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Behavioural adaptations in host finding by *Trichogramma evanescens*: the influence of oviposition experience on response to host contact kairomones

Sara M. Gardner, Marleen Dissevelt, Joop C. van Lenteren
Laboratory of Entomology, Wageningen University, The Netherlands

Abstract

The influence of oviposition experience on the response of the egg parasitoid *Trichogramma evanescens* Westwood (Hymenoptera Trichogrammatidae) towards the contact kairomones of two different host species, *Mamestra brassicae* (L.) and *Pieris brassicae* L., is described. The response of *T. evanescens* was influenced by the number of eggs it had laid, but time since oviposition did not result in a significant change in behaviour. Parasitoids readily accepted an egg of a second species and the time spent searching in a particular kairomone area would appear to depend on the reproductive state and expected survival of a parasitoid, rather than the development of any host preference. *Trichogramma* seems to select patches on the basis of reward probability rather than maximising reward size. Such behaviour would assist parasitoids to respond to fluctuations in host availability.

Key words: *Mamestra brassicae*, *Pieris brassicae*, egg parasitoid, host searching behaviour, host preference, reproductive state, egg load.

Introduction

The central task facing a population of animals is to maximise the number of offspring that survive to reproduce in the next generation. Based on this problem, a number of optimal foraging models has been developed which assume that animals search in a manner that maximises their net foraging reward, and use this as a criterion for ranking different patches or types of prey (for reviews, see Krebs and McCleery, 1984; Godfray, 1994). For predators, foraging reward is usually assumed to be net rate of energy gain while for insect parasitoids the appropriate quantity is the number of host parasitised (Hubbard and Cook, 1978; Godfray, 1994). Such models predict that specialisation on the most profitable patches will occur when the value of the foraging reward on these is greater than that to be attained from foraging on all available patches. The inclusion of lower ranking patches is dependent upon the encounter rate with the most profitable patch type.

Two assumptions fundamental to many optimal foraging models are that foragers are "aware" of available patches and that the value of a foraging award is fixed and independent of changes in an animal's internal state (Houston, 1980; Bukovinszky *et al.*, 2007). Animals base their foraging "decisions" on approximate "rules of thumb" (e.g. Waage, 1979; Godfray, 1994) which are continuously updated. The information available to a forager concerning the occurrence and profitability of different patch types is necessarily incomplete, and variation in patch reward probability may influence the decision making process (Caraco, 1980; Real, 1980; Bukovinszky *et al.*, 2007).

Behavioural changes that occur as a result of foraging experience can be broadly defined as learning (Shettleworth, 1984; Vet *et al.*, 1995). Such changes can arise from the association of a particular stimulus with a subsequent foraging reward (e.g. Arthur, 1966, 1971; Vet *et al.*, 2003) or from non-associative processes such as habituation and sensitisation (Mackintosh, 1983; Vet *et al.*, 1995), and may enable foragers to respond to fluctuations in foraging reward (Jaenike, 1982; Vet, 1983; Vet *et al.*, 2003).

Specialisation on a particular host or patch type may under some circumstances result in reproductive isolation of individuals within a species (Bush, 1972, 1975). Although learning may contribute to this process, it is of itself unlikely to lead to significant isolation (Diehl and Bush, 1984). Learning does not necessarily result in exclusive preferences (Lester, 1984), but little information is available on the flexibility of the learning process, particularly with respect to the acceptance of subsequent host species or strains over the period during which "learned responses" are retained, but see Vet *et al.* (1995), Bleeker *et al.* (2006) and Smid (2006). This information is, however, crucial not only for understanding of learning behaviour and its consequences on the host and parasitoid population dynamics, but also for several high priority applied aspects of parasitoid – host studies, such as environmental risks of the introduction of exotic natural enemies (e.g. van Lenteren *et al.*, 2006) and the quality of natural enemies when reared on a factitious host (e.g. van Lenteren, 2003).

Recent studies have indicated that the foraging behaviour of many insects is modified as a result of their ovipositional experience (e.g. Jaenike, 1982, 1983; Prokopy *et al.*, 1982; Vet, 1983; Vet *et al.*, 2003; van Lenteren, 1991; Bukovinszky *et al.*, 2007). *Trichogramma* are egg parasitoids of mainly, but not exclusively, Lepidoptera and are the world's most widely used parasitoids in biological control of pests (van Lenteren and Bueno, 2003). *Trichogramma evanescens* is known to respond to chemical stimuli produced by its lepidopteran hosts using them as "indicators" of host presence (e.g. Lewis *et al.*, 1976; Noldus and van Lenteren, 1983, 1985a, b; Gardner and van Lenteren, 1986; Fatouros *et al.*, 2005;

Romeis *et al.*, 2005). A study of the influence of oviposition experience on the response of *T. evanescens* towards kairomones of two lepidopteran species, *Mamestra brassicae* (L.) and *Pieris brassicae* L., and the consequences for host selection behaviour are reported in this paper.

