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Adaptive superparasitism and patch time allocation in solitary parasitoids: the influence of pre-patch experience

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Summary. Dynamic optimal diet models predict that host selection decisions and patch time allocation are influenced by the resource value of the habitat. We tested these predictions using the solitary parasitoid *Leptopilina heterotoma.* Assuming that travel times between patches, the quality of previously visited patches and parasitoid density affect the parasitoids' estimation of the resource value of the habitat, different treatments were given before introducing parasitoids singly to a patch containing 5 unparasitized and 15 parasitized hosts. The decision to superparasitize is only slightly influenced by the rate of patch encounter. The quality of the previously visited patch has a strong influence. When a poor patch has been visited on the previous day, more superparasitism is observed in the partly depleted patch than when a rich patch has been searched. More superparasitism is also observed when the parasitoids are kept with conspecifics before the experiment than when they are kept alone. Increasing patch residence times are observed as the quality of the previously presented patch decreases. Host selection decisions and patch time allocation are thus clearly influenced by the pre-patch experience of the parasitoid, as predicted by dynamic optimal diet models. This can also explain why females that have never oviposited in unparasitized hosts will superparasitize readily.

Introduction

Parasitic insects search for hosts (usually other insects) to lay eggs in or on. In contrast to prey eaten by predators, parasitized hosts remain in the habitat and can thus be re-encountered by either the same or another parasitoid. Oviposition in a host parasitized by a conspecific or by the female itself is termed superparasitism, a phenomenon which is found commonly in both field and laboratory studies (see van Alphen and Visser 1990 for a review). One situation in which superparasitism can be adaptive is when a number of parasitoids deplete a patch simultaneously (Visser et al. 1992a, 1990). Another is when a parasitoid searches a patch that has already been depleted to a certain extent by conspecific females. In that case, the patch contains a number of host types, differing in the number of parasitoid eggs they contain. If a female is able to distinguish between the different host types, then she needs to decide which host types to accept and which to reject. Adaptive superparasitism when a number of parasitoids deplete a patch has been demonstrated by Visser et al. (1992a) and Visser et al. (1990). Here we will consider the other situation mentioned above: superparasitism when a parasitoid encounters a partly depleted patch.

When only parasitized hosts are present in a patch, parasitoids that have never oviposited in an unparasitized host (so-called inexperienced females) will superparasitize more readily than females that have oviposited in unparasitized hosts (experienced females) (van Lenteren 1976). This has been interpreted as due to the inability of inexperienced parasitoids to distinguish unparasitized from parasitized hosts (host discrimination) until they have encountered an unparasitized host (van Lenteren and Bakker 1975; van Lenteren 1976; Klomp et al. 1980). Van Alphen et al. (1987) have, however, shown convincingly that parasitoids are able to discriminate, even when they have never oviposited in an unparasitized host. Van Alphen et al. (1987) also propose a functional explanation of why inexperienced females superparasitize more readily: "... when an experienced parasitoid arrives in an exploited patch, she may reject the parasitized hosts and leave the patch, because her experience in the previous patch supplied her with the information that unexploited or less exploited patches exist within her habitat." Inexperienced females have no such information and may therefore stay and superparasitize.

This explanation is formalized in dynamic optimal diet models, which predict that the resource value of the habitat influences host selection decisions within a patch. In a poor habitat, the parasitoid searching a patch

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should accept less profitable host types, but when searching a similar patch in a good habitat it should not (Mangel 1989; Visser 1991; Visser et al. 1992a). More specifically, Visser (1991) predicts that when a female searches a patch alone, it should either always or never accept a host type; it should always reject hosts of type i if:

$$R^* > g_i/h_i$$

where R^* is the resource value of the habitat (offspring per unit time), g_i is the pay-off from an egg laid in a host already containing i eggs and h_i is the time needed to handle such a host.

This prediction can be understood intuitively: when R^* is so high that a parasitoid obtains more offspring when foraging for h_i units of time elsewhere in the habitat than when it accepts a host of type i when foraging in the patch, it should always reject such hosts. In this way, the patch will be left h_i units of time earlier, and more time can be spent foraging in the habitat. If at some moment during the depletion of the patch a parasitoid should start to accept hosts of type i, than there is no point in rejecting such hosts first and searching for them again later. This would be a waste of searching time that could otherwise be used to forage outside the patch (Mitchell 1990; Visser 1991).

When a parasitoid depletes a patch, the time spent in the patch is influenced by the resource value of the habitat. The rate of offspring gain decreases with patch residence time when a patch is being depleted. According to the marginal value rule (Charnov 1976), a parasitoid should leave the patch when its rate of offspring gain has decreased to the resource value of the habitat. In a habitat of low value this threshold will be lower and a patch will be further depleted. Therefore, females in such habitats should stay longer in a patch than those in a similar patch within a habitat of a high resource value.

We studied the influence of the resource value of the habitat on host selection decisions and patch time allocation of a solitary parasitoid experimentally by altering the resource value R^*. We predict that (a) at high values of R^*, no superparasitism will occur, and at lower values it will, and (b) patch time will increase with decreasing values of R^*.

How can the resource value of the habitat be altered? For a particular parasitoid, the resource value of the habitat is determined by (a) the characteristics of the habitat, (b) the decisions of the parasitoid and (c) the decisions of conspecific females. The characteristics of a habitat are the average travel time between patches, the number of hosts of various types in the patches and the number of competitors. The latter can superparasitize hosts parasitized by a given female and thus decrease that female's probability of obtaining offspring from those hosts. The resource value of the habitat is also influenced by the decisions of the parasitoid concerning host selection and patch time. This makes the prediction of optimal decisions within a patch difficult when such decisions depend on the resource value of the habitat (Charnov 1976; Visser 1991).

