Adaptive superparasitism and patch time allocation in solitary parasitoids: searching in groups vs sequential patch visits

J. J. M. VAN ALPHEN, M. E. VISSER and H. W. NELL

Department of Population Biology, University of Leiden, PO Box 9516, 23300 RA Leiden, The Netherlands

Summary

1. A deterministic ESS model was made to predict optimal degrees of superparasitism, when solitary parasitoids exploit a patch simultaneously or sequentially.
2. Some predictions of this model are: (1) increasing levels of superparasitism and (2) longer patch times (measured as the sum of search times of all females visiting a patch) with increasing numbers of females visiting the patch. (3) More superparasitism and (4) longer patch times were predicted when females visited a patch simultaneously than when the same number of females visited a patch sequentially.
3. Experimental tests of this model with the solitary larval *Drosophila* parasitoid *Asobara tabida* were in agreement with predictions (1), (2) and (3), but no differences were found between the sums of patch times of females visiting patches simultaneously and those visiting patches sequentially.
4. Thus, superparasitism contributes to the aggregation of parasitoids, by generating longer patch times.
5. It is not only the number of parasitoids that search a habitat which determines the level of superparasitism, but also the way they are distributed over patches.

Key-words: Aggregation, *Asobara tabida*, ESS model

Functional Ecology (1992) **6**, 528–535

Introduction

An important difference in the lifestyle of insect parasitoids in comparison to that of predators is that, unlike prey caught by a predator, parasitized hosts are not removed from the habitat and thus can be re-encountered. Hymenopterous parasitoids are able to recognize parasitized hosts (an ability referred to as host discrimination) and thus are able to avoid oviposition in such hosts. Yet, oviposition in or on parasitized hosts (an act called superparasitism) often occurs. When superparasitism increases the probability for a female to obtain offspring from that host, or increases the number of offspring obtained from it, it can be an adaptive strategy (see for a review van Alphen & Visser 1990).

To understand the adaptive significance of superparasitism, we must distinguish between oviposition in a host previously parasitized by a conspecific, and oviposition in a host previously parasitized by the same female (van Alphen & Nell 1982). The difference between 'conspecific' and 'self'-superparasitism (van Dijken & Waage 1987) is that eggs deposited in a host parasitized by another female are

potential competitors of other females' offspring, whereas eggs deposited in a host parasitized by the same female will increase competition among sibs. This distinction is most obvious in solitary parasitoids, where only one of the eggs deposited in a host will develop into an adult. For this reason, a gain in fitness from self-superparasitism is not likely and therefore often a waste of oviposition time and eggs. Conspecific superparasitism can be advantageous under a wider range of conditions because of the probability of elimination of the non-sib competitor from the parasitized host (van Alphen & Visser 1990).

Since this was recognized in the early 1980s (van Alphen & Nell 1982), a number of theoretical studies have been published that predict when gregarious parasitoids should superparasitize (Parker & Courtney 1984; Charnov & Skinner 1985; Strand & Godfray 1989). For solitary parasitoids, a quantitative analysis of superparasitism has lagged somewhat behind. Iwasa, Suzuki & Matsuda (1984), Hubbard *et al.* (1987) and Janssen (1989) have used static optimal diet models to predict adaptive superparasitism in solitary parasitoids. Visser, van Alphen & Hemerik

(1992a) point out that two common features in the ecology of parasitoids, i.e. that they often forage in the same patches as their competitors and that they deplete unparasitized hosts in the patches they visit — mean that static optimization models are not particularly appropriate for the analysis of adaptive superparasitism. For that reason they advocate a game-theoretical approach and show that two interdependent decisions affect superparasitism: when to start superparasitizing and when to leave a patch.

Two situations in which a parasitoid may encounter hosts parasitized by conspecifics are (1) when it searches a patch together with conspecifics (searching in groups) or (2) when it searches a patch that has (partly) been depleted by a conspecific previously (sequential patch visits). Superparasitism can be adaptive in both situations (van Alphen & Visser 1990; Visser *et al.* 1992a), and experimental tests have shown that the solitary parasitoid, *Leptopilina heterotoma* (Hymenoptera: Eucoilidae), indeed superparasitizes in both situations (Visser, van Alphen & Nell 1990; M.E. Visser, J.J.M. van Alphen & H.W. Nell, submitted for publication). In this paper we compare oviposition decisions and the patch time allocation of females of the solitary parasitoid *Asobara tabida* Nees (Hymenoptera: Braconidae), searching a patch simultaneously with that of the same number of females visiting a patch sequentially.