Materials and methods

Parasitoids and hosts

The parasitoids used in these experiments originated from a population of *Trichogramma evanescens* Westwood collected in The Netherlands in 1981 on *M. brassicae* in cabbage (strain II in Pak and van Lenteren, 1984). Since then the population has been reared in the laboratory on *Ephestia kuehniella* Zeller. Parasitoids were reared at 25 °C and were offered honey after emergence.

General method

Experiments were carried out at 20 °C using two day old females. Parasitoids were transferred to the experimental room (20 °C) on the previous day. Both inexperienced and experienced females were used. The latter had oviposited in one or five eggs of *M. brassicae* or *P. brassicae* one hour before the experiment. Inexperienced females had not oviposited.

Each parasitoid was released into a Petri dish (diameter 9.0 cm), the base of which was covered with filter paper. Wing and body scales of either *M. brassicae* or *P. brassicae* were brushed onto the filter paper in a discrete area (0.78 cm^2), subsequently referred to as a kairomone area. A fresh arena was used for each female. For some experiments a larger kairomone area (4.0 cm^2) was used. Parasitoid behaviour was observed throughout each experiment. Each visit to a kairomone area was divided into time spent searching within (T_K) and around (T_S) a kairomone area. The total time spent searching is shown as T_T in tables 1-4. A visit was completed once a single period of 90 s had been spent by a parasitoid outside the kairomone area. After this period less than 10% of females returned to the kairomone area. The time spent searching by the parasitoids within and around kairomone areas (=T_T) of *M. brassicae* or *P. brassicae* of different size did not differ significantly (table 1).

A summary of the experimental regimes used in the three experiments described below is given in figure 1.