We consider time-limited parasitoids, and therefore the probability of death (which can depend on the age of female) has no influence on the value of R^*, provided that it is equal in the patch and in the rest of the habitat. R^* is expressed in offspring per unit time, and is therefore independent of the time to be spent in the habitat. A number of factors which may influence the resource value of the habitat for a particular forager can be manipulated. The habitat value increases with: (a) an increasing average patch quality, (b) an increasing patch encounter rate and (c) a decreasing number of competitors in the habitat.

Animals will not have complete information on all these factors and thus we assume that they will have to estimate the resource value of the habitat. We suppose that animals have an expectation of some of the parameters at the beginning of their lives and are able to update these values as they sample the habitat. Such "initial" values might themselves be subject to natural selection, as well as the habit of under- or overestimating the habitat value from the information obtained (Roitberg 1990). The importance of sampling is likely to be correlated with the predictability of the environment over the generations. For animals that live in an environment that varies widely over the generations, sampling is essential to adjust the estimation of the resource value of the habitat. Information obtained before arriving at a patch (which we will refer to as "pre-patch experience"), and possibly also obtained within that patch, will influence these estimates and thus the host selection decisions and patch time allocation.

Here, we study the influence of pre-patch experience on the decisions of *Leptopilina heterotoma* (Hymenoptera: Eucoilidae), encountering a partly depleted patch. *L. heterotoma* is a solitary parasitoid of larvae of *Drosophila* species that breed in sap fluxes, fermenting fruits, decaying plant material and fungi (Janssen et al. 1988). The hosts of *L. heterotoma* occur on patchily distributed substrates, and in the field females will encounter partly depleted patches. Within a patch, *L. heterotoma* searches randomly for hosts (van Batenburg et al. 1983). The life expectancy of the females in the field is 11 days (variance 24; A. Janssen, pers. comm.).

Our aim is to test the predictions that (a) at high values of R^* no superparasitism will occur, while at lower values it will and (b) patch time will increase as the value of R^* decreases. All females are presented with a first and a second patch and we influence the parasitoids' estimation of R^* by altering the three factors that determine the resource value of the habitat mentioned above: the quality of the first patch, the way parasitoids were kept before the first patch (alone or with conspecifics) and the rate of encounter with patches (the number of patches visited divided by the age of the parasitoid). The latter is altered by keeping the number of patches visited the same for all females, and using females of different age. We assume that both intervals (from emergence to first patch and from first to second patch) are used by the animal to estimate the encounter rate. It is however not unlikely that in real animals the last interval has a larger impact on this estimation. The parasitoids are kept in vials before the first patch visit and between the first and second patch visits to simulate travel times between patches, but this obviously differs from real travelling since no energy is spent in flying. We want to stress that we are not calculating the exact value of R^* using the marginal value theorem (MVT; Charnov 1976), but assume that pre-patch experience influences the parasitoids' estimation of the resource value of the habitat.

We use laboratory reared animals in order to control for age and experience, but also use some wild-caught females to see whether their decisions fall within the range of those obtained from females reared and manipulated in the laboratory.

Methods

In the experiments we used *L. heterotoma* females and early second instar larvae of *Drosophila subobscura.* Both species originated from specimens collected near Leiden, the Netherlands in August 1988. All parasitoids were reared from isolated pupae. After emergence, they were mated and kept at 20° C, in vials containing an agar layer and some honey. All parasitoids were given a first and a second patch and had no experience with hosts previous to the first patch visit. Initially, six different treatments were given, with 15 replicates per treatment (the first six treatments in Table 1). The treatments are coded in the following way: kept *AL*one or kept *TO*gether/age on second patch (*5* or *12* days)/interval between patches (*1* or *8* days)/hosts on first patch *U*nparasitized, *P*arasitized or an *E*mpty patch.

Parasitoids were kept alone in a vial, except those used in the treatment in which the females were kept in groups of four between mating and introduction to the first patch (TO5/1/U treatment).

The first patch to which the females were introduced singly contained either 20 unparasitized hosts, 20 parasitized hosts or no hosts. The patches consisted of a viscous suspension of live baker's yeast ("Engedura"). They had a diameter of 3 cm and were about 1 mm deep, and were fitted into circular depressions in an agar layer (4 mm in depth) in a 12 cm diameter plastic dish. Sixteen hours before an experiment, the unparasitized hosts were placed in the patches; 20 h after introduction 90–100% of the hosts were recovered from such patches. In the case of a patch with parasitized hosts, five third-instar hosts were introduced 16 h before the experiment. Fifteen minutes before the experiment, they were replaced by 20 second-instar hosts that had been parasitized 30 min prior to the experiment. In this way, secretions of hosts that function as a kairomone for the parasitoids, are present in the patch, while the mark in the parasitized hosts is still well detectable (Visser et al. 1992b). In the case of an empty patch, no hosts were introduced to the patch at any time. All experiments were performed at 20° C and 70–80% relative humidity. Females were observed continuously. A female that had left the patch for more than 10 min was removed, and the hosts dissected in a droplet of water in order to count the number of eggs laid in each host. Between the first and the second patch, all parasitoids were kept alone in a vial at 20° C.

