Oecologia (Berlin) (1985) 67:352–359

Oecologia

Why is there no interspecific host discrimination in the two coexisting larval parasitoids of *Drosophila* species; *Leptopilina heterotoma* (Thomson) and *Asobara tabida* (Nees)

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Summary. (1) The parasitic wasps *Leptopilina heterotoma* (Thomson) and *Asobara tabida* (Nees) usually refrain from laying eggs in hosts that have already been parasitized by themselves or by a conspecific (= intraspecific host discrimination).

(2) In contrast to intraspecific host discrimination, interspecific host discrimination, in which females refrain from laying eggs in hosts that have already been parasitized by the other species, is not found in these sympatric parasitoid species.

(3) Because we expected that development of interspecific host discrimination would increase the fitness of the wasps, we wondered why this strategy had not evolved in *L. heterotoma* and *A. tabida.*

(4) We therefore developed a simulation model of the parasitization process, in which interspecific host discrimination can be included.

(5) By varying the time needed for host location, survival chances and the proportions of hosts parasitized, we obtained estimates for the number of offspring in situations with and without interspecific host discrimination.

(6) The results imply that, assuming that female wasps carry an ample supply of eggs, the development of interspecific host discrimination by *L. heterotoma* or *A. tabida* will not lead to increased fitness, even under extreme circumstances. Hence, interspecific host discrimination will not evolve.

Since the publication of MacArthur and Pianka (1966) much work has been done to verify the hypothesis that selective forces mould foraging behaviour, thereby maximizing fitness. The foraging behaviour of *Leptopilina heterotoma* (Thomson 1862) (Eucoilidae) and that of *Asobara tabida* (Nees von Esenbeck 1834) (Braconidae: Alysiinae) seem in agreement with optimal foraging theory (Bakker et al. 1967; van Lenteren 1976; van Lenteren and Bakker 1978; Galis and van Alphen 1981; van Alphen and Janssen 1982; van Alphen and Nell 1982; van Alphen and Galis 1983). These solitary larval endoparasitoids of *Drosophila* species concentrate their searching on places with high host densities and seem to select host species in which their offspring have a high chance of survival. They also practice intraspecific host discrimination, avoiding superparasitism by not laying eggs in hosts that have already been parasitized by conspecifics.

There is one aspect of their behaviour, however, that seems to conflict with the theory of optimal foraging. Both *L. heterotoma* and *A. tabida* show no interspecific host discrimination. They accept hosts that have already been parasitized by the other species (van Strien-van Liempt and van Alphen 1981).

It would be expected that intra- and interspecific host discrimination confer similar advantages to *L. heterotoma* and *A. tabida*. These are:

1. Discrimination may prevent wastage of eggs. In solitary wasps (like *L. heterotoma* and *A. tabida*) only one parasitoid can develop per host. Therefore the average survival chance of an egg of a non-discriminating wasp is expected to be lower.
2. Discrimination may save time. Oviposition takes much longer than testing and rejecting a host.
3. Discrimination may provide clues as to when to leave a patch, by giving the parasitoid females information about the profitability of the patch.

In this paper we try to elucidate the 'paradoxical' absence of interspecific host discrimination in *L. heterotoma* and *A. tabida.*

Two possible functional explanations for the absence of interspecific host discrimination have to be considered. (1) Interspecific host discrimination would have no function if parasitoid species rarely meet the same hosts in the field. However, eggs or larvae of *L. heterotoma* and *A. tabida* are frequently found in the same hosts (van Strien-van Liempt and van Alphen 1981). (2) Discrimination may after all confer no advantages to *L. heterotoma* and *A. tabida*, so that discrimination would not increase fitness.

The aim of our study was to determine whether or not the latter possibility could explain the absence of interspecific host discrimination. To estimate the number of offspring in situations with and without interspecific host discrimination, we developed a computer model that simulates the foraging behaviour of the wasps.

Relevant to modelling are the following aspects of the parasitization process (Fig. 1).

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Table 1. Numbers of parasitizations and rejections and values for the time components

Parasitoid species	Host age (h)	Mean number of parasitizations $n=9$	Expected number of rejections	Total time (s)	Mean oviposition time (s)	Mean rejection time (s)	Calculated host location time (s)
L. heterotoma	24 h	28	5	10,800	32	2	300
	48 h	28	5	10,800	40	2	293
A. tabida	24 h	20	2	10,800	24	2	469
	48 h	44	14	10,800	28	2	164

A female wasp searches for hosts. After she hits a larva and pierces it with her ovipositor, she tests its suitability. If a larva is still unparasitized or if it is parasitized by the other species only, it is accepted and oviposition occurs. If a larva has already been parasitized by the female herself or by a conspecific, it is rejected.