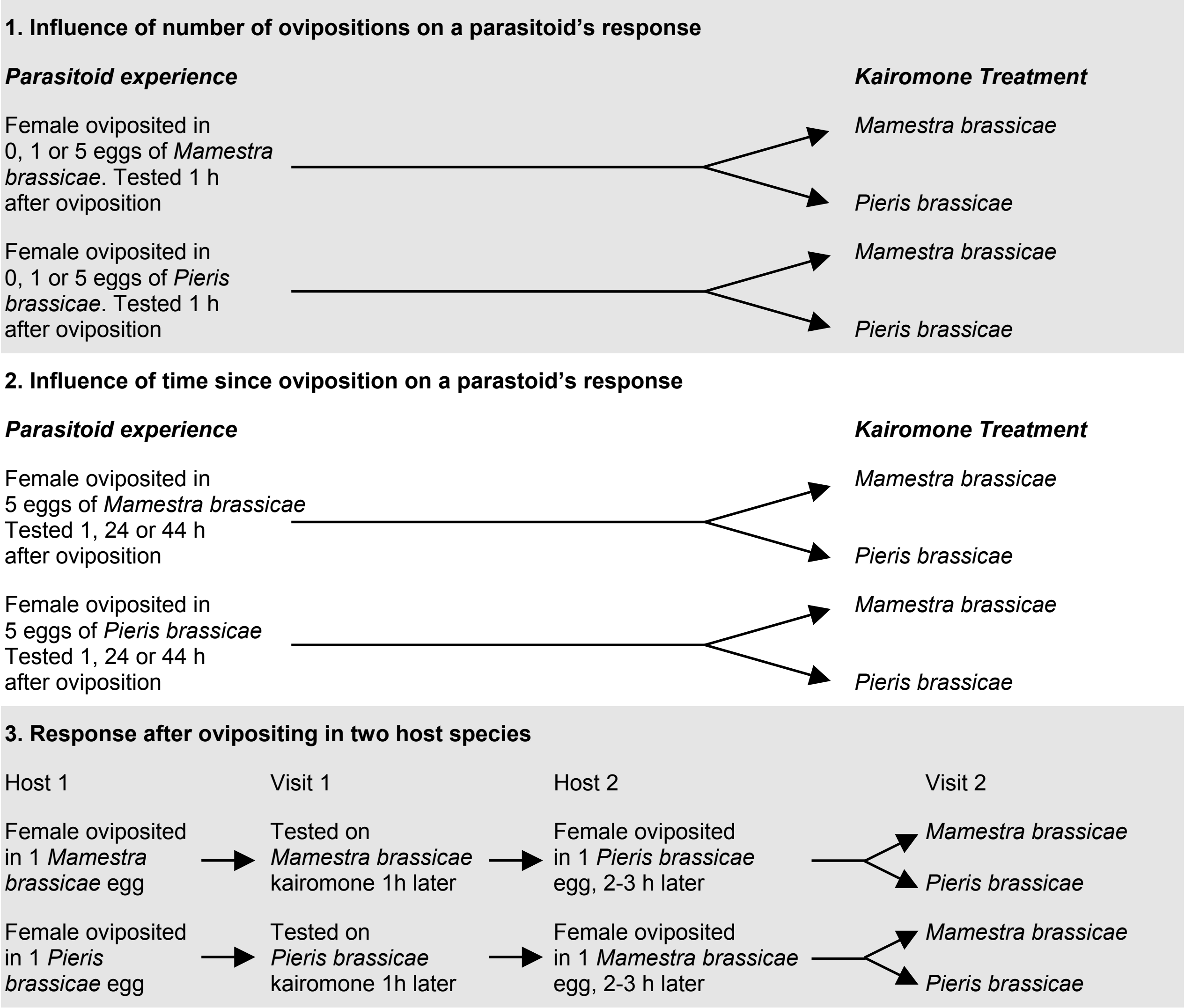

Figure 1. Outline of experimental regime.

Table 1. Time spent by inexperienced *Trichogramma evanescens* on kairomone areas of different size (mean ± S.E., time in s). Time spent searching within kairomone area = T_K; around kairomone area = T_S; within and around kairomone area = T_T.

Size of kairomone area	Response to *Mamestra brassicae* kairomone T_K	T_S	T_T
0.78 cm^2 n=47	46.3 a (±4.7)	46.4 b (±7.4)	92.6 d (±10.2)
4.00 cm^2 n=38	50.9 a (±6.9)	57.7 b (±11.5)	117.6 d (±18.8)

Size of kairomone area	Response to *Pieris brassicae* kairomone T_K	T_S	T_T
0.78 cm^2 n=53	84.7 a (±14.9)	26.6 c (±7.6)	111.3 d (±19.4)
4.00 cm^2 n=46	45.7 a (±4.7)	23.1 c (±4.0)	75.5 d (±7.9)

Figures followed by the same letter are not significantly different.

Comparisons made between rows only using Mann Whitney U test.

1. Influence of number of ovipositions on a parasitoid's response to the contact kairomones of *M. brassicae* and *P. brassicae*

Inexperienced and experienced parasitoids were used in this experiment, the latter had oviposited in one or five eggs of either *M. brassicae* or *P. brassicae* one hour previously. The time spent searching by each parasitoid on a single kairomone area of either *M. brassicae* or *P. brassicae* was recorded.

2. Influence of time since oviposition on a parasitoid's response to the contact kairomones of *M. brassicae* and *P. brassicae*

The response of experienced parasitoids to the kairomones of either *M. brassicae* or *P. brassicae* were observed at intervals of 1, 24 and 44 h after oviposition. Each parasitoid had oviposited in a clump of five *M. brassicae* or *P. brassicae* eggs.

3. Response to host contact kairomones following oviposition in two host species

Parasitoids were offered a single egg of either *M. brassicae* or *P. brassicae*, and one hour later released into an arena containing a single kairomone area of the host in which they had oviposited. A couple of hours later, parasitoids were allowed to oviposit in an egg of a different host and after one hour their response to the kairomone of either *M. brassicae* or *P. brassicae* was observed.

Results

1. Influence of number of ovipositions on a parasitoid's response to the contact kairomones of *M. brassicae* and *P. brassicae*

Inexperienced females spent a similar amount of time searching within the kairomone area (T_K) of each host, but more time was spent searching around the kairomone area (T_S) of *M. brassicae* than that of *P. brassicae* (compare table 2a and b). This difference in response suggests that parasitoids may react to different components in the scales of the two host species. The total time spent examining the kairomone areas of *M. brassicae* and *P. brassicae* did not differ significantly (table 2a and b). The behaviour of experienced females to the kairomones of the host in which they had oviposited was not influenced by their oviposition experience (table 2a and b), and did not differ from that of inexperienced females. Parasitoids that had oviposited in one host egg only, were, however, less responsive to the kairomones of a "novel" host, than inexperienced females, or those that had oviposited in five host eggs (table 3a and b). The behaviour of 5-egg experienced females did not differ from that of inexperienced females.

These results indicate that oviposition experience does influence a parasitoid's response to host kairomones. It is, however, difficult to determine whether the changes in behaviour observed were due to the number of hosts parasitised of the number of parasitoid eggs laid. Since the responses of parasitoids towards the kairomones of hosts in which they had oviposited were independent of their oviposition experience, it would seem unlikely that the changes in behaviour towards kairomones of "novel" hosts would be influenced by the number of hosts parasitised. Parasitoids laid significantly more eggs in five hosts than on one (table 2a and b).