Table 1. The eight different treatments of female *Leptopilina heterotoma* before they are individually introduced to a patch containing 5 unparasitized and 15 parasitized *Drosophila subobscura* larvae

Treatment[a]	Before 1st patch, parasitoid kept	Age on second patch (days)	Interval between patches (days)	Hosts on first patch	*n*
AL5/1/U	alone	5	1	unparasitized	15
AL12/1/U	alone	12	1	unparasitized	15
AL12/8/U	alone	12	8	unparasitized	15
AL5/1/P	alone	5	1	parasitized	15
AL5/1/E	alone	5	1	empty patch	15
TO5/1/U	4 together	5	1	unparasitized	15
AL40/1/U	alone	40	1	unparasitized	10
AL5/0/U	alone	5	0.0417[b]	unparasitized	10

[a] The treatments are coded in the following way: kept ALone or kept TOgether/age on second patch/interval between patches/hosts on first patch Unparasitized, Parasitized or an Empty patch

[b] =1 h

For a second patch, all parasitoids were introduced singly to a patch containing 15 parasitized hosts and 5 unparasitized hosts. The parasitized hosts had been parasitized 30 min before the experiment. The unparasitized hosts were coloured with carmine (Bakker et al. 1972). All hosts were introduced into the patch 15 min before the experiment. Again, females that had left the patch for more than 10 min were removed and the hosts were dissected.

Wild parasitoids were collected on 1 and 2 August 1990 on decaying cucumbers placed in a woodland at the east side of the coastal dunes in Wassenaar, the Netherlands. They were taken to the laboratory, one female per vial, and stored at 20° C. On 3 August, the females were introduced individually to a patch containing 15 parasitized hosts and 5 unparasitized hosts.

Differences between treatments in the distribution of eggs over hosts were tested on mean and variance of the distribution per replicate. A significant difference means that the P value from the Mann-Whitney U-test is less than 0.025 for either the mean or variance of the distributions. The patch time was tested as the patch time per parasitoid, also with the Mann-Whitney U-test.

Results

Before discussing the influence of each of the three variables on the distribution of eggs over hosts (Fig. 1) and the patch residence time (Fig. 2), some clarification is needed on the distribution of eggs over the initially parasitized hosts (on the second patch). In some of these hosts, no egg was found at dissection (Fig. 1). There are three possible explanations: (a) the egg was present in the host, but not found at dissection, (b) when collecting parasitized hosts, an unparasitized one was collected, either by mistake or because the wasp behaved as if laying an egg, but did not, and (c) the red colour of an initially unparasitized host was lost during the experiment and the host was therefore classified as initially parasitized. The overall distribution is not altered by the latter two explanations. The former explanation would alter the distribution (more hosts in the once-parasitized category) but only weakly. Moreover, none of the explanations depend on the treatment and therefore the initially parasitized hosts in which no egg was found at dissection are ignored in the conclusions.

Quality of patches

Not surprisingly, on the first patch, the distribution of eggs over hosts of the parasitoids that were introduced to a patch initially containing 20 parasitized hosts (AL5/1/P treatment), differs significantly from those that

