

PATCH TIME ALLOCATION AND PARASITIZATION
EFFICIENCY OF *ASOBARA TABIDA*, A LARVAL
PARASITOID OF *DROSOPHILA*

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SUMMARY

(1) Patch time allocation by the parasitoid *Asobara tabida* Nees was studied on patches with different host densities.

(2) The parasitoid increased its searching time and giving up time with increasing host density. These increases were caused by a response of the parasitoid to the number of encounters with unparasitized hosts; the amount of kairomone in a patch may have had an additional incremental effect on patch time.

(3) Encounters with parasitized hosts had no effect on searching time and giving up time.

(4) The percentage of hosts parasitized first increased with host density and then levelled off at densities of more than four host larvae per patch, thus producing an accelerating functional response.

(5) The foraging behaviour of *A. tabida* is compared to that predicted by optimal foraging models.

INTRODUCTION

In the analysis of foraging behaviour of predators and parasitoids, the question of how foraging time is allocated between patches of different profitability by a foraging predator or parasitoid has received a lot of interest. The question has been studied by investigators whose main interest was to show that certain behaviour patterns may enhance population stability (e.g. Royama 1971a; Hassell & May 1973, 1974; Murdoch & Oaten 1975) as well as by those who wanted to show that certain behaviour patterns are adaptive and help to maximize the numbers of offspring of individual foragers (Charnov 1976; Cook & Hubbard 1977; Comins & Hassell 1979; Waage 1979; Royama 1971b). Both approaches lead to the question of efficiency of foraging behaviour.

The response of an individual predator to prey density, the functional response, was classified by Holling (1959) into three types: type I, in which there is a linear rise to a maximum in the number of prey eaten per unit of time as prey density increases; type II, where the response rises at a decreasing rate towards a maximum value; type III, where the response is sigmoid and also approaches an upper asymptote. The type III response may have a regulating potential over the range of densities where the curve is accelerating and, therefore, may enhance population stability.

To discuss the stabilizing properties of sigmoid functional responses it is necessary to distinguish the different situations in which they may occur.

One prey or one host species

Two situations have been studied where individual predators search for a single prey species. The first situation is represented by a model of Hassell, Lawton & Beddington (1977) and by experiments in which different individual predators are offered different prey densities, to each individual predator a fixed number of prey. Examples of sigmoid functional responses found with this experimental set-up are Takahashi's (1968) study of *Nemeritis canescens* ('confined experiment' only) and the examples given by Hassell *et al.* (1977). A special case are the experiments by van Lenteren & Bakker (1976, 1978) with *Leptopilina heterotoma*, in which this parasitoid itself determined the time spent on a patch. These experiments resulted in a sigmoid relation between patch density and average number parasitized per patch (series 2 and 3), but this is no functional response according to the definition, which requires a sigmoid relation between patch density and the number of hosts parasitized *per unit of time*. However, this distinction is not of great biological importance. The different prey or host densities in these experiments can be considered as differences occurring through time and the question of whether functional responses can stabilize host populations is concerned with the relation between host or prey density and the number taken through time.

Hassell & Comins (1978) studied the stabilizing properties of sigmoid functional responses using difference equations based on Rogers' 'Random Parasite Equation' (Rogers 1972). They concluded that due to the one generation time delay the sigmoid functional response could not stabilize an otherwise unstable parasitoid-host model. However, Nunney (1980), also working with difference equations, demonstrated a stabilizing effect of a sigmoid functional response in a model which included the ability of parasitoids to discriminate between parasitized and unparasitized hosts. Even when the sigmoid functional response alone cannot stabilize a system by itself, the presence of a sigmoid response adds to the likelihood of stability when other density-dependent factors operate on the system.

The second situation in which a sigmoid functional response may occur is represented by experiments in which the predators or parasitoids search for simultaneously available patches with different prey or host densities. Murdoch & Oaten (1975) have demonstrated with a model based on differential equations that in such a system the overall functional response through time (not to be confused with the functional response to patch density, the response in space) may be powerful enough to stabilize the model. Murdoch & Oaten's (1975) model has a greater complexity than that of Hassell & Comins (1978): the most important parameters affecting its stability was the amount of time spent in travelling between the patches ('transit time').

Two or more prey or host species

When a predator or parasitoid distributes its attacks in response to the relative frequencies of the prey or host species, concentrating its attacks disproportionately on the more abundant prey (a phenomenon called 'switching') this may also produce sigmoid functional responses with stabilizing properties (Hassell 1978; Murdoch & Oaten, 1975). Sigmoid functional responses of polyphagous predators and parasitoids are discussed in more detail by van Alphen & van Harsel (unpubl.).