2. Influence of time since oviposition on a parasitoid's response to the contact kairomones of *M. brassicae* and *P. brassicae*

Both *M. brassicae* and *P. brassicae* experienced females spent a similar amount of time searching within the kairomone areas (T_K) of the two host species after 1, 24 and 44 h (table 4a and b). *Mamestra brassicae* experienced females spent longer searching around (T_S) the kairomone area of *P. brassicae,* when tested at 44 h than those tested 1 or 24 h after oviposition (table 4a). In all other cases, time since oviposition did not influence the duration of T_S (table 4a and b).

Comparisons were made of the responses of experienced females towards the kairomones of *M. brassicae* and *P. brassicae* within a single time interval since oviposition. There were no significant differences between the T_K and the T_T values of the two host kairomones for either *M. brassicae* or *P. brassicae* experienced females. More time was spent by both *M. brassicae* and *P. brassicae* experienced females tested one hour after oviposition, searching around the kairomone are of *M. brassicae* compared to *P. brassicae*. This difference was also observed in *M. brassicae* experienced females

Table 2. Response of *Trichogramma evanescens* to the contact kairomones of hosts in which they have oviposited (mean ± S.E., time in s). Time spent searching within kairomone area = T_K; around kairomone area = T_S; within and around kairomone area = T_T.

a. *Mamestra brassicae* experienced females

Oviposition experience		Response to *Mamestra brassicae* kairomone		
No. of host oviposited in	No. of parasitoid eggs laid	T_K	T_S	T_T
0 eggs (n=15)	0	55.9 a (±8.7)	42.5 b* (±9.7)	98.4 c (±9.7)
1 *M. brassicae* egg (n=38)	2.5 (±0.4)	50.9 a (±6.9)	57.7 b (±11.5)	111.9 c (±13.9)
5 *M. brassicae* eggs (n=13)	8.3 (±0.9)	31.0 a (±3.2)	43.7 b (±17.3)	74.6 c (±21.5)

b. *Pieris brassicae* experienced females

Oviposition experience		Response to *Pieris brassicae* kairomone		
No. of host oviposited in	No. of parasitoid eggs laid	T_K	T_S	T_T
0 eggs (n=18)	0	64.5 a (±18.9)	25.3 b (±18.1)	89.1 c (±35.1)
1 *P. brassicae* egg (n=46)	4.3 (±0.5)	45.7 a (±4.7)	23.1 b (±4.0)	97.2 c (±12.9)
5 *P. brassicae* eggs (n=16)	12.1 (±1.4)	52.8 a (±19.6)	33.4 b (±13.7)	86.3 c (±24.9)

Figures followed by the same letter are not significantly different. Comparisons made between rows only using Kruskal Wallis test: response of inexperienced and *M. brassicae* experienced parasitoids to *M. brassicae*, comparison of T_T values: H=2.87, d.f.=2, p NS; response of inexperienced and *P. brassicae* experienced parasitoids to *P. brassicae*, comparison of T_T values: H=1.16, d.f.=2, p NS. Mann Whitney U test used to compare response of inexperienced females to kairomones of both host species. * indicates a significant difference from T_S value for response to *M. brassicae* kairomone of inexperienced females ($z=2.09$, $n_1=15$, $n_2=18$, $p<0.02$).

Table 3. Response of *Trichogramma evanescens* to the contact kairomones of "novel" hosts (mean ± S.E., time in s). Time spent searching within kairomone area = T_K; around kairomone area = T_S; within and around kairomone area = T_T.

a. *Mamestra brassicae* experienced females

Oviposition experience		Response to *Pieris brassicae* kairomone		
No. of host oviposited in	No. of parasitoid eggs laid	T_K	T_S	T_T
0 eggs (n=18)	0	64.5 a (±18.9)	25.3 b (±18.1)	89.9 c (±35.1)
1 *M. brassicae* egg (n=20)	2.5 (±0.4)	26.0 d (±6.0)	5.0 e (±4.3)	31.1 f (±9.7)
5 *M. brassicae* eggs (n=10)	8.3 (±0.9)	117.8 a (±44.0)	16.5 b (±9.9)	134.3 c (±52.7)

b. *Pieris brassicae* experienced females

Oviposition experience		Response to *Mamestra brassicae* kairomone		
No. of host oviposited in	No. of parasitoid eggs laid	T_K	T_S	T_T
0 eggs (n=15)	0	55.9 a (±8.7)	42.5 b (±9.7)	98.4 c (±13.3)
1 *P. brassicae* egg (n=20)	4.3 (±0.5)	45.4 a (±11.5)	16.4 d (±5.3)	61.8 e (±13.0)
5 *P. brassicae* eggs (n=16)	12.1 (±1.4)	45.9 a (±10.0)	52.9 b (±14.0)	98.7 c (±19.8)