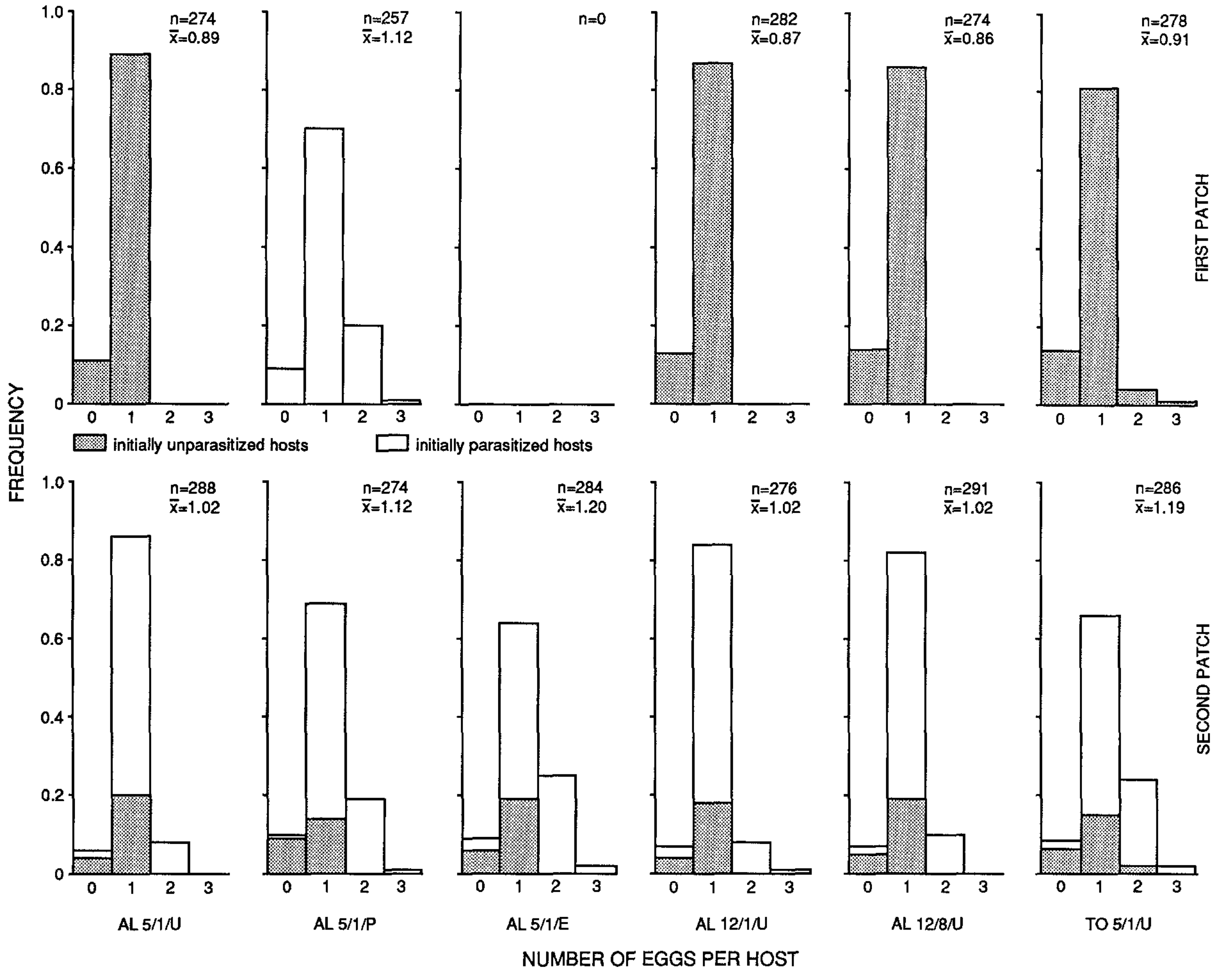

Fig. 1. Frequency histograms of the distribution of eggs over hosts for six treatments of females (see the first six treatments in Table 1), for the first patch (initially containing either 20 unparasitized, 20 parasitized or no hosts) and the second patch (initially containing 5 unparasitized and 15 parasitized hosts). The *shaded part* of the bars represents the initially unparasitized hosts, the *open part* of the bars the initially once-parasitized hosts (each distribution is the average of 15 replicates; n = number of dissected hosts; $\bar{x}$ = mean number of eggs per host)

searched a patch initially containing 20 unparasitized hosts (AL5/1/U) (Fig. 1). On the second patch, two aspects of the egg distributions can be studied: the distribution of eggs over the initially unparasitized hosts and that over the initially parasitized hosts (Fig. 1). The distributions of eggs over the initially unparasitized hosts are not significantly different for the three treatments. The egg distribution over the initially parasitized hosts of the parasitoids presented with a first patch containing only unparasitized hosts (AL5/1/U) differs significantly from those previously presented with a patch containing only parasitized hosts (AL5/1/P) or an empty patch (AL5/1/E): when the quality of the patch previously searched is low (AL5/1/P, AL5/1/E) more superparasitism is observed on the second patch.

The patch times on the first patch (Fig. 2) of the parasitoids introduced to a patch containing only parasitized hosts (AL5/1/P), are significantly shorter, and the patch times of those introduced to an empty patch (AL5/1/E) significantly even shorter, than those of parasitoids that searched a patch initially containing only unparasitized hosts (AL5/1/U). The quality of a patch strongly influences the time spent in the patch, as is predicted by theory. The time spent in the second patch (Fig. 2) is significantly longer when parasitoids have previously searched an empty patch (AL5/1/E treatment) than when they have searched a patch containing unparasitized hosts (AL5/1/U treatment). Thus, both host selection decisions and patch time allocation of a parasitoid searching a partly depleted patch is influenced by the quality of the patch searched previously.

Encounter rate with patches

Both for the first and the second patch, the egg distributions of the three treatments (AL5/1/U, AL12/1/U, AL12/8/U) are not significantly different (Fig. 1). Neither are the patch times on the first patch and on the second patch of the three treatments (AL5/1/U, AL12/1/U, AL12/8/U) are significantly different (Fig. 2). The encounter rate with patches seems not to affect patch time allocation and host selection decisions.

It might be that the difference between an encounter rate of 2 patches in 5 days or 2 patches in 12 days

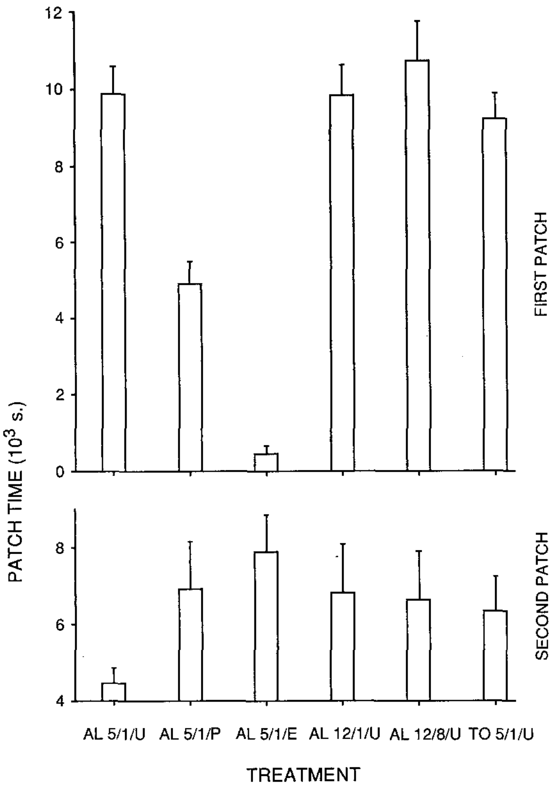

Fig. 2. The average observed patch times (s) with SE for the six treatments of females (see the first six treatments in Table 1), for the first patch (initially containing either 20 unparasitized, 20 parasitized or no hosts) and the second patch (initially containing 5 unparasitized and 15 parasitized hosts)