Though Murdoch & Oaten (1975) already distinguished the different situations in which sigmoid functional responses can occur, later papers discussing the meaning of functional responses for population stability (van Lenteren & Bakker 1976, 1978; Hassell *et al.* 1977; Hassell & Comins 1978) do not make this distinction. We believe that it is important

to realize that different behaviour patterns on a different scale in space and/or time may produce sigmoid functional responses, and that therefore one should make explicit which particular situation is discussed. In this paper we present experiments that describe patch time allocation and parasitization efficiency of the larval *Drosophila* parasitoid *Asobara tabida* Nees (Braconidae; Alysiinae).

Galis & van Alphen (1981), studying patch time allocation and searching intensity by *A. tabida* found that:

(i) *Asobara tabida* reacts to a water-soluble kairomone produced by the host *Drosophila melanogaster* in that (a) time spent on the patch (yeast patch in which *D. melanogaster* larvae had crawled and fed) increased in an S-shaped fashion with increasing numbers of host larvae that had produced kairomone in the patch, until it levels off at higher concentrations, and (b) the searching intensity by the parasitoid (defined as the number of times the parasitoid stood motionless per unit of time) increased with increasing kairomone concentration until it levels off at higher concentrations;

(ii) *A. tabida* recognized areas previously searched by a conspecific and spent less time and searched less intensively in such patches as compared to those that had not been searched before;

(iii) patches with a reduced quality (reduced amount of living yeast) for the host are less attractive for the parasitoid which spends less time and searches less intensively on such patches than on patches with a better resource quality for the host.

We concluded that the response of the parasitoid to these three factors contributes to the optimization of time allocation and that an increase in search intensity may lead to a type III functional response.

Here we present experiments in which we measured the functional response of *A. tabida*. The experiments are of the kind in which each parasitoid only visits one patch which contains a specific number of individuals of one host species and thus they represent the simplest situation of those described above.

MATERIAL AND TECHNIQUES

Adult female *A. tabida* wasps, 'Leiden' strain (for origin and rearing see van Alphen & Nell 1982) were stored at 10 °C until required for experimentation. One day prior to an experiment the wasps were allowed to oviposit in hosts for 1.5–2 h at 20 °C to gain experience (see Samson-Boshuizen Lenteren & Bakker 1972). Experienced females were then kept at 20 °C with sugar water as source of carbohydrates and moisture. Early second instar larvae of *D. melanogaster*, strain WW were used as hosts (for rearing and origin see Bakker 1961).

Preparation of the patches

A viscous suspension of yeast, 2 cm diameter, was placed on a layer of agar in a 5 cm Petri dish. The yeast suspension contained 0.125 g of yeast. In these patches 1, 2, 3, 4, 8, 16, 32 or 64 host larvae were allowed to crawl and feed for 18 h. During this period the patch was enclosed within a perspex ring (2 mm high) to prevent the larvae from leaving the patch. After 18 h the larvae and the perspex ring were removed. We then added 1.5 ml water to the yeast and filtered this liquid. To the filtrate we added an amount of fresh yeast of the same age, equal to the original amount. The excess water was evaporated to provide a suitable substrate for the searching parasitoid. Using this procedure we obtained patches containing an amount of kairomone produced by the different numbers of host larvae, all

having the same yeast quality (Galis & van Alphen 1981). Then we added the same number of host larvae that had previously crawled in the yeast spot half an hour prior to offering the patch to individual wasps.

The experiments

Four series of experiments were done. The first series of experiments (series I) consisted of exposing a patch to a single female of *A. tabida*. An experiment was terminated when the wasp left the patch for more than 1 min or when she attempted to migrate. This latter was manifested when a parasitoid walked to the lid of the Petri dish and attempted to leave. In practically all experiments both of the above criteria were applicable. We recorded the experiments on videotape, while simultaneously observing the parasitoid's behaviour with a stereomicroscope. At the end of an experiment we dissected the larvae to check for superparasitization. The following parameters were measured:

- (i) duration of the experiment;
- (ii) time spent on the patch;
- (iii) time spent searching;
- (iv) time spent locating larvae before parasitization and after detection;
- (v) time spent parasitizing;
- (vi) time spent rejecting;
- (vii) time spent in unsuccessful host location (iv + v + vi + vii = total handling time);
- (viii) giving up time (g.u.t., the time spent on the patch after the last parasitization, and, if no parasitization occurred, the total time spent on the patch);
- (ix) number of parasitizations;
- (x) number of superparasitizations;
- (xi) number of rejections;
- (xii) number of contacts after the last parasitization;
- (xiii) number of stops.

For a detailed description of the searching and parasitization behaviour of *A. tabida* see van Alphen & Drijver (1982).