In the model it has to be possible to introduce interspecific host discrimination, which means that hosts parasitized by another species will be rejected. Interspecific host discrimination will lead to more rejections. Rejections take far less time than parasitizations. Therefore interspecific host discrimination may save time, thereby influencing the time budget of the wasps. Consequently, time has to be one of the factors in the model.

Four time components will be used in the model:

1. Total time (total amount of time that a parasitoid spends on a patch with hosts).
2. Host location time (mean time between successive host encounters).
3. Oviposition time (including probing time).
4. Rejection time (equivalent to probing time).

Not all parasitoid eggs develop into adults. A number of them will die (van Strien-van Liempt, in prep.). In the strains used for our experiments a high proportion of this mortality is due to encapsulation of the eggs by the host's blood cells. In multi-parasitized hosts, one of the parasitoids will be eliminated by its competitor. The outcome of this competition is correlated with the sequence of and the time between the ovipositions. To accommodate the influence of differences in the time of parasitization by the two parasitoid species in the same host, host larvae were offered at two different stages: early second (one day old) and early third (two days old) instar larvae. These are the two suitable stages for *L. heterotoma* and *A. tabida* (van Lenteren 1976; van Alphen and Drijver 1982).

The survival rates determined by van Strien-van Liempt were used in the model for the calculation of the expected numbers of offspring of both parasitoid species. These results are used to compare the fitness of hypothetical discriminating females with that of the non-discriminating females.

The robustness of our conclusion is tested by varying the values of those parameters that can be expected to be variable in the field.

Material and methods

Parasitoid and host species

The data used in the simulation stem from experiments with sympatric strains of *L. heterotoma* and *A. tabida* from The Netherlands. These strains, both named "Rosenburgh '81", had been reared in the laboratory for over a year when the experiments started. Both parasitoid species were reared on larvae of *Drosophila melanogaster,* strain "WW" (strain W, Bakker 1961). Larvae of the same strain were also used as hosts during the experiments. Rearing techniques for parasitoids and hosts have been described by van Strien-van Liempt and van Alphen (1981) and Bakker (1961).

Time components

Data on the proportions of one-day-old and two-day-old hosts parasitized by *L. heterotoma* and *A. tabida* are derived from the results of the following experiments. Females of both parasitoid species were introduced to petri dishes filled with a mixture of fruit pulp and agar. Each petri dish contained 100 one-day-old and 100 two-day-old host larvae. After having had the opportunity to lay eggs for three hours, the wasps were removed and the host larvae were dissected to check them for eggs of *L. heterotoma* and *A. tabida.* Nine of these experiments have been done. Table 1 gives the mean numbers of hosts parasitized in the experiments.

With these mean values the values for the time components were determined. Unless stated otherwise, the total time is considered to be 3 h (=10,800 s; the time that the experiments lasted). Oviposition and rejection times were derived from other experiments (Hofker, unpubl.). Host location time was determined from the given parameters using the following equation.

$$\text{Host location time} = \frac{\text{TT-(NO} \times \text{OT} + \text{NR} \times \text{RT)}}{\text{NO} + \text{NR}}. \qquad (1)$$

TT = total time; OT = oviposition time; RT = rejection time; NO = number of ovipositions; NR = number of rejections.

This host location time not only includes time spent searching for hosts, but of all other other activities of the wasp between host encounters. The only parameter in the equation of which the value could not directly be determined from the experiments, is the number of rejections.

A simple computer model was used to estimate the number of rejections (NR). This model simulates a wasp that parasitizes randomly chosen hosts from a group of 100 healthy and unparasitized host larvae. Larvae that are encountered after they have been parasitized earlier during the simulation are rejected. The number of rejections (NR) is counted until the wasp has parasitized the correct number of hosts (NO = the mean number found in the experiments).

All parameters and their values are presented in Table 1.

Table 2. Survival chances of sympatric strains of *L. heterotoma* and *A. tabida* for eight possible parasitization combinations (van Strien-van Liempt, in prep.)

Parasitization combination	Survival chance	
	L. heterotoma	*A. tabida*
L1	0.76	–
L2	0.40	–
A1	–	0.50
A2	–	0.30
L1A1	0.20	0.26
L1A2	0.29	0.33
L2A1	0.17	0.50
L2A2	0.20	0.07

Table 3. List of parameters used in the model with their original values

Parameter	Parameter value	
Number of larvae	100	
Total time	10,800	
	L. heterotoma	*A. tabida*
Host location time		
24-h-larvae	300	469
48-h-larvae	293	164
Oviposition time		
24-h-larvae	32	24
48-h-larvae	40	28
Rejection time (both ages)	2	2
Survival chances		
L1	0.76	–
L2	0.40	–
A1	–	0.50
A2	–	0.30
L1A1	0.20	0.26
L1A2	0.29	0.33
L2A1	0.17	0.50
L2A2	0.20	0.07
Interspecific host discrimination	yes/no	yes/no

Survival rates

Van Strien-van Liempt (in prep.) studied the outcome of competition between *L. heterotoma* and *A. tabida*. She offered hosts to both parasitoids in succesion, removed the multiparasitized ones and reared them until wasps and flies had emerged. Thus, she determined the outcome of competition in the four different kinds of multi-parasitized larvae.