Patches are depleted in both situations, and therefore static optimal diet models (that assume constant encounter rates with the different host types) cannot be applied. Furthermore, such models make no predictions on patch times. We therefore use the game-theoretic model of Visser *et al.* (1992a, see description below) to make predictions on the level of superparasitism and patch residence times for both types of experiments. We present experimental evidence to test these predictions and address the question whether the degree of superparasitism and the time spent searching in the patch increases with the number of parasitoids visiting a patch, and how this is affected by whether the patch is visited sequentially or simultaneously.

Description of the model

A deterministic simulation model is developed to study the pay-off from decisions by the parasitoids with respect to oviposition and patch leaving. This dynamic optimal diet model, which is fully described in Visser *et al.* (1992a), is here adjusted to the characteristics of *A. tabida*. We assume that females have an unlimited egg supply and are unable both to assess the number of eggs already present in a host and to discriminate between hosts parasitized by

themselves and hosts parasitized by conspecifics. Rejection time (11 s) is shorter than oviposition time (31 s) (van Alphen & van Harsel 1982). Females search randomly for hosts, with an encounter rate with hosts of λ , which is a constant because parasitized hosts are not removed from the patch ($\lambda = 0.0377$ encounters s^{-1} in the simulations presented here, the average encounter rate observed in the experiments). Depletion of the patch occurs because unparasitized hosts become parasitized and thereby become less valuable.

Females leave the patch when the gross rate of offspring gain has dropped to the threshold rate for patch leaving (called leaving threshold R^*). All females use the same R^* of 0.005 offspring s^{-1} , both in the sequential and in the simultaneous patch visits. The value of 0.005 was chosen to scale the model in such a way that comparable amounts of superparasitism in simulations and experiments were found. The female's gross rate of offspring gain is calculated according to the pay-off from parasitism and conspecific superparasitism; self-superparasitism does not add offspring. The pay-off from conspecific superparasitism decreases with the number of eggs already present in the host, the pay-offs of the first, second, third and fourth egg are 1.00, 0.43, 0.25 and 0.15 respectively, given that no further eggs will be laid in that host.

When a patch is visited by a number of parasitoids simultaneously, the parasitoids arrive all at the same time on the patch, which initially only contains unparasitized hosts. Unparasitized hosts are always accepted for oviposition, parasitized hosts are either accepted or rejected, depending on the strategy the female plays upon encountering such a host. The Evolutionary Stable Strategy (ESS) threshold rate (also expressed in gross offspring gain) at which parasitoid should switch from rejecting parasitized hosts to superparasitism is calculated with the model, given the number of hosts and the number of parasitoids visiting the patch. When a patch is visited sequentially, the first parasitoid arrives on a patch containing only unparasitized hosts. It searches the patch and always accepts unparasitized hosts. An important assumption is that this female does not anticipate the visits of other females. After this parasitoid has left, a second one enters the patch. This female either can accept or reject the parasitized hosts, and the model is used to calculate the optimal strategy. After this second female has left, a third can be introduced, and when it leaves, a fourth one. Again, these females have the option of either accepting or rejecting parasitized hosts.

After the optimal strategies are calculated for each of the situations, they are used in simulations to predict the influence of the number of parasitoids visiting a patch, simultaneously or sequentially, on the degree of superparasitism and on patch residence times.

Predictions of the model

SUPERPARASITISM

Parasitoids visiting a patch alone, and the first parasitoid visiting a patch in the experiments on sequential patch visits, do not superparasitize (prediction 1). The model predicts for both simultaneous and sequential patch visits that superparasitism increases with the number of females visiting a patch (prediction 2). These predictions follow mainly from the difference between self- and conspecific superparasitism; when only one female visits a patch all superparasitism would be self-superparasitism and this would not increase offspring production. The increased occurrence of superparasitism when parasitoids search in a group is expected because of the increasing probability of conspecific superparasitism with increasing number of females searching a patch. Superparasitism becomes more profitable when the probability of self-superparasitism decreases. Another reason is, paradoxically, that self-superparasitism becomes profitable when the probability of superparasitism by other females in the near future is high. Having two (or more) eggs in a host may increase the probability of gaining an offspring from that host in comparison to having only one egg in a host to compete with the eggs of other parasitoids. When a patch is sequentially visited, a parasitoid entering a patch after the previous one has left, oviposits and gains offspring from the patch despite the fact that all parasitoids use the same threshold leaving rate. While the previous female searching the patch has a high probability of encountering hosts containing its own eggs, for the next female this probability is initially 0. The model predicts that either parasitized hosts should always or never be accepted (Visser 1991; Visser *et al.* 1992a). Switching from rejecting parasitized hosts to superparasitism is never the best strategy when searching alone, but it can be the best strategy for females searching in a group.