Ten experiments were carried out for each larval density. In addition we did a series of experiments to investigate the effect of an oviposition on giving up time (series II). Van Lenteren & Bakker (1976, 1978) found that *Leptopilina heterotoma* has a longer giving up time after finding a single host compared with giving up time on a similar patch on which no host is found. A similar increase in giving up time was found by Roitberg *et al.* (1982) for the tephritid fly *Rhagoletis pomonella* after one oviposition in a hawthorn fruit. Luck *et al.* (1979) showed that this increase in giving up time after the first encounter with a host can produce a sigmoid functional response. Because the parasitoids found a host larva at density 1 in only two replicates in series I, we increased the number of experiments at this density until we had ten replicates in which the wasp found the larva. By comparing the results of these experiments with those of Galis & van Alphen (1981) (patches with kairomone produced by one larva) we could determine whether *A. tabida* increases its giving up time after the first encounter with a host.

It has been suggested that a number of probes in already parasitized hosts may initiate migration and, hence, that encounters with parasitized hosts among other factors determine patch time (van Lenteren 1981). We tested this hypothesis in the following experiments (series III). Experienced females of *A. tabida* were allowed to search for half an hour on a patch containing thirty-two host larvae. Four host larvae parasitized during this period were removed and placed in a yeast patch containing an amount of kairomone produced

by four larvae. This patch was prepared in a similar manner as described for those used in the first series of experiments. About 30 min after a wasp was removed from the patch with thirty-two larvae, it was either introduced onto a patch with four larvae parasitized by herself and kairomone produced by four larvae, or onto a patch containing only kairomone produced by four larvae. The experiments lasted until the wasp left the patches containing parasitized larvae and ten experiments with patches with only kairomone were carried out. The behaviour of the wasps was recorded on videotape.

Because *A. tabida* finds its hosts by reacting to their movements (van Alphen & Drijver 1982), a reduced activity of the host larvae after parasitization may result in a reduced chance to be encountered again by the parasitoid after parasitization. We measured the activity of unparasitized and parasitized larvae in the following way (series IV). Patches similar to those in series I were used, each containing eight larvae. To obtain parasitized larvae, an experienced female of *A. tabida* was allowed to search on a patch containing eight larvae until she had parasitized all of them. Then the wasp was removed and the Petri dish was turned upside down. A second Petri dish, containing eight unparasitized larvae that had crawled in the patch for the same period that the other patch had been exposed to the parasitoid, was also turned upside down. The larvae that had buried themselves in the yeast could now be observed through the bottom of the Petri dish and the transparent agar bottom with the aid of a stereomicroscope. Every 15 min we counted the number of active larvae and the mean number of mandibular movements made per 20 s for each active larva. Larvae were classified as active when we saw either mandibular movements or crawling, or both. Each of the twenty experiments lasted 2.5 h. The total number of observations per experiment was ten.

RESULTS AND DISCUSSION

Allocation of time to patches of different densities

The total patch time in the experiments of series I can be subdivided into four categories: searching time, handling time of accepted hosts, handling time of rejected hosts and time spent probing without succeeding parasitization or rejection. Time devoted to other activities (e.g. preening) is less than 1% of the total patch time and is therefore neglected.

The total time spent on a patch increased linearly with increasing larval densities (Fig. 1: abscissa on a log-scale). The searching time also increased linearly with larval densities (Fig. 2). The strong correlation between the number of hosts parasitized in a patch and the time a wasp spent searching on the patch ($r_s = 0.91$; $P < 0.01$; $n = 80$) suggests that encounters with unparasitized hosts have an incremental effect on the searching time. Further evidence for this comes from the comparison of the searching time (= giving up time) in those experiments on patches containing an amount of kairomone produced by one larva (Galís & van Alphen 1981) with the giving up time in those experiments on patches containing a single larva that was found by the parasite (series II; Table 1): giving up time, and hence searching time, is longer in those experiments in which the single larva was found by the parasite than in experiments in which only the kairomone of one larva was present (Mann-Whitney U ; $P < 0.05$). The same can be demonstrated when we compare the searching time on patches containing larvae plus kairomone (series I) with searching time on patches containing only kairomone from a corresponding number of larvae (Galís & van Alphen 1981: series b): at all densities searching time is longer on patches containing the larvae (Table 2).

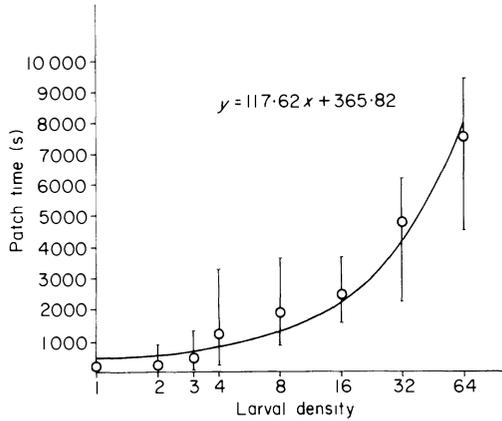


FIG. 1. The relation between larval density and total time spent on the patch (abscissa on log-scale). The vertical bars indicate lowest and highest values. Line drawn from regression analysis ($r_s = 0.93$; $P < 0.01$).