L1A1 – Larvae parasitized by both *L. heterotoma* and *A. tabida* when they were one day old.
L1A2 – Larvae parasitized by *L. heterotoma* when they were one day old and by *A. tabida* a day later.
L2A1 – Larvae parasitized by *A. tabida* when they were one day old and by *L. heterotoma* a day later.
L2A2 – Larvae parasitized by both species when they were two days old.

The survival of the parasitoids in multiparasitized hosts was compared with that in singly parasitized hosts (L1, A1, L2 and A2). The survival rates of both species for all possible parasitization combinations are presented in Table 2. All parameters and their original values are summarized in Table 3.

The model

A discrete Monte-Carlo simulation model was selected because of the comprehensiveness of the separate parts of such a simulation and because of the complex use of time components in the model.

The language used for our model is APLGPSS (van Batenburg and van Baaren unpubl.). This language provides a combination of the simple simulation possibilities that GPSS offers and the powerful APL functions. APLGPSS has been succesfully used to construct models like the one presented in this paper (van Batenburg et al. 1983).

The simulation

The model comprises two phases:

1. The oviposition phase: the wasps search for hosts and oviposit in those that are detected and accepted.

2. The survival phase: the parasitoid eggs either develop into adult wasps or die during their development.

Before starting the actual simulation, the user has the option of changing the values of parameters used in either phase.

The simulation of the oviposition phase. The four empirically derived time components are integrated into this phase. The simulation starts by allowing a female of *L. heterotoma* and a female of *A. tabida* to search and parasitize one-day-old larvae as shown in Fig. 1.

Both species find a randomly chosen larva as soon as their host location time has passed. Whether or not a larva is accepted for oviposition depends on previous ovipositions in that larva. Three alternative conditions of parasitism can occur:

1. The larva has not been parasitized yet, in that case it will be accepted. The first larva encountered is of course always in this category.

2. The larva has been parasitized by the other species only. It is then rejected when interspecific host discrimination is included in the model and accepted when interspecific host discrimination is not included.

In the model, we either allow the parasitoids to show their normal behaviour (no interspecific host discrimination = L – A –) or to become discriminators. In the latter situation interspecific host discrimination is assigned to either *L. heterotoma* (L + A –) or *A. tabida* (L – A +) or to both species (L + A +).

3. The larva has already been parasitized by the same wasp. Such larvae are always rejected.

When a larva is accepted, the oviposition time passes and the larva will be marked as being parasitized. When it is rejected only the rejection time passes.

After handling a larva a wasp starts searching again and finds a larva after the host location time has elapsed once more.

This process is reiterated until the sum of the times needed for host location, oviposition and rejection of one of the wasps equals or exceeds the total time (3 hours). The host age then increases by one day and the time components are adjusted to those for two-day-old larvae.

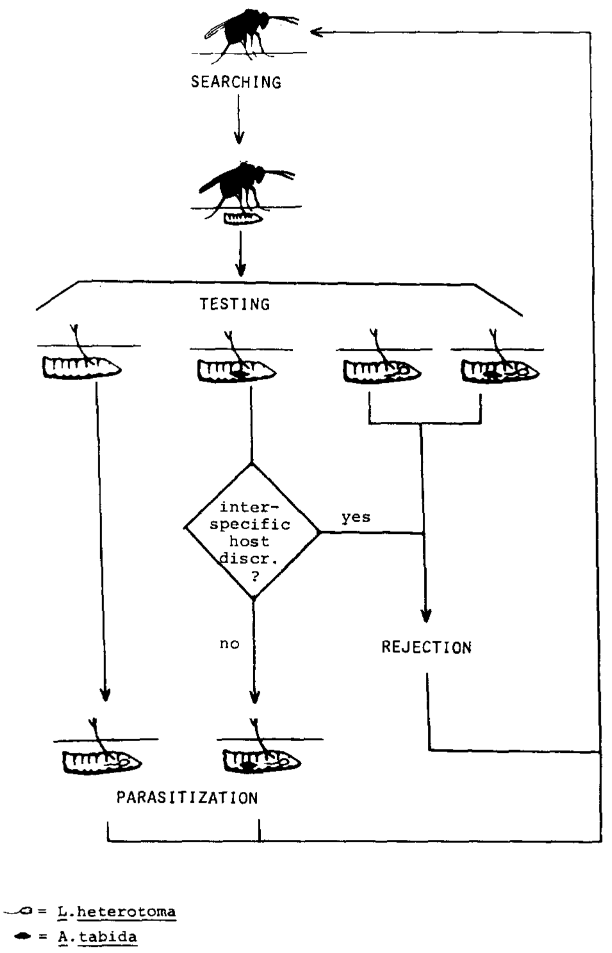


Fig. 1. Outline of the parasitization process for *L. heterotoma*

The process of locating, parasitizing or rejecting hosts starts again and ceases as soon as the total time is reached once more.