The model also predicts that more superparasitism will occur when females visit a patch simultaneously than when they visit sequentially (prediction 3). This is because when females search a patch simultaneously, conspecific superparasitism in the near future is more likely than when females visit a patch sequentially and therefore self-superparasitism has a higher pay-off in that situation. There is, however, a second reason why self-superparasitism is more profitable when a patch is searched simultaneously. When females search in groups, the interval between parasitism and conspecific superparasitism will be shorter than when females visit a patch sequentially. The pay-off from conspecific superparasitism decreases with this interval (Visser *et al.* 1992b) and therefore when a host containing an egg of a particular female is superparasitized with a short interval between ovipositions, the loss in offspring for the first

Table 1. Search times as predicted from the simulations for the first, second, third and fourth female sequentially visiting a patch

	First female	Second female	Third female	Fourth female
Search time	1338	722	332	5

female will be larger. Because self-superparasitism is a way to diminish a possible loss due to conspecific superparasitism, its profitability will not only increase with an increasing probability of conspecific superparasitism, but also with a diminishing interval between parasitism and conspecific superparasitism. It is for these two reasons that self-superparasitism is more profitable when searching a patch in the presence of conspecifics, and thus more superparasitism is predicted in that situation.

SEARCH TIMES

Simulations for sequentially visiting parasitoids show that the search time decreases with an increasing rank number of the visit although the second, third and fourth females visiting a patch all spent some time searching in the patch (Table 1). Therefore, the sums of search times increase with the number of females visiting a patch sequentially. When a patch is searched simultaneously, both self- and conspecific superparasitism become more profitable when more females visit a patch, and therefore it pays to stay longer. Thus, in both situations patch times increase with the number of females searching the patch (prediction 4).

Comparing the two situations, the model predicts that the sums of search times of females visiting a patch sequentially are larger than those of females searching a patch simultaneously (prediction 5). This difference is caused by the time used by the first female visiting a patch in rejecting parasitized hosts.

Materials and methods

We used *A. tabida*, a solitary larval *Drosophila* parasitoid. This species has a holarctic distribution. It attacks *Drosophila* larvae in fermenting substrates (i.e. fermenting fruits and sap streams on wounded trees). Although the main host species of *A. tabida* are in the *obscura*-group, other *Drosophila* species are also used. The parasitoid strain used in this study was collected in 1975 in a city garden in Leiden. It had been reared for at least 150 generations on *D. melanogaster* when we started the experiments. All parasitoids used were 3- to 6-day-old mated females. The day before an experiment parasitoids were individually placed on patches similar to those used in the experiments and allowed to search and parasitize

during 1 h. This training ensures that in the experiment the parasitoids all start searching immediately after introduction, and thus at the same time. Only females which searched and oviposited during this training period were used.

In the experiment we used early second instar larvae of *D. melanogaster*, 24-h-old, reared at 25°C. The same strain was used for rearing the parasitoids.

The experiments were done in small, 5 cm diameter petri dishes, with a circular patch (21 mm diameter) of live baker's yeast (0.125 g) suspended in water on top of a 5-mm thick agar bottom (20 g agar/litre water), at 20°C. Thirty-two host larvae were placed in each patch 1 h before an experiment began.

SEQUENTIAL PATCH VISITS

In the first series, all experiments were started by placing a single female *A. tabida* in a petri dish with a host patch. A parasitoid was allowed to search until it left the patch for longer than 60 s. Female *A. tabida* that have left the patch for longer than 60 s show a strong tendency to migrate and are very likely not to return to the patch at all (van Alphen & Galis 1983). For 10 replicates this was the end of the experiment. In 11 other replicates, a second female was introduced, immediately after the first one had been removed. This parasitoid was also allowed to search until it left the patch for longer than 60 s, when the experiment ended. In a third group of experiments, repeated 11 times, a third female was introduced immediately after the second had been removed, and in the last group of 10 experiments a fourth female was introduced after the third had been removed. Parasitoids were observed continuously and their behaviour was recorded with a digital event recorder.