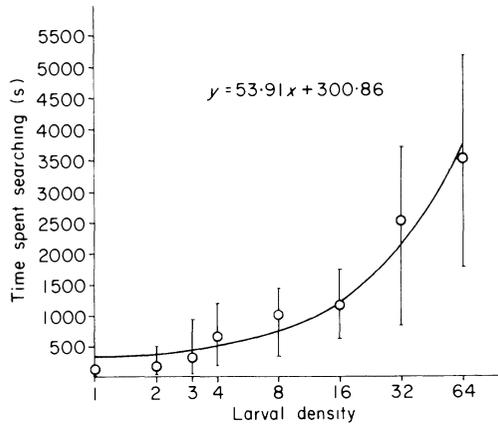


FIG. 2. The relation between larval density and searching time. (Abscissa on log-scale.) The vertical bars indicate lowest and highest values. Line drawn from regression analysis ($r_s = 0.89$; $P < 0.01$).

TABLE 1. Mean giving up time (s) on patches containing only kairomone produced by one larva (kairomone only) or kairomone produced by one larva and one larva which is parasitized during the experiment ($n = 10$)

	Kairomone only	With larvae
Mean g.u.t.	79.6	277.3
S.D.	87.8	165.2

Galis & van Alphen (1981) have shown that the wasp spends most of its searching time standing still. While standing still the parasitoid perceives the movements of the host (van Alphen & Drijver 1982). The increase in the number of stops (not including stops during parasitization or rejection) in patches with an increasing number of larvae thus corresponds with the increase in searching time (Fig. 3).

TABLE 2. Mean searching time (s) of *A. tabida* on patches with kairomone produced by different numbers of larvae and on patches containing different numbers of larvae and an amount of kairomone produced by a corresponding number of larvae

No. of larvae or no. of larvae that produced kairomone	Kairomone only	With larvae
1	79.6 S.D. 87.8	206.0 S.D. 84.9
2	159.4 S.D. 70.8	282.3 S.D. 151.9
4	466.1 S.D. 267.1	700.4 S.D. 363.6
32	425.5 S.D. 189.6	3090.2 S.D. 479.2
64	441.3 S.D. 166.4	3678.8 S.D. 611.5

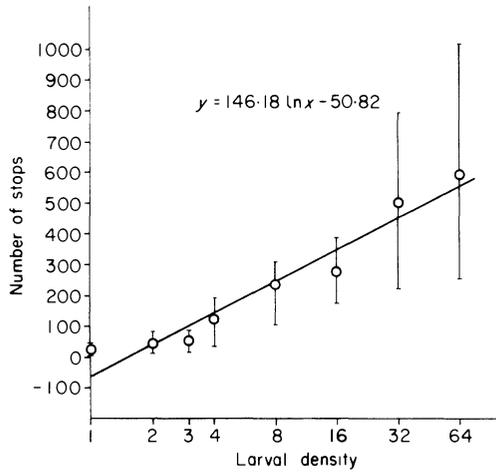


FIG. 3. The relation between larval densities and the number of stops made by *A. tabida*. Standing motionless during oviposition and rejection are excluded. The vertical bars indicate lowest and highest values. Line drawn from regression analysis ($r_s = 0.85$; $P < 0.01$).

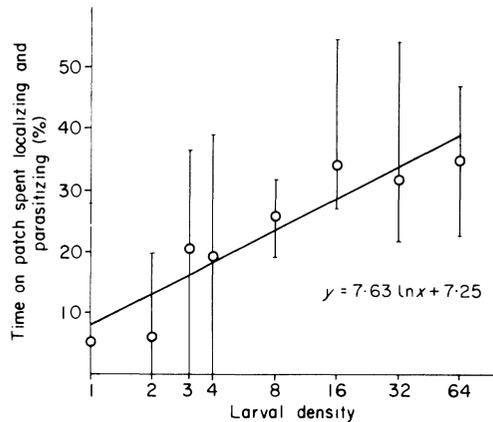


FIG. 4. Total time spent handling hosts (= time spent in parasitization + time spent in rejection + time spent in successful and unsuccessful localizations of hosts) at different host densities. The vertical bars indicate lowest and highest values. Line drawn from regression analysis ($r_s = 0.69$; $P < 0.01$).

Handling time

As expected, the time on the patch spent localizing and parasitizing or rejecting hosts increased with larval density and this increase was steeper than the increase in time on the patch, since the proportion of time spent on the patch spent handling hosts increased with larval density (Fig. 4).

Giving up time and the longest interval between parasitizations

Giving up time (g.u.t.) as well as the longest interval between parasitizations both increased with host density (Fig. 5).

In the models that are based on a fixed g.u.t. for a certain habitat (Krebs, Ryan & Charnov 1974; Cook & Hubbard 1977) it is assumed that in rich habitats the g.u.t. is shorter than in poor habitats. Our results are thus in contradiction with these assumptions, though it must be kept in mind that in our experiments the habitats consisted of one single patch. Furthermore, the longest interval between parasitizations in an experiment was often longer than the g.u.t. (Fig. 5) and this is also in contradiction with the notion of a fixed g.u.t. for a specific habitat. However, McNair (1982) with a model for optimal giving up times, predicts that the g.u.t. should increase with increasing host density in a patch, as we found for *A. tabida*.