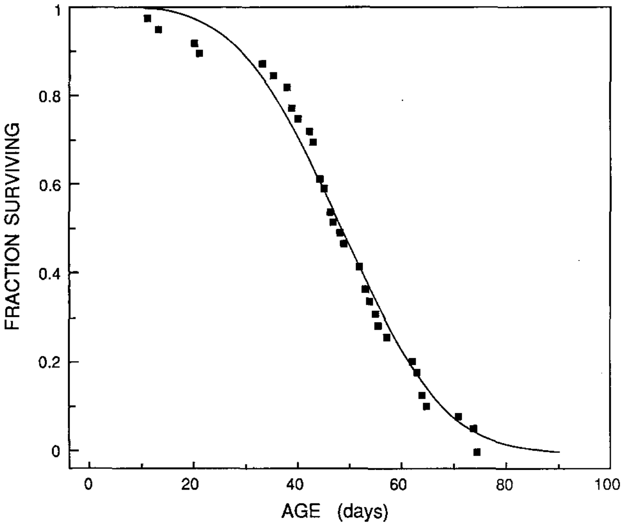

Fig. 3. The fraction of female *Leptopilina heterotoma* surviving plotted against their age when kept alone in a vial (under laboratory conditions: L16:D8, constant 20° C, 70% relative humidity, access to honey). A Weibull distribution is fitted to the observed data ($\alpha = 3.58$ and $\beta = 53.82$)

is not large enough to have an influence. This would be surprising because parasitoids live for only about 11 days in the field. It is possible however that parasitoids in the laboratory live for a longer period and thus that the difference between 5 and 12 days is relatively small.

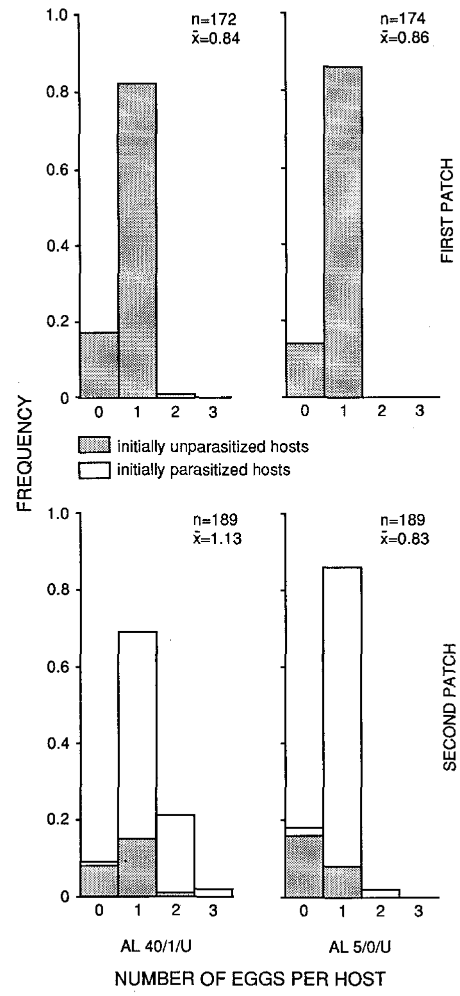

Fig. 4. Frequency histograms of the distribution of eggs over hosts for two treatments of females (see the last two treatments in Table 1), for the first patch (initially containing either 20 unparasitized hosts) and the second patch (initially containing 5 unparasitized and 15 parasitized hosts). The *shaded part* of the bars represents the initially unparasitized hosts, the *open part* of the bars the initially once-parasitized hosts (each distribution is the average of 10 replicates; n = number of dissected hosts, $\bar{x}$ = mean number of eggs per host)

We checked this by keeping mated females alone in vials, with honey but without access to hosts, under laboratory conditions (L16:D8, constant 20° C, 70% humidity). Under those conditions, parasitoids have an average life span of 49 days (var. 245), with a maximum of 75 days (Fig. 3).

We therefore carried out another set of experiments with a much lower patch encounter rate: only 2 patches in 40 days (AL40/1/U treatment, see Table 1). At that age, about half the initial population has died (Fig. 3) and such a low encounter rate should have an influence. The parasitoids were given a patch containing 20 unparasitized hosts, and the next day, when they were 40 days old, a partly depleted patch (15 parasitized and 5 unparasitized hosts). With this treatment (AL40/1/U), more superparasitism is observed in the second patch (Fig. 4) than when the parasitoids are given 2 patches in 5 days (AL5/1/U) or in 12 days (AL12/1/U, AL12/8/U) (Fig. 1), but the differences are, due to the large variation, not significant. On the first patch, the average patch time in the AL40/1/U treatment was 12329 s (SE = 2065). Although on average this is the longest patch time, it is not significantly different from the patch times in the three other treatments. On the second patch, the average patch time was 7613 s (SE = 1445), which is also not significantly different from the other treatments.

Another striking result is that, contrary to the prediction, superparasitism occurs in all treatments, even in the treatment that represents the best habitat (AL5/1/U treatment). An explanation might be that even in such a habitat, the patch encounter rate is too low to allow specialization on unparasitized hosts. To test this, another set of experiments is carried out, identical to the AL5/1/U treatment, but with only 1 h between the two patches, instead of one day (AL5/0/U treatment, Table 1). Now, the encounter rate with patches is 2 in 5 days, but the interval between the patches is extremely short. Hardly any superparasitism in the second patch is found in this treatment (Fig. 4), and the egg distribution differs significantly from those of the four previous treatments. The patch times in the AL5/O/U treatment are 8099 s (SE = 543) on the first patch, which is not significantly different from the other four treatments, and 2419 s (SE = 753) on the second patch. The latter is significantly shorter than the patch times in the other four treatments, which is in agreement with the prediction that patch times will decrease as patch encounter rate increases. Still, the encounter rate with patches only weakly influences decisions made by the parasitoids.