Then the oviposition phase is completed and will have resulted in a number of parasitized hosts (with either one or two eggs). These parasitized hosts will enter the survival phase.

The survival phase. The survival rates included in the model decide the number of adults that emerge. Each parasitization combination has its own survival rate for each species (Table III).

The output of the model is the number of hosts parasitized, and the number of offspring for each parasitoid species, in all situations tested.

As we use a Monte-Carlo simulation for the oviposition phase, we need a number of replicates to obtain an estimate of the average result. The costs of computing time were minimized by limiting the number of replicates. Six runs with each set of parameter values were sufficient to differentiate between situations. Tests with selected parameter sets indicated that larger numbers of replicates produced no alterations at all in the average output values.

Results and discussion

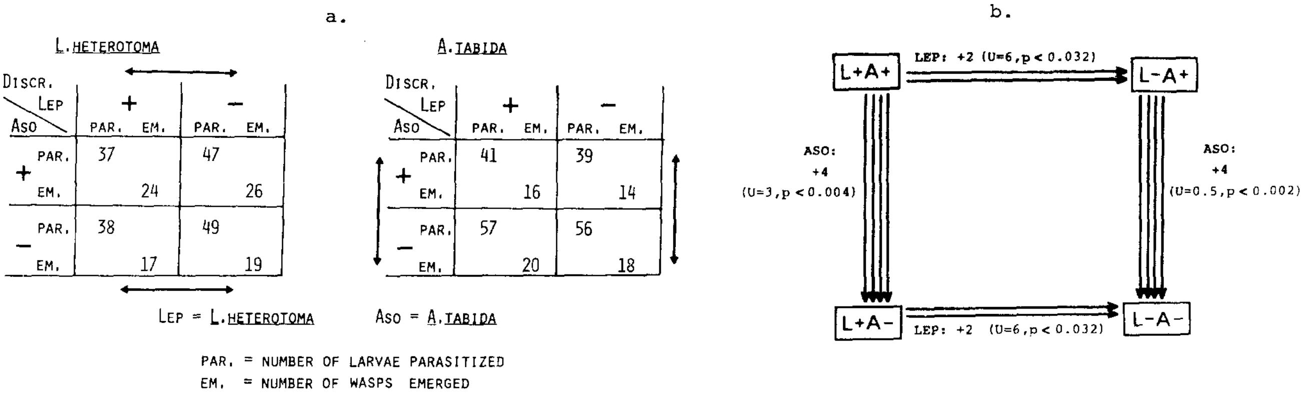
Original parameter values

Initially the parameters were kept at the original values as measured in the experiments (Table 3). Only the discriminative ability of *L. heterotoma* and that of *A. tabida* was varied. For each of the four different combinations of discriminative abilities (L−A−, L+A−, L−A+ and L+A+) the mean numbers of parasitoids emerged are presented in Fig. 2a.

Both *L. heterotoma* and *A. tabida* appear to have the highest number of offspring in situations where they do not discriminate whereas the other species does. Therefore, development of interspecific host discrimination will be improbable: neither *L. heterotoma* nor *A. tabida* will be better off by preventing multiparasitism.

The second best situation for *L. heterotoma* appears to be the one where both species discriminate (L+A+). It is, however, very unlikely that species change their strategy at the same time, therefore the step from L−A− to L+A+ is considered to be impossible. From a situation where both species do not discriminate (L−A−), L+A+ can only be reached via one of the two other situations (L+A− or L−A+). As previously stated those situations are not likely to evolve.

The arrows in figure 2b represent the profitability of steps that could be taken by *L. heterotoma* and *A. tabida.*



a.

