living hosts and the influence of physiological state on oviposition behavior in the field and we finish by discussing optimal patch use in the field.

3.3.1 Host species selection in the field

In a pioneering study using direct observation in the field of a relatively small parasitoid, Janssen (1989) followed females of *Asobara tabida* and *Leptopilina heterotoma*, both parasitoids of *Drosophila* larvae, in natural field settings. Janssen (1989) brought a stereomicroscope into the field, suspended it on a tripod, and observed these parasitoids searching for and attacking their hosts on fermenting apples and pears and on sap fluxes of wounded trees. He recorded details of foraging behavior by speaking into a tape recorder or by entering data into a portable data logger. A total of 19.5 hours of observations were logged in this way over the summers of 1984 and 1985, providing novel data on encounter rates and handling times in the field of these parasitoids whose behavior had been well studied in laboratory settings. To help interpret data from these observations, hosts were collected and parasitoids reared from them in the laboratory and handling times for both parasitoid species on nine *Drosophila* spp. were obtained in laboratory studies.

One of Janssen's (1989) key findings was that the encounter rate between both *A. tabida* and *L. heterotoma* and host larvae was rather low, ranging between 0.2 and 5.0 per hour, depending upon the year and substrate. Of the nine *Drosophila* species that were present at the sites that Janssen (1989) studied, three comprised over 97% of the samples reared from field collections of field material in approximately equal proportions (*Drosophila subobscura*, *Drosophila immigrans*, and *Drosophila simulans*). Of these, *D. subobscura* was a highly suitable host for both *A. tabida* and *L. heterotoma*, *D. simulans* was suitable for *L. heterotoma* but a very poor host for *A. tabida*, and *D. immigrans* was a poor host for both parasitoid species. Janssen's (1989) field observations involved host larvae and it was therefore impossible to distinguish between host species. However, given the relative abundance of the various hosts and assuming no differences in detectability of the different host species (as appeared to be the case in the laboratory), it is likely that approximately one-third of *L. heterotoma*'s encounters were with a low-quality host (*D. immigrans*) and approximately two-thirds of *A. tabida*'s encounters were with low quality hosts (*D. immigrans* or *D. simulans*). Despite this, only three of the 33 host encounters observed in the field for both parasitoid species resulted in rejections. Thus, it appears that these parasitoids readily accept very low-quality hosts in the field. Janssen (1989) used this result to conclude that fitness in these parasitoids was limited by time (or the number of hosts that they could encounter during their lifetime) and not by eggs. Indeed, the high acceptance of low-quality hosts that was observed matched the prediction of an optimality model that was based upon an assumption of time limitation (Janssen 1989). The use of low-quality hosts by parasitoids is relatively common (Heimpel et al. 2003) and this is broadly consistent with widespread time limitation.

Janssen's (1989) conclusion of time limitation by *Asobara* and *Leptopilina* has been investigated further. Driessen and Hemerik (1992) used estimates of egg load at emergence, oviposition rates within host patches, patch residence time, travel times between patches, and life expectancy to simulate the time and egg budget of *Leptopilina clavipes* (note that this is not the same species of *Leptopilina* that Janssen (1989) worked with). Their model suggested that a relatively high fraction (13%) of females would deplete their egg supply during their lifetime. Contrary to Janssen (1989), they concluded that at least some of the population was probably under selection to reject low-quality hosts at some times during the season. Females of *A. tabida* were also able to deplete their egg load under field conditions, although seemingly at a lower rate than *L. clavipes*, with most females dying with high egg loads (Ellers et al. 1998, 2001).

Another case in which direct field observations were used to determine host species selection involves the parasitoids *Cotesia glomerata* and *Cotesia rubecula*. Laboratory studies and field data have shown that *C. rubecula* is a specialist, showing a strong preference for larvae of the small cabbage white butterfly *Pieris rapae* over other *Pieris* spp. (Brodeur et al. 1996, 1998, Geervliet et al. 2000). *Cotesia glomerata*, on the other hand, attacks larvae of at least three species of *Pieris*, including *P. rapae* and the large cabbage white butterfly *Pieris brassicae*. Geervliet et al. (2000) set up cabbage plants in the field on which one leaf was provisioned with *P. rapae* larvae and another leaf was provisioned with *P. brassicae* larvae. Observers then sat near the plants and observed naturally foraging *C. rubecula* and *C. glomerata* locate and attack the host larvae. They found, as suspected, that *C. rubecula* attacked exclusively *P. rapae* and that *C. glomerata* attacked both *P. rapae* and *P. brassicae*.