Figures followed by the same letter are not significantly different. Mann Whitney U test: Inexperienced and 5-egg *M. brassicae* experienced females *versus* 1-egg *M. brassicae* experienced females, response to *P. brassicae* kairomone: T_T values $z=2.29$, $n_1=20$, $n_2=28$, $p<0.01$; Inexperienced and 5-egg *P. brassicae* experienced females versus 1-egg *P. brassicae* experienced females, response to *M. brassicae* kairomone: T_T values $z=2.07$, $n_1=20$, $n_2=31$, $p<0.02$. Inexperienced *versus* 5-egg *M. brassicae* experienced females, response to *P. brassicae* kairomone, T_T values: $U=78.5$, $n_1=10$, $n_2=18$, p NS; Inexperienced *versus* 5-egg *P. brassicae* experienced females, response to *M. brassicae* kairomone, T_T values: $U=116$, $n_1=15$, $n_2=16$, p NS. Comparisons made between rows only using Kruskal Wallis test ($p<0.01$).

Table 4. Influence of time since oviposition on a parasitoid's response to the contact kairomones of *Mamestra brassicae* and *Pieris brassicae* (mean ± S.E., time in s). Time spent searching within kairomone area = T_K; around kairomone area = T_S; within and around kairomone area = T_T.

a. *Mamestra brassicae* experienced females				
Time since oviposition		Response to *Mamestra brassicae* kairomone		
		T_K	T_S	T_T
1 h	(n=13)	31.0 (±5.1) a	43.7 (±17.3) b	74.6 (±21.5) c
24 h	(n=14)	42.8 (±6.1) a	36.9 (±14.0) b	79.7 (±17.9) c
44 h	(n=15)	56.0 (±8.9) a	59.1 (±19.8) b	115.1 (±27.2) c
Time since oviposition		Response to *Pieris brassicae* kairomone		
		T_K	T_S	T_T
1 h	(n=10)	117.8 (±44.0) a	16.5 (±9.9) d	134.3 (±52.7) c
24 h	(n=16)	35.7 (±6.2) a	7.7 (±4.7) d	43.7 (±7.9) c
44 h	(n=14)	58.0 (±12.8) a	64.2 (±23.3) b	122.2 (±32.0) c
b. *Pieris brassicae* experienced females				
Time since oviposition		Response to *Pieris brassicae* kairomone		
		T_K	T_S	T_T
1 h	(n=16)	52.9 (±19.6) a	33.4 (±13.7) d	86.3 (±24.9) c
24 h	(n=16)	51.8 (±9.2) a	43.4 (±15.9) bd	95.1 (±22.0) c
44 h	(n=20)	56.5 (±9.9) a	26.6 (±11.0) bd	83.1 (±17.5) c
Time since oviposition		Response to *Mamestra brassicae* kairomone		
		T_K	T_S	T_T
1 h	(n=16)	45.9 (±10.0) a	52.9 (±14.0) b	98.7 (±19.8) c
24 h	(n=16)	34.5 (±6.3) a	21.0 (±7.7) b	50.1 (±9.5) c
44 h	(n=14)	50.7 (±10.4) a	43.2 (±23.3) b	93.9 (±21.2) c

Figures followed by different letters are significantly different (Mann Whitney U test, p<0.01).

tested after 24 h, and is similar to the behaviour of inexperienced females (compare table 2). T_S values for the two host kairomones did not differ significantly within the remaining time intervals. The behaviour of both *M. brassicae* and *P. brassicae* experienced females within each time interval since oviposition did not differ significantly from that of inexperienced parasitoids (compare table 2).

3. Response to host contact kairomones following oviposition in two host species

Data from this experiment were analysed to determine whether oviposition in a host influences the response of *T. evanescens* towards eggs of different host species, and the extent to which the arrestment behaviour of a parasitoid changes following oviposition in a second host species.

Trichogramma evanescens readily accepted eggs of *P. brassicae*, but the acceptance of *M. brassicae* eggs was significantly lower when these were presented as Host 2 (table 5b). The latter observation would suggest that oviposition in *P. brassicae* may influence a parasitoid's acceptance of a second host species. It would, however, seem unlikely that such behaviour would lead to an exclusive preference for *P. brassicae* by *T. evanescens*, since the acceptance of *M. brassicae* eggs was still high. A full discussion of host selection by this strain of *T. evanescens* is given in Brand *et al.* (1984). The number of eggs laid in both host species and the handling time for *P. brassicae* was independent of the sequence of presentation (table 5a and b). Less time was spent handling *M. brassicae* eggs when these were presented as Host 2; with Host 2 the handling time, and with both hosts the number of eggs laid in *M. brassicae* was significantly lower than for *P. brassicae* (table 5a and b).