Number of competitors in the habitat

In the first patch, the distribution of eggs over hosts of the parasitoids that were kept with three conspecifics before the experiment (TO5/1/U treatment) differs significantly from that of the parasitoids treated in the same way, but kept alone (AL5/1/U treatment). Parasitoids that had encountered conspecifics before entering the first patch superparasitize when depleting a patch with initially only unparasitized hosts, while females that were always kept alone do not, although the difference is not as large as in similar experiments in Visser et al. (1990). In the second patch, the distributions of eggs over the initially unparasitized hosts of the TO5/1/U treatment differs significantly from those of the AL5/1/U treatment. This is caused by the proportion of initially unparasitized hosts that contain two eggs in the TO5/1/U treatment.

Self-superparasitism is very rare in the other seven treatments in which parasitoids were kept alone before the experiment. To test this more directly, we compared the distribution of eggs over the initially unparasitized hosts in the TO5/1/U treatment with the total of the seven other treatments (Table 2). These distributions differ significantly (χ^2, $P = 0.001$), due to self-superparasitism in the treatments where the parasitoids were kept together in a vial until introduction to the first patch (TO5/1/U treatments). Apparently, since no self-superparasitism is observed when parasitoids are kept alone, *L. heterotoma* is able to avoid self-superparasitism when searching a patch with hosts containing eggs laid by conspecifics (the initially parasitized hosts) and hosts containing eggs of the female herself (initially unparasitized hosts that have been parasitized by the female during the experiment). From this we can conclude that *L. heterotoma* is able to distinguish between hosts containing eggs laid by a conspecific and those containing eggs laid by herself (see Visser 1992 for a full discussion of this ability). The females that have encountered conspecifics before the experiment therefore self-superparasitize when searching a partly depleted patch, similarly to the first patch.

Table 2. The distribution of parasitoid eggs over the initially unparasitized hosts when a female *L. heterotoma* is introduced on a patch containing 5 unparasitized and 15 parasitized *D. subobscura* larvae

Treatment[a]	# Hosts containing 0 eggs	# Hosts containing 1 egg	# Hosts containing 2 eggs
AL*/*/*[b]	107	240	4
TO5/1/U	13	42	5

[a] Females were either kept alone (AL*/*/*) or in groups of 4 (TO5/1/U) before their introduction to the first patch

[b] AL5/1/U, AL12/1/U, AL12/8/U, AL5/1/P, AL5/1/E, AL40/1/U and AL/5/0/U treatments

With respect to the distribution of eggs over the initially parasitized hosts, the treatment in which females were kept alone (AL5/1/U) differs significantly from those kept in a group (TO5/1/U). Thus, when a female has encountered conspecifics 2 days before, more superparasitism is observed.

The patch times on both the first and the second patch of the TO5/1/U treatment are not significantly different from the AL5/1/U treatment (Fig. 2).

Parasitoids from the field

Only five parasitoids were collected, of which four were willing to search the patch, which contained 5 unparasitized and 15 parasitized hosts. The patch time of these parasitoids was on average 2682 s (SE = 575), which is significantly shorter than the patch time in the AL5/1/U, AL12/1/U, AL40/1/U, AL5/1/E and TO5/1/U treatments. This indicates that these parasitoids estimated the habitat as more profitable than those reared and treated in the laboratory.

The distribution of eggs over the initially unparasitized hosts (Fig. 5) is different from that distribution in the AL5/1/U treatment; fewer initially unparasitized hosts are parasitized by the parasitoids from the field. Searching is random in *L. heterotoma*, and therefore this is probably a direct consequence from the shorter patch times. The distribution of eggs over the initially parasitized hosts is not different from the distributions of the other treatments (with the exception of AL5/0/U): the

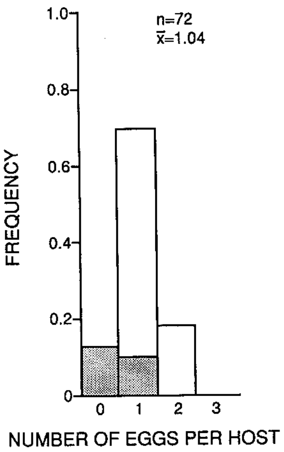

Fig. 5. Frequency histogram of the distribution of eggs over hosts for the females caught in the field, when introduced to a patch initially containing 5 unparasitized and 15 parasitized hosts. The *shaded part* of the bars represents the initially unparasitized hosts, the *open part* of the bars the initially once-parasitized hosts (the distribution is the average of 4 replicates; $n=$ number of dissected hosts, $\bar{x}=$ mean number of eggs per host)

parasitoids caught in the field did superparasitize when introduced to a partly depleted patch, and the egg distribution falls within the range of those obtained from females reared and manipulated in the laboratory.

Discussion

The influence of the resource value of the habitat on decisions of the parasitoid

From dynamic optimal diet models (Mangel 1989; Visser 1991; Visser et al. 1992a), we predict that parasitoids searching a partly depleted patch in habitats of different resource value will take different decisions, both with respect to host selection and to patch time allocation. In patches that are in a habitat of a high resource value no superparasitism should occur, whereas it should occur in similar patches in a habitat of low value. In our experiments with *L. heterotoma*, the degree of superparasitism varies between treatments. In treatments that represent a habitat of low value, more superparasitism is found than in treatments representing a high resource value of the habitat. In the treatment indicating the highest resource value (AL5/0/U), almost no superparasitism is found. We therefore conclude that the prediction of the model is supported, although the parasitoids need to have a very good previous experience to refrain from superparasitism in a partly depleted patch. This is consistent with decisions of the parasitoids collected in the field, which superparasitize readily (Fig. 5).