3.3.2 Host quality and parasitism rate

The low hourly parasitism rate of *A. melinus* observed by Casas et al. (2000, 2004) on the basis of egg load dynamics is due to a high rejection rate of unsuitable hosts. In this case, we are not referring to unsuitable host species, but instead to individuals of high-quality host species that are either a suboptimal stage or previously parasitized or dead. So, finding and even encountering members of the correct host species may not be a problem *per se*. Instead, finding high-quality individuals might be a greater problem. There is a large variety of host types that can be considered unsuitable, including already parasitized hosts, hosts that are too small or otherwise physiologically unsuitable, and even dead hosts. This latter case is particularly interesting, as it is difficult to imagine how spending time examining dead hosts can be considered anything but suboptimal. Dead hosts appear to play a key role in two totally different systems: for eulophids attacking leafminers (Casas 1989, Connor & Cargain 1994) and for *Aphytis* attacking scale insects (Heimpel et al. 1996, Casas et al. 2000, 2004). In both cases, the hosts remain present in their habitat and continue to attract parasitoids long after their death.

This simple fact is in itself already surprising, as it is difficult to reconcile with the highly complex array of sensors that parasitoids are equipped with. *Aphytis melinus* has to insert its ovipositor into the host for examination and most scale probed in the field were recorded dead once dissected in the laboratory (Casas et al. 2004). Heimpel et al. (1996) calculated that over 20% of the scale examined long enough to proceed to ovipositor insertion by *A. aonidiae* were in fact dead. *Sympiesis* also spends time on empty host mines (Casas 1989).

The parasitism rate reported in the field of *A. melinus* (between 0.5 and 1.0 eggs per hour) using behavioral observations is lower than that reported from laboratory experiments (1.5 eggs per active hour). These low attack rates are, however, consistent with the estimates from egg load maturation and egg laying rates obtained through ovarian dynamics in the field (Heimpel et al. 1998, Casas et al. 2000). As stated above, the key difference between laboratory and field observations is in the much lower acceptance rate in the field. The discrepancy is therefore not the result solely of the time spent dealing with dead scale insects. Indeed, a simple calculation gives an increase in search time of only 20%, once the time spent on dead scale is added to the actual search time (Casas et al.

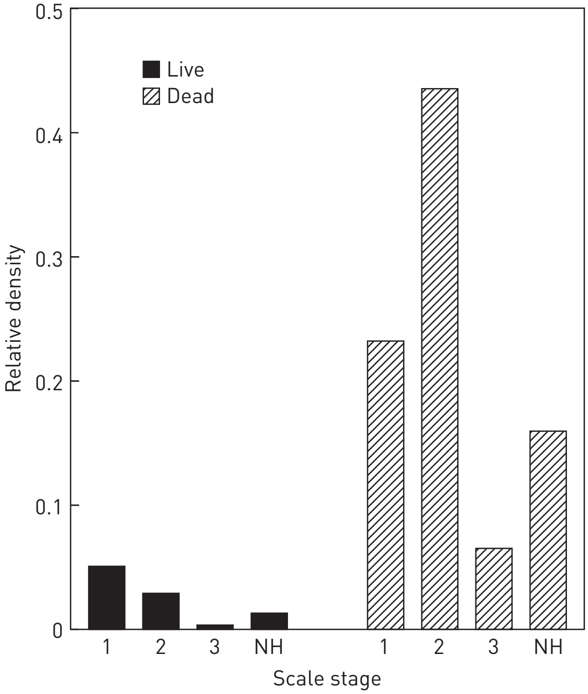

Fig. 3.1 Relative density of live and dead California red scale in a sample from the bark in the interior of a tree. A scale of stage 1 to 3 can be use as hosts (the smallest for host feeding) and NH represents non-host stages. Even though *Aphytis* foraging in such an environment has enough hosts within reach to use up its egg load in a few minutes, it will use the whole day to lay its eggs, rejecting most scale, 90% being dead.