Table 5. Response of *Trichogramma evanescens* to the eggs of *Mamestra brassicae* and *Pieris brassicae*.

a. Host 1		
	Mamestra brassicae	*Pieris brassicae*
% females accepting eggs at first encounter	95 a n=39	90 a n=39
Handling time (min)	18.5 (±1.2) a n=39	20.0 (±1.3) a n=39
No. of eggs laid in host	3.3 (±0.3) a n=35	6.3 (±0.5) b n=46
b. Host 2		
	Mamestra brassicae	*Pieris brassicae*
% females accepting eggs at first encounter	76 b n=33	100 a n=31
Handling time (min)	11.0 (±1.1) b n=33	23.7 (±1.9) a n=31
No. of eggs laid in host	4.0 (±0.3) a n=40	6.0 (±0.8) b n=29

Figures followed by different letters are significantly different (Mann Whitney U test and chi-squared contingency table, p<0.01). Comparisons made for each trait between columns and Host 1 and Host 2.

Table 6. Response of *Trichogramma evanescens* to the contact kairomones of *Mamestra brassicae* and *Pieris brassicae* following oviposition in two different host species (mean ± S.E., time in s). Time spent searching within kairomone area = T_K; around kairomone area = T_S.

a. Parasitoid oviposition experience -	Host 1 *Mamestra brassicae* Host 2 *Pieris brassicae*		
	Kairomone	T_K	T_S
Visit 1	*M. brassicae* (n=38)	50.9 (±6.9) a	57.7 (±11.5) c
Visit 2	*M. brassicae* (n=16)	18.6 (±2.4) b	21.4 (±7.0) d
Visit 2	*P. brassicae* (n=13)	33.3 (±8.1) ab	16.1 (±7.2) d
b. Parasitoid oviposition experience -	Host 1 *Pieris brassicae* Host 2 *Mamestra brassicae*		
	Kairomone	T_K	T_S
Visit 1	*P. brassicae* (n=46)	45.7 (±4.7) a	23.1 (±4.0) d
Visit 2	*P. brassicae* (n=21)	25.2 (±3.4) b	24.0 (±5.0) d
Visit 2	*M. brassicae* (n=18)	42.0 (±9.0) ab	42.9 (±14.1) c

Figures followed by different letters are significantly different (Mann Whitney U test $p<0.05$). Comparisons made between rows, and a. and b.

Following oviposition in a second host species, parasitoids did not differ in their response to *M. brassicae* and *P. brassicae* kairomones (table 6a and b). Comparisons were made of the time spent visiting the kairomone area of Host 1 before and after oviposition in Host 2. In both cases, less time was spent searching within, and for *M. brassicae* experienced females, around the scale area of Host 1 at a second visit (table 6a and b). For an individual host species, the responses of parasitoids to the kairomones of the host in which they had most recently oviposited did not differ significantly between visits 1 and 2 (table 6a and b).

Discussion

Trichogramma evanescens exhibited a significant change in response to host kairomones following successful oviposition in a host egg. Previous exposure to a host has been shown to result in an enhanced preference for that host type in several insects and has been attributed to associative learning (e.g. Jaenike, 1983; Prokopy *et al.*, 1982; Vet, 1983; Lewis *et al.*, 2003; Vet *et al.*, 1995, 2003). This process does not adequately explain the behaviour observed in *T. evanescens*. Oviposition experience did not influence the response of parasitoids to the kairomone associated with the host in which they had oviposited. Less time was, however, spent initially in searching kairomone areas of hosts not previously encountered.

Mackintosh (1983) has suggested that the conflicting processes of sensitisation and habituation can lead to an initial increase (or decrease in the case of a negative stimulus) in response to a particular stimulus, followed by a gradual decline. Sensitisation to a conditional stimulus (CD) may be elicited by presentation of the unconditional stimulus (UCS) alone, without previous CD-UCS pairing (Mackintosh, 1983). This process could account for the initial decrease in response to kairomones of "novel" hosts observed in *T. evanescens* following oviposition. Such behaviour will enable *Trichogramma* to concentrate its foraging efforts in kairomone areas of hosts in which it has most recently oviposited and may thus increase its chance of reproducing. These results provide an interesting contrast to those of Jaenike (1982, 1983), who showed that oviposition in a preferred host may lead to increased acceptance of a less preferred host – a behaviour referred to as "cross-induction". For *Trichogramma* a reverse effect occurred, and oviposition in one of two similarly preferred hosts led to reduced acceptance of the second host type.

The time spent searching in the kairomone area of a "novel" host was dependent on a parasitoid's oviposition experience. Females that had oviposited in five host eggs spent longer searching in the kairomone areas of "novel" hosts, than those that had oviposited in one host egg. Such behaviour is difficult to explain in terms of learning, without a detailed examination of the physiological processes involved. It did not arise from habituation to kairomones of the encountered host, but rather from removal of some "inhibitory effect" towards kairomones of "novel" hosts.