L.HETEROTOMA

DISCR. LEP / ASO		+ PAR.	+ EM.	− PAR.	− EM.
+	PAR.	37		47	
	EM.		24		26
−	PAR.	38		49	
	EM.		17		19

A.TABIDA

DISCR. LEP / ASO		+ PAR.	+ EM.	− PAR.	− EM.
+	PAR.	41		39	
	EM.		16		14
−	PAR.	57		56	
	EM.		20		18

LEP = L.HETEROTOMA ASO = A.TABIDA

PAR. = NUMBER OF LARVAE PARASITIZED
EM. = NUMBER OF WASPS EMERGED

Fig. 2a, b. Simulation with the original parameter values in situations with (+) and without (−) interspecific host discrimination. **a** Simulation results summarized in payoff matrices. **b** Consequences of changing discrimination strategy for *L. heterotoma* (*L*) and *A. tabida* (*A*). Example: If both *L. heterotoma* and *A. tabida* discriminate, then the average number of offspring for *L. heterotoma* is 24 and for *A. tabida* 16 (see *matrices*). If *A. tabida* stops discriminating interspecifically, it will produce 20 offspring. This profit of 4 is indicated by the 4 downward pointing *arrows* on the left side of **b**

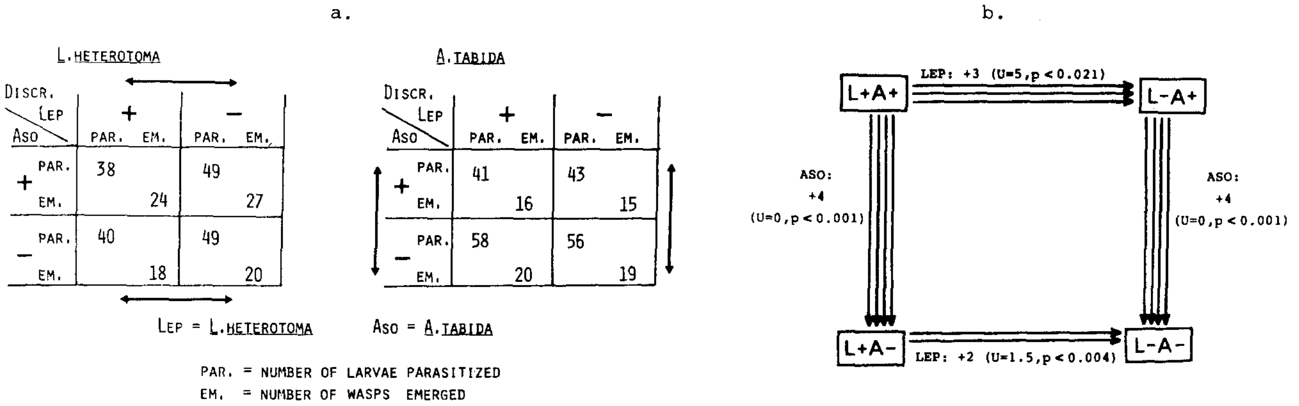


Fig. 3a, b. Simulation with a total time of 1 h in situations with (+) and without (−) interspecific host discrimination. **a** Simulation results summarized in payoff matrices. **b** Consequences of changing discrimination strategy for *L. heterotoma* (*L*) and *A. tabida A*

The mean profit (number of extra offspring) for the species that takes the evolutionary step, is tested with Mann-Whitney-U (Fig. 2b). In all cases a significant difference is found. Following the arrows one will always end up with the actual situation where both *L. heterotoma* and *A. tabida* do not discriminate. So, these results imply that the development of interspecific host discrimination is unlikely. For these parasitoids the situation in which both species do not discriminate interspecifically appears to be the stable state.

To test the robustness of the conclusion that developing interspecific host discrimination is not advantageous other parameter values have to be tried out. The values used sofar have been derived from lab-experiments. However, in the field considerable variation can be expected in total time, host location time and survival rates. These are therefore selected for sensitivity analysis.

The number of hosts is not varied because it would have the same effect as varying the total time or the host location time. Because the values used for the oviposition time and the rejection time will not vary substantially in the field, they are not varied either.

Reduced total time

So far we kept the total time (TT) during simulation time at 3 h because the fractions of parasitized hosts were determined in experiments that lasted 3 h. The wasps, however, were not constantly observed during the experiments. It is quite possible that the wasps had been active for less than 3 h; in that case the total time should be shortened. In consequence the host location time will also be shorter (equation 1).

The time gained by rejecting less suitable hosts becomes available to search for other hosts. During this "extra" time more hosts can be detected as host location time is shorter. By drastically reducing the total time we checked whether the consequences of developing interspecific host discrimination changed.

A total time of 1 h and adjusted host location times were used for new simulation runs. An even shorter total time would result in an irrealistically short host location time for each parasitoid.

The shorter host location time does result in a few more parasitizations but the effect is the same for all four situations (Fig. 3a). The consequences of interspecific host discrimination hardly differ when simulating with a total time of 1 hour and adjusted host location times (compare Fig. 3b with Fig. 2b).