2004). If *Aphytis* in the field had shown the same acceptance rate as in the laboratory, they would have laid their entire egg complement (up to 12 eggs) in only a few minutes, as the females were literally surrounded by live hosts (three hosts per square centimeter (Fig. 3.1)). The results for the leafminer systems are less clear, but dead hosts and empty mines are an impediment to the female's search here as well. More work is needed on the lack of mechanisms to recognize dead hosts and their impact on behavioral decisions, as it is difficult to envision adaptive explanations for the lack of recognition and the time spent dealing with dead hosts.

3.3.3 Physiological state and host use patterns

Further work on the importance of egg versus time limitation and its influence on reproductive decisions in the field was done on *Aphytis* parasitoids, which attack armored scale insects.

Heimpel and colleagues conducted observations of female *A. aonidiae* and *Aphytis vandenboschi* foraging for and attacking the San Jose scale in California almond orchards (Heimpel et al. 1996, 1997b, 1998, Heimpel & Rosenheim 1998). These observations were focused primarily on the decision of the parasitoids to use hosts for oviposition or host feeding. Previous laboratory studies had shown that *A. melinus* were more likely to oviposit when they had high egg loads and host feed when they had low egg loads (Collier et al. 1994, Heimpel & Rosenheim 1995) and the question was whether this trend would be upheld in the field. A sufficient number of observations to address this question was obtained for *A. aonidiae* and, indeed, females with lower egg loads were more likely to use hosts for host feeding than oviposition (Heimpel et al. 1996), supporting predictions from dynamic host use models (Chan & Godfray 1993, Heimpel et al. 1994, Collier 1995, Heimpel & Collier 1996, McGreggor 1997, Heimpel et al. 1998, see also Chapter 7 by Bernstein and Jervis). Using these results, it was possible to derive a simple behavioral rule that takes into account only the parasitoid egg load and host size. In this rule, a parasitoid with a given egg load oviposits on hosts that are larger than a particular size and host feed on hosts that are below this size. In simulation models, this simple (empirically derived) behavioral rule was compared to 'optimal' dynamic behavior as a predictor of field egg loads. The rule was much better at predicting field egg loads than the dynamic model. In particular, the dynamic model predicted that many more females should deplete their egg loads than actually did. One implication of this discrepancy is that parasitoids engaged in more host feeding than was deemed optimal. And while it is possible that the high level of host feeding observed was suboptimal or maladaptive, it is also possible that the estimates of host feeding gain were underestimated in laboratory studies (Heimpel et al. 1997a). An alternative explanation is the lack of a clear relationship between the time spent host feeding and the amount obtained, as well as the small quantities of food often obtained (Rosenheim & Rosen 1992, Giron et al. 2004).

Measuring the oviposition rate per hour in the field is a daunting task. Statistical inference using the dynamics of egg load is much easier, a case where physiology is the best route to quantify behavior rather than measuring behavior directly. By conducting both a series of cage experiments in the field on *A. melinus* and stochastic modeling of the egg maturation and egg laying rates using wild females caught the same day in the same environment, Casas et al. (2000) showed that the oviposition rate is a positive function of the egg load itself. Parasitoids either pause more or get choosier as they deplete their egg load. The stochastic model developed also showed that a major portion, up to 40%, of the *A. melinus* population was experiencing transient time and egg limitation, sometimes in sequence during a single day. A similar result was found for the *A. aonidiae* system discussed above in which an increased tendency to host feed versus oviposit was documented as the egg load declined (Heimpel et al. 1998). The time window for foraging becomes crucial and a female can end up being time limited one day and being egg limited the next, depending on weather conditions.

We know surprisingly little about the daily time window for foraging and its influence (see Casas 2000, for a quantification in the field). In collaboration with J. Casas, P. D'Ettorre measured the egg load of the parasitoid *Pteromalus sequester* attacking a seed weevil (*Apion ulicis*) on *Ulex europeaus* in the field over the entire daily foraging over three days. As shown in Fig. 3.2, the egg load declined over the day for this species, but did not reach zero. Why not lay all of the eggs? Is the female unable to assess her own ovarian state closely enough? Does the entire machinery of hormonal control and egg production maintain a minimal supply of eggs (see also Chapter 7 by Bernstein and Jervis)? Is it optimal to behave in a way that leads to some small leftover at the end of the day, given the stochastic nature of host availability and metabolic needs? This is not some oddity of this biological