SIMULTANEOUS PATCH VISITS

Two, three or four females of *A. tabida* were introduced simultaneously in a petri dish with a host patch, and their behaviour recorded on video tape. Females which left the patch for more than 60 s were removed. An experiment ended when the last female had left the patch for more than 60 s. Videotapes were played back, and behaviour of individual parasitoids was recorded with the digital event recorder.

After each experiment, hosts were removed from the patch and dissected in a droplet of water under a stereomicroscope to determine the number of parasitoid eggs in each host.

Results

EGG DISTRIBUTIONS

When only one female visited a patch, it oviposited in on average 66% of all hosts before leaving. In

contrast with the predictions of the model 12% of the parasitized hosts had been superparasitized (Fig. 1a). When more than one female visited a patch, both when these visits were simultaneous and sequential, more superparasitism occurred than when a single female searched the patch ($P = 0.004$ and $P = 0.01$ for simultaneous and sequential patch visits respectively; Mann-Whitney *U*-test on the average number of eggs per host for patches visited by one female *vs* patches visited by two females, *P*-values for one female *vs* three or four females are smaller than 0.001 for both set ups). The degree of superparasitism increased for both sequential and simultaneous patch visits with the number of females visiting a patch (Fig. 1b-d), but only for the simultaneously searching females were differences significant [$P = 0.003$ and $P = 0.002$ for two *vs* three females and two *vs* four females respectively ($P = 0.08$ for three *vs* four females), Mann-Whitney *U*-test on the average number of eggs per host per patch].

More superparasitism occurred when females searched a patch simultaneously than when the same number of females visited a patch sequentially ($P = 0.62$, $P = 0.05$ and $P = 0.004$ for two, three and four females respectively, Mann-Whitney *U*-test on the average number of eggs per host per patch). This difference is due to the decisions of the parasitoids, because no differences in the number of encounters with hosts of parasitoids visiting a patch sequentially compared to those visiting simultaneously were found (Table 2). Thus, females visiting a patch sequentially more frequently rejected parasitized hosts and thus superparasitized less.

SEARCH TIMES

The sum of the search times of females visiting a patch increased with the number of females visiting a patch, although not all differences are significant ($P = 0.04$, $P = 0.05$ and $P = 0.16$ for the simultaneously searching parasitoids and $P = 0.007$, $P = 0.06$ and $P = 0.10$ for the sequentially searching parasitoids, when comparing one *vs* two, two *vs* three and three *vs* four introduced females respectively; Mann-Whitney *U*-test on the sum of patch times of all females per patch). No differences in the sums of search times were found between females visiting a patch simultaneously and females visiting sequentially (Fig. 2; $P = 0.32$, $P = 0.41$, and $P = 0.31$ when comparing sequential *vs* simultaneous patch visits for two, three and four females respectively; Mann-Whitney *U*-test on the sum of patch times of all females per patch).

Discussion

The predictions of the model for superparasitism by females visiting a patch sequentially illustrate an important difference between predators and parasitoids. When an optimally foraging predator depletes

Fig. 1. Frequency histograms of the distribution of eggs over hosts for the seven experiments (a) one female, (b) two females, (c) three females and (d) four females. Each distribution is the average of a number of replicates; see last column of Table 3.

Table 2. Mean number of encounters per experiment $\pm$ standard deviation, summation for all females searching the patch

No. of females	Visits sequentially	Visits simultaneously	Mann-Whitney <i>U</i> -test
2	230.7 $\pm$ 80.7	177.4 $\pm$ 87.7	$P = 0.15$
3	304.9 $\pm$ 164.6	305.0 $\pm$ 33.4	$P = 0.43$
4	318.3 $\pm$ 103.3	298.5 $\pm$ 50.4	$P = 0.30$

a patch until the marginal value (Charnov 1976) is reached, a second predator finding that patch should reject it, because it will find a higher reward elsewhere in the habitat. However, when an optimally foraging parasitoid depletes the unparasitized hosts in a patch and leaves at the marginal value, a second parasitoid can still gain offspring from that patch before it, on its turn, reaches the marginal value. This is possible because the gain from conspecific superparasitism is higher than that from self-superparasitism, and self-superparasitism is the only option available to the first female visiting the patch. In an analogous way it can be explained why even for a third and a fourth parasitoid foraging in the patch can be profitable, albeit for a short time.