Lower survival chances in multi-parasitized hosts

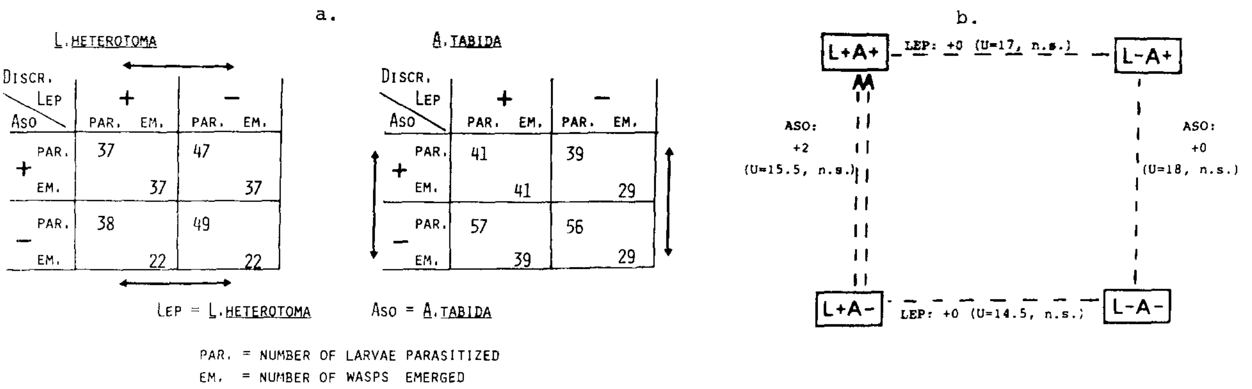
Parameters that probably vary considerably in the field are the survival chances. The hypothesis – interspecific host discrimination is a good strategy for *L. heterotoma* and *A. tabida* – was, among other things, based on the survival chances that we found in the laboratory. Simulation however, showed that interspecific host discrimination is not a good strategy. We wondered whether the result would be different if a larger difference between survival in multi-parasitized and singly parasitized hosts was included in the simulation. We decided to test the extreme situation, where all parasitoids survive in singly parasitized hosts and none of them survives in multi-parasitized hosts.

Although L+A+ appears to be much more profitable than L−A−, the intermediate situations (L+A− and L−A+) are not preferable above the L−A− situation (Fig. 4a). The species that developed discrimination would not benefit from it as long as the other species still multi-parasitizes and thereby lowers the number of offspring of the discriminating species.

As compared to the runs with the former parameter sets the results are different, none of the possible traits will alter the number of offspring significantly (Fig. 4b). Even now, with no survival in multi-parasitized hosts, no advantages will be scored when the parasitoids develop interspecific host discrimination. In other words: none of the possible traits results in a significantly higher number of offspring. Therefore no selective forces will encourage the development of interspecific host discrimination.

Higher proportional parasitization

The proportions of hosts parasitized are not used directly as parameters in the model, but they were used to calculate values for the host location time (equation 1). In the field situations might occur (e.g. in patches with clusters of hosts) where many more hosts are parasitized in 3 h than was



L. HETEROTOMA

Discr. Aso \ Lep		+ PAR.	+ EM.	− PAR.	− EM.
+	PAR.	37		47	
	EM.		37		37
−	PAR.	38		49	
	EM.		22		22

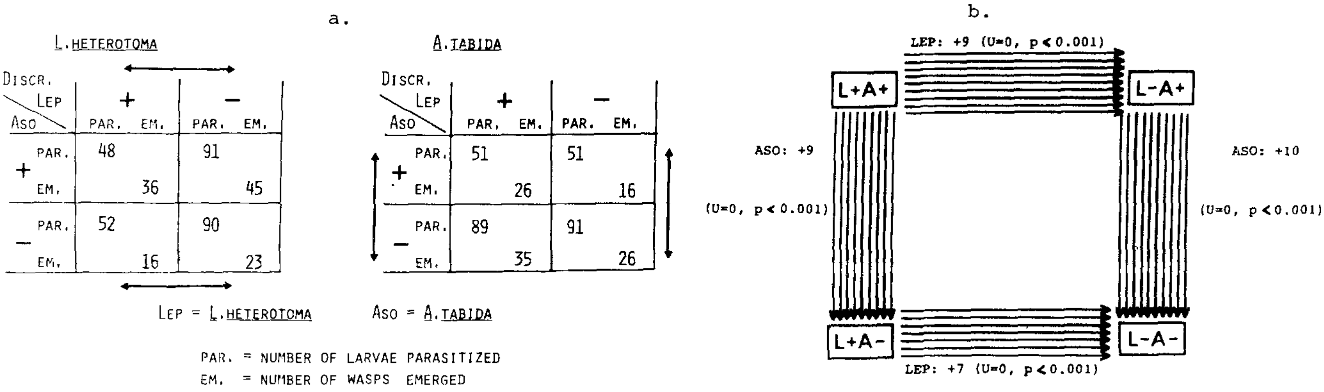
A. TABIDA

Discr. Aso \ Lep		+ PAR.	+ EM.	− PAR.	− EM.
+	PAR.	41		39	
	EM.		41		29
−	PAR.	57		56	
	EM.		39		29