The second prediction tested is that patch residence time increases with a decreasing value of R^*. This prediction is confirmed in the experiments. The average patch time is the shortest in the "richest habitat" (AL5/0/U) and the longest in the "poorest habitat" (AL5/1/E), while the other categories are somewhere in between these two. This is in agreement with the prediction that patch times will decrease with an increasing resource value of the habitat.

In this respect, it is remarkable that the parasitoids caught in the field have such short patch times. This indicates either that they estimate the habitat as very good or that they search the patch more efficiently than parasitoids reared in the laboratory. We can test the latter hypothesis by calculating the searching efficiencies on the patch, s', of the females in the different treatments and of those obtained from the field. From the number of hosts parasitized and the patch time, we can estimate s' (Free et al. 1977; Visser and Driessen 1991). The value for the animals collected in the field (3.2×10^{-4}) falls within the range of the values for the seven treatments in which laboratory animals were used (1.4×10^{-4}–4.1×10^{-4}, on average 2.2×10^{-4}). For this reason, we conclude that animals from the field do not search more efficiently in a patch, and therefore that the short patch times are due to a relatively high estimate of R^* by those females.

Time versus egg limitation in L. heterotoma

Why do the field-caught parasitoids superparasitize when they have such a high estimation of R^*, and more generally: why do egg distributions differ between categories with similar average patch times (AL12/1/U, AL12/8/U, AL5/1/P, TO5/1/U)? This difference in egg distribution implies that different host selection decisions are made, which is not predicted by dynamic optimal diet models: a host type should either always or never be accepted. The model of Visser et al. (1992a) shows that for time-limited parasitoids this host selection decision is optimal, but the predicted egg distributions from that model are more skewed to the right than the observed distributions (more superparasitism predicted). A similar difference was also found between predicted and observed distributions in Visser et al. (1990). This indicates that *L. heterotoma* rejects hosts where a model assuming time-limitation predicts that they should accept them.

One explanation is that *L. heterotoma* is not strictly time-limited. Parasitoids are not either egg- or time-limited as a species, but as individuals. Some are egg-limited (they are still alive with no further eggs available) while other females of the same species are time-limited (they die with eggs still available) (Driessen and Hemerik 1992). When a parasitoid estimates that it will become egg limited, it should not superparasitize as readily as predicted by a model assuming an unlimited egg supply. At first, it seemed that under our experimental conditions *L. heterotoma* would be time limited: it has a large number of eggs (200–250) in its ovarioles upon emergence (Jenni 1951) and lays at most 35 eggs during the experiments. When encountering the second patch it is either 5 or 12 days old, i.e. either halfway or at the end of its life (11 days under field conditions; A. Janssen, pers. comm.). The parasitoids can however live much longer under laboratory conditions, and it might be that the parasitoids in the experiment behaved as though they were egg limited and therefore did not superparasitize as much as predicted by a model assuming time limitation. The field-caught parasitoids might have a different estimation of the probability of death and therefore behave as though they were time limited, explaining the observed superparasitism at short patch times. Analysis of the behaviour of the parasitoids is needed to gain more insight into this problem (Visser, in prep.)

We used females of different ages, which might alter their estimation of survival. As argued in the introduction, for time-limited animals, the probability of death is not expected to affect the resource value of the habitat, or thereby to affect the host selection decisions and patch time allocation. Roitberg et al. (1992), however, used another method to alter the probability of death and did find such an effect. They compared the oviposition decisions and patch time allocation of *L. heterotoma* when the females were kept either under summer (L16:D8, 22 C) or fall (L12:D12, 22 C) conditions. The latter stayed longer in a patch, and superparasitized more hosts when introduced to a patch containing 30 parasitized *D. simulans* larvae, than females kept under summer conditions. They argue that females in the fall have a lower life expectancy, for instance because they are closer to the first frost. Although the probability of death has no influence on the resource value of the habitat, it will have an influence on whether a parasitoid is time or egg limited, and thereby on the decisions of the parasitoid.

Unexperienced versus experienced parasitoids

We can now return to the phenomenon discussed in the introduction: parasitoids that have never oviposited in an unparasitized host (inexperienced females) will superparasitize more readily than experienced females. Dynamic optimal diet models by Mangel (1989), Visser (1991) and Visser et al. (1992a) predict this phenomenon when experienced parasitoids estimate the resource value of the habitat as higher than inexperienced ones, due to their better pre-patch experience. This prediction is tested in our experiments in a more general way: the pre-patch experience of a parasitoid is found to have an effect on both the host selection decisions (to reject or accept parasitized hosts) and the patch time allocation. Experienced and inexperienced females are just special cases in the range of treatments in our experiments (the AL5/1/U and AL5/1/E treatments respectively). There is therefore no need to assume that inexperienced females are unable to discriminate, as did van Lenteren and Bakker (1975) and van Lenteren (1976), to explain this difference in behaviour by experienced and inexperienced females. Van Alphen et al. (1987) indeed show that inexperienced *L. heterotoma* females are able to discriminate, which can also be concluded from our data: there is a clear difference in patch time on the first patch and in the distribution of the eggs *laid* on this patch between parasitoids that were given a patch with unparasitized hosts and those given a patch with only parasitized hosts.