Optimal foraging models predict that the incorporation of a second host/patch type into the foraging set should depend on the encounter rate with the most profitable patch (e.g. Charnov, 1976; Hubbard and Cook, 1978). For animals searching within a stochastic environment, ranking patches on the basis of reward probability rather than mean value prove to be a better strategy (e.g. Caraco, 1980; Real, 1980; Stephens, 1981). Indeed, many foragers appear to modify their assessment of patches during a foraging bout, as other activities such as predation or foraging for alternative food assume greater importance (e.g. Heller and Milinski, 1979; Lima *et al.*, 1985; Lewis *et al.*, 2003).

Females of *T. evanescens* are small and short-lived, and emerge with an almost full complement of eggs and limited energy reserves. Each female must therefore search in a manner that maximises its chance of finding hosts within her lifespan, assuming that she remains reproductively active throughout her adult life. The time spent searching in a particular patch will be governed by a parasitoid's expectation of finding hosts and her expected survival, as determined from age and/or energy constraints. This trade off between survival and foraging reward probability forms the basis of models of risk sensitive foraging (Caraco, 1980, 1981; Caraco and Chasin, 1984; Caraco and Lima, 1985; Houston and McNamara, 1982; Real, 1980; Stephens, 1981). Since *Trichogramma* relies on tactile cues for the location of hosts within a patch, some time should be spent in each patch (e.g. Laing, 1938; Gardner and van Lenteren, 1986; Schmidt and Smith, 1989). It should be noted in this context that the term patch refers to kairomone area. The amount of time spent in a patch may be expected to vary according to foraging experience. Inexperienced parasitoids should spend a similar amount of time in all patch types. Females that have successfully oviposited should concentrate their searching activities in patches associated with the highest reward probability. As the number of eggs laid increases but with little change in expected survival, parasitoids should spend more time searching "novel" patches since by parasitising several host types an individual may increase the probability of survival and the genetic diversity of its offspring (den Boer, 1968). Finally, parasitoids that have laid few eggs and have a low survival expectation should not differentiate between patch types (Caraco, 1980; Burger *et al.*, 2003).

It is clear that a detailed analysis of behavioural changes with respect to egg load, time and energy constraints, is required before the proposed hypothesis can be substantiated. It would, however, appear to explain the behaviour observed in *T. evanescens* rather well. The changes in response towards kairomones of "novel" hosts cannot be explained in terms of maximising the net rate of oviposition alone. The latter would predict that parasitoids should concentrate their searching effort in the kairomone areas of hosts in which they had successfully oviposited and "ignore" those of "novel" hosts. Such behaviour was not observed.

Results from this study indicate that oviposition experience in *T. evanescens* would not lead to specialisation on a particular host species. Females readily accepted eggs of a second host, although the acceptance of *M. brassicae* was significantly lower when presented as Host 2, and the time spent searching in a particular kairomone area would appear to depend on the reproductive state and expected survival of a parasitoid, rather than the development of any host preference. Such behavioural flexibility will assist *T. evanescens* to respond to fluctuations in host availability and minimise the risk of variation in foraging award.

References

Arthur A. P., 1966.- Associative learning in *Itoplectis conquisitor* (Hymenoptera: Ichneumonidae).- *Canadian Entomologist*, 98: 213-223.

Arthur A. P., 1971.- Associative learning by *Nemeritis canescens* (Hymenoptera: Ichneumonidae).- *Canadian Entomologist*, 103: 1137-1141.

Bleeker M. A. K., Smid H. M., Steidle J. L. M., Kruidhof M., van Loon J. J. A., Vet L. E. M., 2006.- Differences in memory dynamics between two closely related parasitoid wasp species.- *Journal of Animal Behaviour*, 71: 1343-1350.

Boer P. J. den, 1968.- Spreading of risk and stabilization of animal numbers.- *Acta Biotheoretica*, 18: 165-194.

Brand A. M., Dijken M. J. van, Kole M., Lenteren J. C. van, 1984.- Host-age and host-species selection of three strains of *Trichogramma evanescens* Westwood, an egg parasite of several Lepidopteran species.- *Mededelingen Faculteit Landbouwwetenschappen Rijksuniversiteit Gent*, 49: 839-847.

Bukovinszky T., Gols R., Hemerik L., Lenteren J. C. van, Vet L. E. M., 2007.- Time allocation of a parasitoid foraging in heterogeneous vegetation: implications for host-parasitoid interactions.- *Journal of Animal Ecology*, in press.

Burger J. M. S., Hemerik L., Lenteren J. C. van, Vet L. E. M., 2003.- Reproduction now or later: optimal host-handling strategies in the whitefly parasitoid *Encarsia formosa*.- *Oikos*, 106: 117-130.

Bush G. L., 1972.- The mechanism of sympatric host race formation in the true fruit flies (Tephretidae), pp. 3-23. In: *Genetic Mechanisms of Speciation in Insects* (White M. J. D., Ed.).- Australian and New Zealand Book Co., Pty. Ltd., Sydney, Australia.