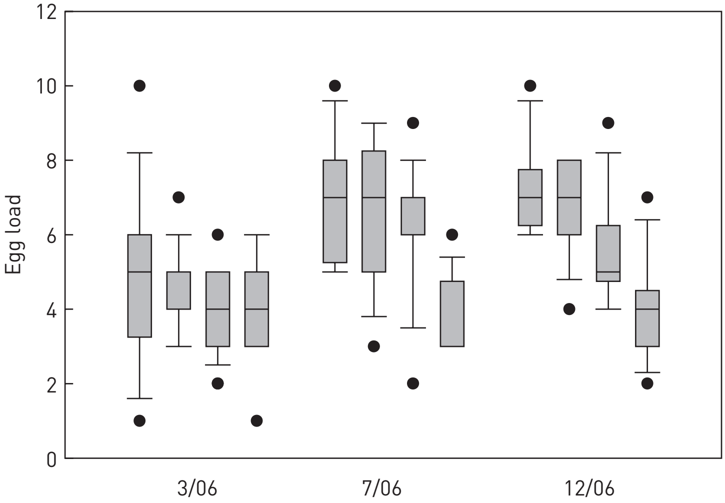

Fig. 3.2 Daily egg load dynamics of *P. sequester* in the wild under high host density conditions over 3 days corresponding to the peak activity of this species. The sampling times were 09:00, 12:00, 15:00, and 19:00 hours. A clear decrease in egg load can be observed, as well as the conspicuous absence of females without any mature eggs. In the vertical direction, the boxes extend from the lower to the upper quartile (25th, 50th, and 75th empirical quartiles). Whiskers are drawn for the largest and lowest observations at a distance of 1.5 the interquartile range. All observations, if any, lying beyond the whiskers are marked by a dot.

system, as it was also observed for *A. melinus* (Casas et al. 2000). The documentation of switching between time and egg limitation implies that the debates about whether time or eggs limit may be misleading. Indeed, models of the dynamics of synovigenic parasitoids predict transient egg (and time) limitation (Heimpel et al. 1998, Rosenheim et al. 2000). This switching is bound to occur often for synovigenic species having only a few eggs at a time, much like a reflecting random walk hovering near the origin. Selection may rather act upon the speed at which the physiological machinery is able to increase and decrease in speed as a function of egg load and host availability.

3.3.4 Optimal patch use in the field

One of the key reproductive strategies that parasitoids face is how long to stay in a patch of hosts (Godfray 1994, see also Chapter 8 by van Alphen and Bernstein). In an earlier section of this chapter, we discussed observations of patch use behavior and the effect of patch leaving on density-dependent parasitism. Here, we focus on tests of optimal patch use theory done on parasitoids in the field. While these studies have implications for density dependence, their main purpose was to test behavioral optimality models.

Much of the work on patch use by parasitoids and other animals has been done in the context of Charnov's (1976) marginal value theorem (MVT), which posits that foragers should leave a patch of resources in search of another only once it has been depleted to the average level of other patches in the habitat. A number of tests of this theory have been conducted on parasitoids in laboratory settings (Godfray 1994, van Alphen et al. 2003, Wajnberg et al. 2003, Wajnberg 2006) and the first explicit field test of predictions associated with the MVT using parasitoids that we are aware of was done by Tenhumberg et al. (2001). These researchers evaluated the patch leaving behavior of *C. rubecula*, a parasitoid of larvae of cabbage white butterflies *P. rapae*, by releasing laboratory-reared parasitoids into matrices of 16 potted cabbage plants that harbored varying densities of host larvae. They monitored the oviposition and flight behavior of the released parasitoids and investigated the effect of per-plant host density and parasitoid oviposition rate on the tendency of parasitoids to leave a plant. As predicted by the MVT, parasitoids were more likely to leave plants with low rather than high host density and a high oviposition rate increased the tendency to leave the patch. Interestingly, these effects had not been previously found in greenhouse studies on the same host–parasitoid system performed by Vos et al. (1998). No effect of per-leaf host density was found in these studies. In addition, rather than decreasing the patch residence time as found by Tenhumberg et al. (2001), contacts with hosts increased patch residence times in the study by Vos et al. (1998). Why these differences? Tenhumberg et al. (2001) speculated that strain differences may be involved since they worked with Australian *C. rubecula* and Vos et al. (1998) worked with a native Dutch strain. Another possibility is that the fact that one study from the field and the other from the laboratory somehow caused the differences, although it is not clear how this would lead to the different results obtained by the two research groups.