Adaptive superparasitism

That *L. heterotoma* females superparasitize readily when inexperienced, self-superparasitism when conspecifics are encountered before the experiment, and are able to distinguish hosts parasitized by herself from those parasitized by conspecifics, are all consistent with predictions from the theory that superparasitism in solitary parasitoids can be adaptive. We can distinguish two situations in which we expect superparasitism to occur: parasitoids depleting a patch simultaneously (Visser et al. 1990, 1992a) and females encountering a partly depleted patch. In both situations, the degree of superparasitism is strongly influenced by the resource value of the habitat. When this value is high, because unparasitized hosts are abundant in the habitat, no superparasitism is expected. When e.g. during a part of the season a large proportion of the hosts is parasitized, superparasitism will occur. This causes temporal patterns in the degree of superparasitism in the field, as has been reported by for instance Takagi (1987) and Barrett and Brunner (1990). Such patterns can thus be understood when superparasitism is approached from a functional point of view.

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References

Alphen JJM van, Visser ME (1990) Superparasitism as an adaptive strategy for insect parasitoids. Annu Rev Entomol 35:59–79

Alphen JJM van, Dijken MJ van, Waage JK (1987) A functional approach to superparasitism: host discrimination needs not to be learnt. Neth J Zool 37:167–179

Bakker K, Eijsackers HJP, Lenteren JC van, Meelis E (1972) Some models describing the distribution of eggs of the parasite *Pseudeucoila bochei* (Hym., Cynipidae) over its hosts, larvae of *Drosophila melanogaster*. Oecologia 10:29–57

Barrett BA, Brunner JF (1990) Types of parasitoid-induced mortality, host stage preferences, and sex ratios exhibited by *Pnigalio flavipes* (Hymenoptera: Eulophidae) using *Phyllonorycter elmaella* (Lepidoptera: Gracillariidae) as a host. Environ Entomol 19:803–807

Batenburg FHD van, Lenteren JC van, Alphen JJM van, Bakker K (1983) Searching for and parasitization of *Drosophila melanogaster* (Dipt., Drosophiladae) by *Leptopilina heterotoma* (Hym., Eucoilidae): a Monte Carlo simulation and the real situation. Neth J Zool 33:306–336

Charnov ER (1976) Optimal foraging, the marginal value theorem. Theor Popul Biol 9:129–136

Driessen G, Hemerik L (1992) The time and egg budget of *Leptopilina clavipes*, a parasitoid of larval *Drosophila*. Ecol Entomol 17:17–27

Free CA, Beddington JR, Lawton JH (1977) On the inadequacy of simple models of mutual interference for parasitism and predation. J Anim Ecol 46:543–554

Janssen A, Driessen G, Haan M de, Roodbol N (1988) The impact of parasitoids on natural populations of temperate woodland *Drosophila*. Neth J Zool 38:61–73

Jenni W (1951) Beitrag zur Morphologie und Biologie der Cynipide *Pseudocoila bochei* Weld, eines Larvenparasiten von *Drosophila melanogaster* Meig. Acta Zool 32:177–254

Klomp H, Teerink BJ, Ma WC (1980) Discrimination between parasitized and unparasitized hosts in the egg parasite *Trichogramma embryophagum* (Hym.: Trichogrammatidae): a matter of learning and forgetting. Neth J Zool 30:254–277

Lenteren JC van (1976) The development of host discrimination and the prevention of superparasitism in the parasite *Pseudocoila bochei* (Hym.: Cynipidae). Neth J Zool 26:1–83

Lenteren JC van, Bakker K (1975) Discrimination between parasitised and unparasitized hosts in the parasitic wasp *Pseudocoila bochei*: a matter of learning. Nature 254:417–419

Mangel M (1989) An evolutionary interpretation of the "motivation to oviposit". J Evol Biol 2:157–172

Mitchell WA (1990) An optimal control theory of diet selection: the effects of resource depletion and exploitative competition. Oikos 58:16–24

Roitberg BD (1990) Optimistic and pessimistic fruit flies: measuring the costs of estimation errors. Behaviour 114:65–82

Roitberg BD, Mangel M, Lalonde RG, Roitberg CA, Alphen JJM van, Vet L (1992) Seasonal dynamic shifts in patch exploitation by parasitic wasps. Behav Ecol 3:156–165

Takagi M (1987) The reproductive strategy of the gregarious parasitoid, *Pteromalus puparum* (Hymenoptera: Pteromalidae). 3. Superparasitism in a field population. Oecologia 71:321–324

Visser ME (1991) Prey selection by predators depleting a patch; an ESS model. Neth J Zool 41:63–79

Visser ME (1992) Adaptive self- and conspecific superparasitism in the solitary parasitoid *Leptopilina heterotoma* (Hymenoptera: Eucoilidae). Behav Ecol (in press)

Visser ME, Driessen G (1991) Indirect mutual interference in parasitoids. Neth J Zool 41:214–227

Visser ME, Alphen JJM van, Nell HW (1990) Adaptive superparasitism and patch time allocation in solitary parasitoids: the influence of the number of parasitoids depleting a patch. Behaviour 114:21–36

Visser ME, Alphen JJM van, Hemerik L (1992a) Adaptive superparasitism and patch time allocation in solitary parasitoids: an ESS model. J Anim Ecol 61:93–101

Visser ME, Luyckx B, Nell HW, Boskamp GJF (1992b) Adaptive superparasitism in solitary parasitoids: marking of parasitized hosts in relation to the pay-off from superparasitism. Ecol Entomol 17:76–82