The strong correlation between the number of parasitizations and the g.u.t. ($r_s = 0.74$; $P < 0.01$; $n = 80$) indicates that encounters with unparasitized hosts have an incremental effect on the g.u.t. This impression is further corroborated by the observation that the g.u.t. in patches containing larvae plus kairomone (series I) is always longer than in those containing only kairomone from a corresponding number of larvae (Galis & van Alphen 1981), as well as by the comparison of the g.u.t. on patches only containing the kairomone

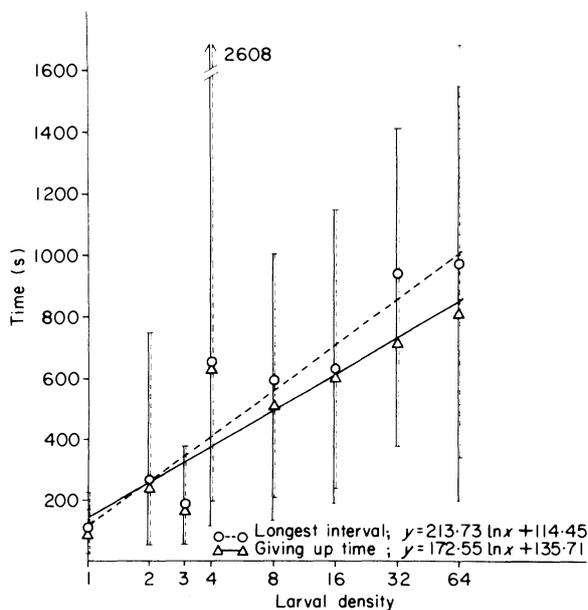


FIG. 5. Giving up time and longest intervals between parasitizations at different host densities. The vertical bars indicate lowest and highest values. Lines drawn from regression analysis (giving up time: $r_s = 0.53$; $P < 0.01$; longest interval: $r_s = 0.62$; $P < 0.01$).

from one larva with those in which one larva was parasitized (Table 1). Our conclusions differ from those of van Lenteren & Bakker (1978). They concluded that in *Leptopilina heterotoma* giving up time is independent of host density. They based their conclusion on patch time of females that searched at different densities of hosts and left *before* a host was found. However, they did not measure giving up time in experiments in which the wasps found host larvae. Therefore, their conclusion that giving up time is independent of host density is premature.

Number of contacts with unparasitized and parasitized hosts

If we assume that *A. tabida* searches randomly on the patch and that a parasitized larva has the same probability of being encountered as an unparasitized one, then the relation between the number of unparasitized hosts found and the total number of encounters with hosts (either parasitized or unparasitized) is given by:

$$N_a = N_t [1 - \exp(-N_e/N_t)]$$

(Thompson 1924; Nicholson & Bailey 1935), in which N_a is the number of hosts parasitized, N_t is the total number of hosts in the patch and N_e is the total number of encounters. A comparison of the total number of encounters from our data with those predicted by the model shows that the observed total number of encounters for a given number of ovipositions is always lower than expected. Figure 6 shows this for three wasps at density 64. The difference between the expected and the actual number of encounters is significant at all larval densities for which enough encounters occurred to allow analysis (larval densities of 8 and more; chi-square; $P < 0.001$). The low number of rejections is advantageous for *A. tabida*, since much time is saved this way: if the wasps had encountered the expected number of parasitized host larvae, the total handling time (of both parasitized and unparasitized larvae) would approximately have been doubled.

The lower number of encounters with parasitized hosts, as compared to the prediction of a random search model has two possible causes: either *A. tabida* does not search randomly, but more or less systematically, or the parasitized hosts have a lower chance to be encountered. Because *A. tabida* locates its hosts by sensing their movements in the medium, and because *A. tabida* partly paralyzes its hosts during parasitization (van Alphen & Drijver 1982), a lower encounter chance of parasitized larvae could be caused

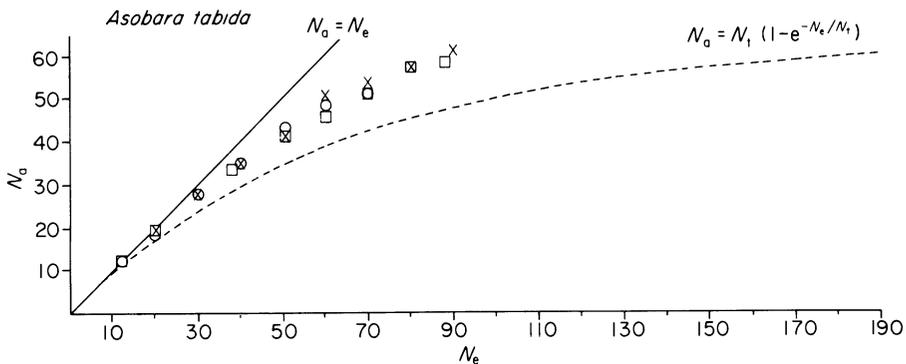


FIG. 6. The relation between the total number of encounters and the number of hosts parasitized: data of three experiments (\square , \circ and \times) and density 64 compared with a random search model (---) and with a model for systematic search (—). N_a = number of hosts parasitized; N_e = number of encounters with hosts; N_t = number of hosts.