For predators depleting a patch simultaneously and leaving when the marginal value has been reached, the sum of their search times should equal the time spent searching by a single predator when it searches the patch alone, assuming no interference between the predators. When parasitoids search a patch simultaneously, the sum of their search times exceeds that of a single parasitoid because the advantage of conspecific superparasitism allows them

Fig. 2. The average observed patch times (s) with SE for the seven experiments (for the number of replicates; see last column of Table 3).

to stay longer. Therefore, competition through parasitism generates aggregation in parasitoids (van Alphen 1988; see also G. Driessen & M.E. Visser, submitted for publication) and aggregation can contribute significantly to the stability of parasitoid and host population interactions (Hassell & May 1974).

A qualitative agreement between the following predictions of the model and the results of the experiments was found. More superparasitism is observed when a number of parasitoids deplete a patch compared to when a patch is searched by one female, both for simultaneous patch visits and for sequential patch visits. In the experiments with simultaneously searching females, superparasitism increases as a function of the number of females in the patch (prediction 2). More superparasitism occurred when females visited a patch simultaneously than when they visited it sequentially (prediction 3). The total amount of search time spent in a patch increases with the number of females visiting the patch (prediction 4).

A discrepancy between the predictions of the model and results from the experiments is that females, exploiting a patch alone, superparasitized: 8% of all hosts, or 12% of the parasitized hosts, contained more than one egg (prediction 1). Because the model does not attribute any value to self-superparasitism when a female searches a patch alone, it predicts that no superparasitism should occur. However, when other females visit the same patch later, the risk is high that a host will be attacked by a conspecific and self-superparasitism can be advantageous. Visser *et al.* (1990) have shown for *L. heterotoma* that females which have been stored together with conspecifics prior to an experiment do self-superparasitize, whereas for parasitoids that had been isolated from conspecific females during their whole life as adult, hardly any self-superparasitism was found. The *A. tabida* females used in our experiments had been stored with other females in the same jar prior to the experiment. This may have caused the observed self-superparasitism.

The model predicts that the sums of search times for females visiting a patch together should be considerably smaller than those of females visiting a patch sequentially (prediction 5). This difference is caused by the time used by the first female visiting a patch in rejecting parasitized hosts. In the experiments no significant differences were found between the sums of search times of females visiting a patch simultaneously and females visiting a patch sequentially. This is due to the third and fourth parasitoid visiting a patch in the experiments, which stayed much longer than our model predicts. One explanation for this observation is that parasitoids that find a patch already exploited by competitors, perceive the habitat as less valuable than when they are the first to find a patch and leave at a lower threshold rate. Another reason for this discrepancy between

model and experiments is that the model assumes that parasitoids are omniscient, and the parasitoids in the experiments have to spend some time foraging in the patch before they can assess its value.

The patch times found in the experiments were considerably longer than those predicted by the model, even though the encounter rate used in the model was set to that measured in the experiments. An assumption in the model is that the parasitoids search randomly, and hence, that each host has the same probability of being encountered. We checked whether this was true in the experiments, by calculating for each replicate the expected search time (T_s) from the number of hosts attacked (N_a):

$$N_a = N_i (1 - e^{-\left(\frac{\lambda T_s}{N_i}\right)}) \quad \text{eqn 1}$$

with N_i = number of hosts offered and λ = encounter rate with hosts, calculated as the number of encounters per unit of time spent searching. The search time observed was much longer than expected (Table 3). The explanation for this is that a number of hosts escaped parasitism by leaving the patch. This happened because we used very thin layers of yeast, to be able to see ovipositions and rejections. Host larvae that leave the patch sometimes crawl into the crevice between the side of the petri dish and the agar bottom and so become unavailable to the parasitoids. A second reason for this difference is that the number of ovipositions in the experiments estimated from the number of eggs found at dissection, is an underestimate. In most experiments, more ovipositions were observed than eggs found (Table 4). This indicates that parasitoids used a lower threshold rate for patch leaving than we had assumed on the basis of the number of eggs found, and explains the longer patch times in the experiments.

Three of the predictions of the model are met in the experiments (predictions 2, 3 and 4), the discrepancy between the other two predictions and the results of the experiment are due to the fact that the assumptions of the model are not met in the experiments. The first female visiting a patch does anticipate the visits of other females in the near future (possibly due to the way of storing the females before the experiment), and therefore superparasitizes (opposite to prediction 1). And secondly, females introduced second, third or fourth on the patch, and thus encountering a partly depleted patch, take this into account in their patch time allocation. It seems that they use a lower value for the leaving threshold, where the model assumes that all females use the same value. We therefore conclude that the model is not falsified due to the fact that two of its predictions are not met.