LEP = L. HETEROTOMA   ASO = A. TABIDA

PAR. = NUMBER OF LARVAE PARASITIZED
EM. = NUMBER OF WASPS EMERGED

Fig. 4a, b. Simulation with survival in singly parasitized hosts of 100% and in multi-parasitized hosts of 0%, in situations with (+) and without (−) interspecific host discrimination. **a** Simulation results summarized in payoff matrices. **b** Consequences of changing discrimination strategy for *L. heterotoma* (*L*) and *A. tabida* (*A*). *Dashed lines* indicate non-significant differences



L. HETEROTOMA

Discr. Aso \ Lep		+ PAR.	+ EM.	− PAR.	− EM.
+	PAR.	48		91	
	EM.		36		45
−	PAR.	52		90	
	EM.		16		23

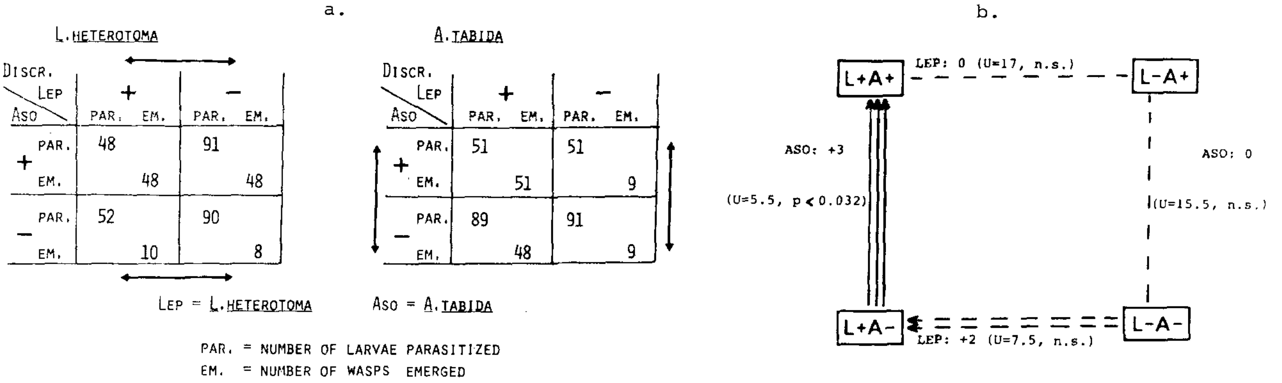
A. TABIDA

Discr. Aso \ Lep		+ PAR.	+ EM.	− PAR.	− EM.
+	PAR.	51		51	
	EM.		26		16
−	PAR.	89		91	
	EM.		35		26

LEP = L. HETEROTOMA   ASO = A. TABIDA

PAR. = NUMBER OF LARVAE PARASITIZED
EM. = NUMBER OF WASPS EMERGED

Fig. 5a, b. Simulation with a proportional parasitization of 90% of the 1-day old larvae, in situations with (+) and without (−) interspecific host discrimination. **a** Simulation results summarized in payoff matrices. **b** Consequences of changing discrimination strategy for *L. heterotoma* (*L*) and *A. tabida* (*A*)



L. HETEROTOMA

Discr. Aso \ Lep		+ PAR.	+ EM.	− PAR.	− EM.
+	PAR.	48		91	
	EM.		48		48
−	PAR.	52		90	
	EM.		10		8

A. TABIDA

Discr. Aso \ Lep		+ PAR.	+ EM.	− PAR.	− EM.
+	PAR.	51		51	
	EM.		51		9
−	PAR.	89		91	
	EM.		48		9

LEP = L. HETEROTOMA   ASO = A. TABIDA

PAR. = NUMBER OF LARVAE PARASITIZED
EM. = NUMBER OF WASPS EMERGED

Fig. 6a, b. Simulation with a proportional parasitization of 90% of the 1-day-old larvae and with survival in singly parasitized host of 100% and in multi-parasitized hosts of 0%, in situations with (+) and without (−) interspecific host discrimination. **a** Simulation results summarized in payoff matrices. **b** Consequences of changing discrimination strategy for *L. heterotoma* (*L*) and *A. tabida* (*A*). *Dashed lines* indicate non-significant differences

found in the experiments. This means that the host location time will be lower, while the total time remains the same. To measure the effect of higher proportional parasitization, simulations were run with host location times adjusted to a 90% parasitization of 1-day-old larvae.