TABLE 3. The activity of unparasitized and parasitized larvae expressed as the percentage of active larvae and the number of mandibular movements made by active larvae during 20 s. Ten observations of eight individuals were made per experiment

Experiment number	Moving larvae				Mean no. of mandibular movements of active larvae per 20 s	
	Parasitized %	no.	Unparasitized %	no.	Parasitized	Unparasitized
1	26.8	2.14	37.5	3.00	13.4	15.0
2	35.8	2.86	44.6	3.57	18.4	14.9
3	51.8	4.14	60.5	4.84	14.0	17.7
4	21.4	1.71	42.9	3.43	30.0	14.4
5	28.6	2.29	33.9	2.71	24.9	17.7
6	32.1	2.57	37.5	3.00	22.1	18.9
7	56.5	3.72	71.5	5.72	20.0	20.0
8	39.1	3.13	62.5	5.00	18.9	18.3
9	29.8	2.38	54.4	3.63	16.9	13.3
10	37.5	3.00	39.1	3.13	21.9	17.4
11	43.8	3.50	43.8	3.50	20.9	15.5
12	26.6	2.13	56.3	4.50	16.5	19.4
13	21.9	1.75	39.1	3.13	18.5	18.4
14	23.3	1.86	56.5	3.72	15.4	25.1
15	30.4	2.43	66.1	5.29	16.0	20.3
16	35.8	2.86	44.6	3.57	18.0	20.6
17	50.0	4.00	55.4	4.43	22.4	22.1
18	42.8	3.42	50.0	4.00	18.6	21.0
19	28.6	2.29	44.6	3.57	20.7	25.6
20	26.8	2.14	53.5	4.28	17.9	21.9
Mean	34.5	2.72	49.3	3.90	18.3	18.9
S.D.		0.74		0.83	3.65	3.35

by a lower activity of parasitized larvae. Indeed, the number of active parasitized larvae counted was significantly lower than the number of active unparasitized larvae (Wilcoxon matched pairs; $P < 0.01$) (Table 3). But active larvae of parasitized and unparasitized hosts did not show a difference in the mean number of mandibular movements per 20 s (Table 3). Therefore, we conclude that parasitized larvae spent more time motionless than unparasitized larvae, and that the former category has a smaller chance to be detected by the parasitoid.

Asobara tabida females are able to recognize a previously searched area and spend less time searching there than in an unsearched area (Galis & van Alphen 1981). This could enable them to search more or less systematically, and could be an additional explanation for the lower number of contacts with parasitized hosts than a random search model predicts. However, the host larvae are able to move freely in the patch and while searching on a patch *A. tabida* frequently crosses its own path and returns to previously searched parts of the patch. Hence, systematic search is unlikely.

Number of encounters after the last parasitization

The number of encounters after the last parasitization increased with the number of larvae that were present in the patches (Fig. 7). This increase corresponds with an increase in the g.u.t.. Because the percentage of parasitism is always high in patches in which at least one larva is parasitized (next section), most, if not all, contacts after the last parasitization must have been rejections of parasitized hosts. To investigate whether probes in parasitized hosts initiate migration, we did the experiments of series III: there was no difference in the time spent searching by *A. tabida* on patches containing only the kairomone produced by

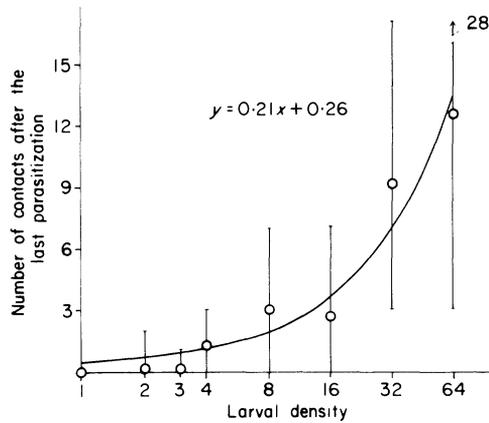


FIG. 7. The number of contacts after the last parasitization at different host densities. The vertical bars indicate lowest and highest values. Line drawn from regression analysis ($r_s = 0.94$; $P < 0.01$).