One of the main questions we addressed was whether there is a difference in the level of superparasitism when the same number of parasitoids search a patch either sequentially or simultaneously. More

Table 3. Mean observed search times and predicted search times for the seven experiments. Replicates in which all hosts were parasitized are excluded from the analysis because in those cases the predicted search time is infinitely large (see equation 1). Number of replicates on which the mean is calculated is n , the number of excluded replicates is m

Experiment	Mean search time observed	Search time predicted	Wilcoxon MPSR test	$n (m)$
One female	2836.6	920.8	$P < 0.01$	20 (1)
Two females, seq.	4766.0	1641.4	$P < 0.01$	9 (2)
Two females, sim.	3877.5	1667.6	$P < 0.01$	11 (0)
Three females, seq.	6490.4	1752.7	$P < 0.05$	8 (2)
Three females, sim.	6007.4	1777.3	$P < 0.05$	8 (1)
Four females, seq.	7702.0	2160.5	$P = 0.06$	5 (0)
Four females, sim.	8592.5	2765.4	$P = 0.37$	2 (4)

Table 4. Mean number of observed ovipositions and mean number of eggs found in the hosts for the seven experiments

Experiment	Mean number of ovipositions observed	Mean number of eggs found	Wilcoxin MPSR test
One female	29.9	23.6	$P < 0.01$
Two females, seq.	46.8	36.8	$P < 0.01$
Two females, sim.	37.7	34.4	$P < 0.01$
Three females, seq.	53.9	41.3	$P < 0.01$
Three females, sim.	78.6	57.2	$P = 0.11$
Four females, seq.	61.9	48.7	$P = 0.06$
Four females, sim.	59.0	76.3	$P = 0.06$

superparasitism is predicted and found in the latter situation. This difference is due to the higher gain from self-superparasitism when searching in the presence of other parasitoids. Females visiting a patch after the previous female has left will only benefit from self-superparasitism when other females will arrive in that patch in the near future (see predictions of the model).

This difference in gain from self-superparasitism between females searching a patch simultaneously and females visiting a patch sequentially may provide a functional explanation for the observation that some parasitoids are able to discriminate between hosts parasitized by themselves from hosts parasitized by conspecifics (Hubbard *et al.* 1987; Völkl & Mackauer 1990; van Dijken, van Stratum & van Alphen 1992; M.E. Visser, submitted for publication; M.E. Visser, J.J.M. van Alphen & H.W. Nell, submitted for publication) whereas other species seem to lack this ability (van Dijken & Waage 1987; Bai & Mackauer 1990). When simultaneous patch visits are common, the gain from self-superparasitism means that it does not pay to discriminate between hosts parasitized by oneself and those parasitized by others. On the other hand, when parasitoids rarely meet, it may pay to distinguish the two categories of parasitized hosts (M.E. Visser, submitted for publication). The latter is a common condition when hosts occur singly or in small groups.

Superparasitism is a common phenomenon in the field, especially when parasitoid numbers are high

(Takagi 1987; Barrett & Brunner 1990). When parasitoids are abundant, there is a high probability that more than one female will visit a patch. Both when a patch is searched sequentially and when parasitoids search the patch simultaneously, superparasitism may pay. In the latter situation however, it pays more and the level of superparasitism is therefore higher. It is thus not only the number of parasitoids that search a habitat that will determine the level of superparasitism, but also the way they are distributed over the patches. Differences in the distribution of parasitoids may therefore influence the distribution of eggs also in a more indirect way than assumed in population dynamic models.

Acknowledgements

We thank G. Boskamp and K. van Wijk for their assistance with the experiments. This investigation was supported by the Foundation for Biological Research (BION-code 436-026), which is subsidized by The Netherlands Organization for Scientific Research (NWO).