Fig. 5a and b shows that *L. heterotoma* and *A. tabida* will be far better off when they do not discriminate under these circumstances. This is mainly due to the fact that a discriminating parasitoid can only accept about half the larvae for oviposition, the other half is rejected because it has already been parasitized by the other species. For non-discriminating females all larvae are acceptable and can be parasitized once.

Higher proportional parasitization and lower survival chances in multi-parasitized larvae

We found that large changes in survival chances and proportional parasitization do not affect our conclusion, but a higher proportional parasitization does lead to substantially more multi-parasitized hosts. To test whether a low survival chance in these hosts will affect the conclusion, simulations were run with a combination of the two former parameter sets. Therefore we increased the proportion of one-day-old larvae parasitized to 90%, and reduced survival in multi-parasitized hosts to 0, while survival in singly parasitized hosts was set 100%.

Figure 6a and b shows that even under these extreme circumstances, there is only one trait (i.e. from L+A− to L+A+) where developing interspecific host discrimination results in significantly more offspring.

General discussion

If we accept the model as a good representation of the parasitization process, we may conclude that the selective forces do not favour the development of interspecific host discrimination. All variations of the parameters that might falsify this conclusion have been checked. They show that *L. heterotoma* and *A. tabida* are in almost all cases better off when they do not discriminate interspecifically. The situation in which both species do discriminate (L+A+) is very improbable:

1. *L. heterotoma* and *A. tabida* are unlikely to start interspecific host discrimination simultaneously. A situation where only one of them discriminates (L+A− or L−A+) will develop first. Such a situation, however, appears to be disadvantageous for the species that takes the step (develop discrimination), and will therefore not evolve.
2. Although in some cases L+A+ appears to be a better situation than L−A−, it is not a stable one. Wasps that give up discrimination will increase their fitness, they can profit by the fact that the other species never multiparasitizes (Fig. 2–6).

So, according to the model, the only stable situation is the one we find in the field, i.e. the situation in which both species do not show interspecific host discrimination.

However, we have to realize that the model is a simplification of the field situation, and that we might have overlooked some important factors.

The parasitization process in our model was limited to one patch only. Therefore possible advantages gained by discriminating females because they leave less profitable patches earlier can not be traced with this model. For a model that simulates the complete parasitization process in a patchy environment, a lot more has to be known about the time needed to find a new patch and the expected profitability of new patches.

Another point for discussion is the assumption in the model that females of both species carry an ample supply of eggs. We believe that a female wasp normally will not lay all her eggs during her life-time. This seems reasonable because the wasps carry several hundreds of eggs and are believed to be time optimizers (van Lenteren and Bakker 1976, 1978; Galis and van Alphen 1981; van Alphen and Galis 1983). One of the functions of optimizing time allocation could be that the parasitoids can lay as many eggs as possible. This would not apply if the parasitoids easily can lay all their eggs.

If, however, the number of eggs is a limiting factor, the conclusion that the parasitoids should not develop interspecific host discrimination is completely wrong. If a female easily gets rid of all her eggs in any of the discrimination situations, the number of offspring only depends upon the survival chance of these eggs. Species that discriminate will have a higher number of offspring, because a larger proportion of the eggs will be laid in unparasitized hosts (in which survival chance is highest).

Objections against the chosen parameter values can hardly be made because our conclusion is valid for a wide range parameter sets. The real situation has to be within the variation we looked at.

We expected that interspecific host discrimination would result in higher fitness for the wasps because of prevention of egg wastage, time gain and because it might provide information about patch suitability. The model shows that these advantages do not lead to a higher number of offspring. The same advantages were suggested for intraspecific host discrimination. Our interpretation of the results for interspecific host discrimination raises doubts about the profitability of intraspecific host discrimination. Obviously, not discriminating intraspecifically, will have some extra consequences. The eggs in detected hosts may have been laid by the female herself or by a closely related female. By superparasitizing those hosts, the wasp will lower the survival chance of a relative.

Still, the question arises whether superparasitism (more eggs of one species in one host) is sometimes favourable. In fact, studies have demonstrated that intraspecific host discrimination is not absolute in *L. heterotoma* and *A. tabida*, and that superparasitism frequently occurs, especially in situations where there is more than one wasp on a patch (Bakker et al. submitted).

Acknowledgement. We would like to extend our thanks to J.J.M. van Alphen, K. Bakker, A.J. Davis, G.J.J. Driessen, A.R.M. Janssen and M. Sabelis for their helpful comments on this paper; C.D. Hofker for his excellent assistance in collecting data and G.J.F. Boskamp for rearing the hosts and parasitoids.

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Received April 18, 1985