TABLE 4. Searching time (s) on patches containing kairomone produced by four larvae and on patches containing kairomone produced by four larvae and four parasitized larvae. The last column gives the number of encounters with parasitized larvae. Data on the number of encounters in the first five experiments were lost

Experiment number	Searching time (s)		No. of contacts with parasitized hosts
	kairomone only	kairomone + 4 parasitized larvae	
1	170	846	—
2	130	206	—
3	170	135	—
4	520	179	—
5	289	235	—
6	214	206	3
7	499	531	15
8	437	315	6
9	128	278	4
10	865	366	3
Mean	342.2	329.7	6.2
S.D.	237.6	213.8	5.1

four larvae and patches containing four parasitized larvae plus the kairomone produced by four larvae (Mann-Whitney U ; $P < 0.05$) (Table 4).

Similarly we observed no difference in the percentage of time spent standing still in both type of patches (Mann-Whitney U ; $P < 0.05$). Hence, there is no decremental effect on searching time resulting from encounters with parasitized hosts. Van Lenteren (1981) in his review of host discrimination, states 'Discrimination initiates migration after a number of probes at or in parasitized hosts. This advantage was discovered only recently, and bears important consequences for theories on optimal foraging (van Lenteren 1976; Hassell & Southwood 1978; van Lenteren & Bakker 1978; Waage 1979).' However, none of the cited papers presents data substantiating this statement. As far as we are aware, no data exist that support the theory that encounters with parasitized hosts have a decremental effect on patch time.

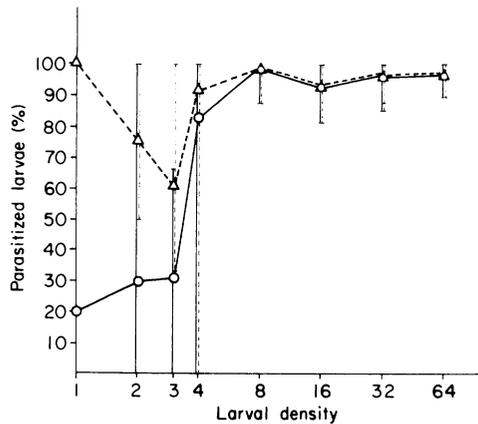


FIG. 8. The percentage of larvae parasitized at different densities. The vertical bars indicate highest and lowest values for all experiments (O—O) and experiments in which at least one larva is parasitized (Δ---Δ).

Percentage of parasitizations

The percentage of larvae that were parasitized increased with the number of larvae that the patch contained (Fig. 8). This increase levelled off at densities of four and more larvae. Hence, the relation between the density of larvae in a patch and the mean number of larvae parasitized is accelerating at low densities. The percentage of parasitism increased from an average of 20% at a larval density of one to an average of 95% at larval densities of four and more. Luck *et al.* (1979) have shown that an increase in g.u.t. after the first host has been found is enough to generate an accelerating relation between patch density and number of hosts parasitized.

This is probably not the only behavioural component that determines the relation between patch density and the number of hosts parasitized at a given density: other factors which may affect the shape of the curve include a host-density dependent increase in giving up time (Fig. 5), an S-shaped relation between searching time and the kairomone concentration in the patch (Galis & van Alphen 1981) and the incremental effect on searching intensity of an increasing amount of kairomone (Galis & van Alphen 1981). The latter produces an increase in the instantaneous attack rate. Hassell *et al.* (1977) have suggested that either an increase in the instantaneous attack rate or a decrease in handling time with increasing host densities could produce a sigmoid functional response. However, they did not discriminate between the two possibilities. Luck *et al.* (1979) studied the effect of handling time with increasing host density in a computer simulation and found that it failed to produce a sigmoid response. An increase in the instantaneous attack rate may therefore be more important than a decrease in handling time in generating sigmoid functional responses. Handling time (= time spent localizing + time spent parasitizing a host) does not vary with host density in our experiments with *A. tabida*, hence it has no influence on the sigmoid shape of the functional response.

Patch time spent per parasitization

At higher host densities, less searching time is spent per host larva that is parasitized, therefore patch time spent per parasitization decreases considerably with increasing larval density (Fig. 9).

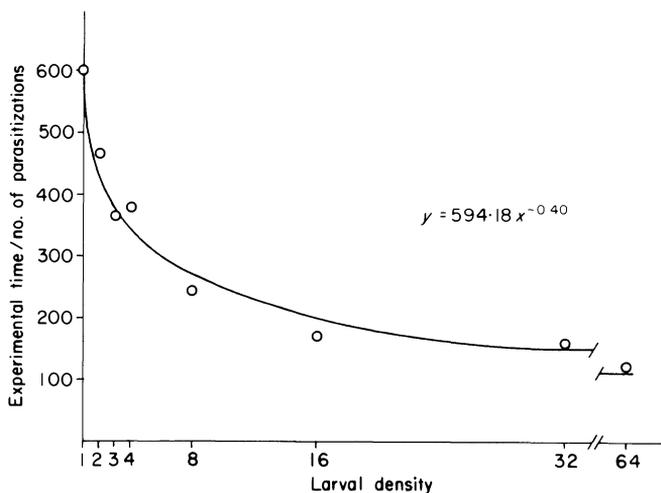


FIG. 9. Time spent per parasitization at different host densities. Line drawn from regression analysis ($r_s = 0.99$; $P < 0.01$).