References

- van Alphen, J.J.M. (1988) Patch time allocation by insect parasitoids: superparasitism and aggregation. *Population Genetics and Evolution* (ed. G. de Jong), pp. 215–221. Springer-Verlag, Heidelberg.
- van Alphen, J.J.M. & Galis, F. (1983) Patch time allocation and parasitization efficiency of *Asobara tabida*, a larval

- parasitoid of *Drosophila*. *Journal of Animal Ecology* **52**, 937–952.
- van Alphen, J.J.M. & van Harsel, H.H. (1982) Host selection by *Asobara tabida* Nees (Braconidae; Alysiinae), a larval parasitoid of fruit inhibiting *Drosophila* species. III. Host species selection and functional response. *Foraging Behaviour of Asobara tabida* (ed. J.J.M. van Alphen) pp. 61–93. PhD thesis, University of Leiden, The Netherlands.
- van Alphen, J.J.M. & Nell, H.W. (1982) Superparasitism and host discrimination by *Asobara tabida* Nees (Braconidae: Alysiinae), a larval parasitoid of Drosophilidae. *Netherlands Journal of Zoology* **32**, 232–260.
- van Alphen, J.J.M. & Visser, M.E. (1990) Superparasitism as an adaptive strategy for insect parasitoids. *Annual Review of Entomology* **35**, 59–79.
- Bai, B. & Mackauer, M. (1990) Self and conspecific host discrimination by the aphid parasitoid *Aphelinus asychis* Walker (Hymenoptera: Aphelinidae). *Canadian Entomologist* **122**, 363–372.
- Barrett, B.A. & Brunner, J.F. (1990) Types of parasitoid-induced mortality, host stage preferences, and sex ratios exhibited by *Phygadeuon flavipes* (Hymenoptera: Eulophidae) using *Phyllonorycter elmaella* (Lepidoptera: Gracillariidae) as a host. *Environmental Entomology* **19**, 803–807.
- Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology* **9**, 129–136.
- Charnov, E.L. & Skinner, S.W. (1985) Complementary approaches to the understanding of parasitoid oviposition decisions. *Environmental Entomology* **14**, 383–391.
- van Dijken, M.J. & Waage, J.K. (1987) Self and conspecific superparasitism by the egg parasitoid *Trichogramma evanescens*. *Entomologia experimentalis et applicata* **43**, 183–192.
- van Dijken, M.J., van Stratum, P. & van Alphen, J.J.M. (1992) Recognition of individual-specific marked parasitized hosts by the solitary parasitoid *Epidinocarsis lopezi*. *Behavioral Ecology and Sociobiology* **30**, 77–82.
- Hassell, M.P. & May, R.M. (1974) Aggregation in predators and insect parasites and its effect on stability. *Journal of Animal Ecology* **43**, 567–594.
- Hubbard, S.F., Marris, G., Reynolds, A. & Rowe, G.W. (1987) Adaptive patterns in the avoidance of superparasitism by solitary parasitic wasps. *Journal of Animal Ecology* **56**, 387–401.
- Iwasa, Y., Suzuki, Y. & Matsuda, H. (1984) Theory of oviposition strategy of parasitoids. I. Effect of mortality and limited egg number. *Theoretical Population Biology* **26**, 205–227.
- Janssen, A. (1989) Optimal host selection by *Drosophila* parasitoids in the field. *Functional Ecology* **3**, 469–479.
- Parker, G.A. & Courtney, S.P. (1984) Models of clutch size in insect oviposition. *Theoretical Population Biology* **26**, 27–48.
- Strand, M.R. & Godfray, H.C.J. (1989) Superparasitism and ovicide in parasitic Hymenoptera: a case study of the ectoparasitoid *Bracon hebetor*. *Behavioral Ecology and Sociobiology* **24**, 421–432.
- 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, M.E. (1991) Prey selection by predators depleting a patch; an ESS model. *Netherlands Journal of Zoology* **41**, 63–79.
- Visser, M.E., van Alphen, J.J.M. & Nell, H.W. (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, M.E., van Alphen, J.J.M. & Hemerik, L. (1992a) Adaptive superparasitism and patch time allocation in solitary parasitoids: an ESS model. *Journal of Animal Ecology* **61**, 93–101.
- Visser, M.E., Luyckx, B., Nell, H.W. & Boskamp, G.J.F. (1992b) Adaptive superparasitism in solitary parasitoids: marking of parasitized hosts in relation to the pay-off from superparasitism. *Ecological Entomology* **17**, 76–82.
- Völkl, W. & Mackauer, M. (1990) Age-specific host discrimination by the aphid parasitoid *Ephedrus californicus* Baker (Hymenoptera: Aphididae). *Canadian Entomologist* **122**, 349–361.

Received for publication 1 July 1991; revised 18 November 1991; accepted 3 March 1992