In a recent set of studies, White and Andow (2007) explored a different kind of patch use behavior in the parasitoid *M. grandii* (= *M. cingulum*). *Macrocentrus grandii* attacks larvae of the European corn borer, which spend much of their time in a physical refuge from attack (Edwards & Hopper 1999). The parasitoid can only attack corn borer larvae when they are either outside of their tunnels or within a half centimeter or so from the tunnel entrances. Upon encountering a European corn borer tunnel that does not have an exposed larva, a female parasitoid must 'decide' whether to stay at the tunnel entrance and wait for the larva to emerge and thus be available for oviposition (if indeed there is a larva inside) or to leave in search of other tunnels that may have exposed larvae. White and Andow (2007) modified an optimal foraging model first introduced by McNamara and Houston (1985) that explored the influence of the following factors on the decision to wait or leave: the proportion of tunnels that contain either inaccessible or accessible hosts, the emergence rate of hosts (i.e. the transition probability from an inaccessible to an accessible state), and the travel time between patches. The model distinguished between two strategies: waiting (akin to sit-and-wait foraging) and leaving (akin to active foraging). A robust prediction of this model was that a leaving strategy is favored by low inter-host travel times and a waiting strategy is favored by high inter-host travel times.

White and Andow (2007) were able to test this prediction using direct observations in the field, by using laboratory-reared *M. grandii* and gingerly placing them upon host tunnels in the field. They found that, if the parasitoids were primed by exposure to a dollop of host frass on a forceps arm just prior to being moved onto the host 'patch', they would actively investigate and probe the tunnel entrance and associated frass. Once placed on the tunnel opening, parasitoids were not manipulated further and freely moved to patches other than the one onto which they were placed. Wasps were observed for as long as possible and probed on average between two and three sites, most of which turned out to be empty tunnels. Information of data was recorded via a running commentary into a tape recorder. Parasitoid 'travel time' was investigated by comparing behavior on the first patch encountered (which followed days of host deprivation in the laboratory) to behavior on subsequent patch visits. The assumption was that perceived travel time was 'long' for the first patch visit and 'short' for subsequent patch visits. The results from these observations supported the prediction that a waiting strategy is favored by longer inter-host travel times. Tenure time averaged more than 30 minutes on initial patches and less than 15 minutes on subsequent patches. Observations showed that it takes between 6 and 16 minutes to properly evaluate a potential host patch for *M. grandii*, so that most parasitoids were essentially engaging in 'leaving' behavior on the subsequent patch visits. As may be expected, parasitoids spent longer on occupied than unoccupied patches for both initial and subsequent patch visits. As in the work of Tenhumberg et al. (2001) discussed above, these results provide support, from the field, for the major predictions of the MVT, namely that long patch tenure times are expected for higher quality patches and ones that require more travel time to locate.

3.4 Concluding statements

The gap between the ever-increasing toolbox of laboratory techniques and the paucity of field studies that was alluded to by Casas (2000) is widening. The reasons are well known: fieldwork is tedious, nothing happens much most of the time, and the material worth publication may be meagre for a 3–5-year PhD study. On the positive side, the number of different species studied in the field has increased, giving us a larger base for the statement that can be made. The wave of work dealing with adult nutrition has shown that physiological work in the field is indeed feasible and the last few years have seen a major advance in the way we do this bit of science (Heimpel et al. 2004). After a long period of mainly observational studies of behavior in the field, Geervliet et al. (2000) showed how laboratory studies could be used to generate qualitative predictions of behavior in the field. Casas et al. (2004) carried on this step further to quantitative ethological predictions. What is still missing as of today is the reverse approach: setting up highly controlled conditions in the field and testing females caught on the spot, enabling clear-cut conclusions. The 'lack' of optimality in the behavior of parasitoids in the field, compared to their behavior in the laboratory, should tell us a lot about the constraints acting in the field.

The number of combinations of environmental conditions experienced by an animal in the field is infinite and changes over time and space. Laboratory experiments can therefore be considered an endless chase after the right combination, very much like Alice trying to find her way in a kaleidoscopic wonderland. Ideally, field tests of theory would produce a probabilistic envelope of behavioral trajectories from the field and, hence, a dose or realism into an otherwise deterministic world found only in the laboratory.

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