It seems from the standpoint of optimal foraging theory that too much time is spent in patches with a low host density. However, this discrepancy between expected and observed patch time is probably due in part to the time necessary for sampling. As we concluded in a previous article (Galis & van Alphen 1981) this sampling time is greatly reduced by the presence of kairomone. The explanation of our data in terms of optimal foraging theory raises another problem. The percentage of parasitized hosts was very high ($\pm 95\%$) in patches which contained four or more larvae (Fig. 8). The time necessary for detecting the last unparasitized larvae was considerably longer than that of unparasitized larvae earlier in the experiments. According to Charnov's (1976) model these long giving up times can only be explained by relatively long travel times between the patches. This may in part be the explanation, since intraspecific competition is probably severe in the field and the parasitoids tend to distribute themselves over the different host patches in the habitat according to Fretwell's (1972) 'ideal free distribution' (van Alphen unpubl.); hence the chance of finding a better patch than the one the parasitoid is currently exploiting may be small. On the other hand, Charnov (1976) assumes in his model that the parasitoid knows the average host density of the patches in the habitat. This assumption is unrealistic for a short-lived parasitoid. Therefore, it may on average be more profitable for a wasp to stay somewhat longer on a patch where it can be relatively certain of parasitizing some additional larvae before leaving the patch to search for patches with unknown hosts densities.

CONCLUSIONS AND GENERAL DISCUSSION

Asobara tabida exhibited an increase in the searching time and giving up time with increasing host densities. These increases were caused by the response of *A. tabida* to the number of encounters with hosts, though this may not be the only factor which plays a role: the amount of kairomone in a patch may have had additional influence on searching time and instantaneous attack rate.

On the basis of our results, three of the models concerning time spent on a patch have to be rejected for *A. tabida*: the fixed time hypothesis (Krebs 1973), the fixed number hypothesis (Gibb 1962) and the fixed giving up time hypothesis (Cook & Hubbard 1977; Krebs *et al.* 1974). Our results, however, are in agreement with a model proposed by McNair (1982), which predicts that g.u.t. should increase with increasing host densities and with Waage's (1979) model, in which patch time is determined by the interaction of two incremental processes, the response to host-related chemicals and the response to oviposition and a decremental process, the waning of the response to the patch edge. However, several other factors are involved in the determination of patch time. One factor which has a decremental effect on patch time involves the response of the parasitoid to a mark left at a previous visit to the patch by a conspecific (Galis & van Alphen 1981). Patch marking has also been found by Price (1970) for several species of pupal parasitoids of sawflies, and by Greany & Oatman (1972) for *Orgilus lepidus*. Van Lenteren (1981) erroneously cites van Lenteren & Bakker (1978), Kooloos (unpubl.) and Waage (1979) as authors that have demonstrated patch marking by respectively *Leptopilina heterotoma*, *Opius pallipes* and *Nemeritis canescens*. These authors have demonstrated that the same individual wasp spends less time at the second and subsequent visits to a patch as compared to the duration of the first visit. When the same individual visits a patch for the second time it may recognize the patch from visual landmarks, or stay a shorter time because of a reduced motivation to search due to egg depletion, habituation to kairomone concentration or tiredness. Although patch marking is one of the possible explanations, we do not agree that these papers can be cited as proof that such a marking exists.

We were unable to demonstrate a decremental effect on patch time by encounters with parasitized hosts as proposed by van Lenteren (1981). So far as we are aware there is no published evidence that such an effect exists. Other factors which may influence patch time are: the amount of available food for the hosts (Galis & van Alphen 1981), the presence of conspecifics, the size of the patch (van Lenteren & Bakker 1978) and the distance to other patches.

Asobara tabida parasitized an increasing percentage of the hosts in a patch with increasing larval density. This increase levelled off at densities of four or more larvae. The increase in the proportion of parasitized hosts can be explained by the response of the wasp to successful oviposition in hosts and to kairomone concentrations. Thus, *A. tabida* reacts with an accelerating functional response to host density. In our experiments *A. tabida* only visited a single patch. In a multi-patch laboratory system and in nature, other effects, e.g. experience on previous patches and travel time, are likely to influence the shape of the functional response curve.

The number of parasitizations per unit of time increased with larval density. It is thus functional that *A. tabida* spends little time on patches with low host densities. This efficient time allocation is in agreement with optimal foraging theory. The efficient searching behaviour of *A. tabida* is adaptive for the individual insect. It also generates an accelerating functional response and may therefore contribute to the stabilization of the host and parasitoid populations.

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