Bush G. L., 1975.- Sympatric speciation in phytophagous insects, pp 143-171. In: *Evolutionary Strategies of Parasitic Insects and Mites* (Price P.W., Ed.).- Plenum Press, New York, USA.

Caraco T., 1980.- On foraging time allocation in a stochastic environment.- *Ecology*, 61: 119-128.

Caraco T., 1981.- Risk - sensitivity and foraging groups.- *Ecology*, 62: 527-531.

Caraco T., Chasin M., 1984.- Foraging preferences: response to reward skew.- *Animal Behaviour*, 32: 76-85.

Caraco T., Lima S. L., 1985.- Foraging juncos: interaction of reward mean and variability.- *Animal Behaviour*, 33: 216-224.

Charnov E. L., 1976.- Optimal foraging, the marginal value theorem.- *Theoretical Population Biology*, 9: 129-136.

Diehl S. R., Bush G. L., 1984.- An evolutionary and applied perspective of insect biotypes.- *Annual Review of Entomology*, 29: 471-504.

Fatouros N. E., Huigens M. E., van Loon J. J. A., Dicke M., Hilker M., 2005.- Chemical communication - butterfly anti-aphrodisiac lures parasitic wasps.- *Nature*, 433: 704.

Gardner S. M., Lenteren J. C. van, 1986.- Characterisation of the arrestment responses of *Trichogramma evanescens*.- *Oecologia*, 68: 265-270.

Godfray H. C. J., 1994.- *Parasitoids Behavioural and Evolutionary Ecology*.- Princeton University Press, Princeton, New Jersey, USA.

Heller R., Milinski M., 1979.- Optimal foraging of sticklebacks on swarming prey.- *Animal Behaviour*, 27: 1127-1141.

Houston A., 1980.- Godzilla and the creature from the black lagoon. Ethology v Psychology, pp. 297-318. In: *Analysis of Motivational Processes* (Toates F. M., Halliday T. R., Eds).- Academic Press, London, UK.

Houston A., Mcnamara J., 1982.- A sequential approach to risk-taking.- *Animal Behaviour*, 30: 1260-1261.

Hubbard S. F., Cook R. M., 1978.- Optimal foraging by parasitoid wasps.- *Journal of Animal Ecology*, 47: 593-604.

Jaenike J., 1982.- Environmental modification of oviposition behaviour in *Drosophila*.- *American Naturalist*, 119: 784-802.

Jaenike J., 1983.- Induction of host preference in *Drosophila melanogaster*.- *Oecologia*, 58: 320-325.

Krebs J. R., McCleery R. H., 1984.- Optimization in behavioural ecology, pp. 91-121. In: *Behavioural Ecology and Evolutionary Approach* (Krebs J. R., Davies N. B., Eds), 2nd edition.- Blackwell Scientific Publications, Oxford, UK.

Laing J., 1938.- Host finding by insect parasites. II The chance of *Trichogramma evanescens* finding its hosts.- *Journal of Experimental Biology*, 15: 281-302.

LENTEREN J. C. VAN, 1991.- Encounters with parasitized hosts: to leave or not to leave a patch?- *Netherlands Journal of Zoology*, 41: 144-157.

LENTEREN J. C. VAN (Ed.), 2003.- *Quality Control and Production of Biological Control Agents: Theory and Testing Procedures*.- CABI Publishing, Wallingford, UK.

LENTEREN J. C. VAN, BUENO V. H. P., 2003.- Augmentative biological control of arthropods in Latin America.- *BioControl*, 48: 123-139.

LENTEREN J. C. VAN, BALE J., BIGLER F., HOKKANEN H. M. T., LOOMANS A. J. M., 2006.- Assessing risks of releasing exotic biological control agents of arthropod pests.- *Annual Review of Entomology*, 51: 609-634 + supplemental material.

LESTER N. P., 1984.- The "feed - feed" decision: how goldfish solve the patch depletion problem.- *Behaviour*, 89: 175-196.

LEWIS W. J., JONES R. L., GROSS H. R. JR., NORDLUND D.A., 1976.- The role of kairomone and other behavioural chemicals in host finding by parasitic insects.- *Behavioural Biology*, 16: 267-289.

LEWIS W. J., VET L. E. M., TUMLINSON J. H., LENTEREN J. C. VAN, PAPAJ D. R., 2003.- Variations in natural-enemy foraging behaviour: essential element of a sound biological-control theory, pp. 41-58. In: *Quality Control and Production of Biological Control Agents: Theory and Testing Procedures* (LENTEREN J. C. VAN, Ed.).- CABI Publishing, Wallingford, UK.

LIMA S. L., VALONE T. J., CARACO T, 1985.- Foraging-efficiency-predation-risk trade-off in the grey squirrel.- *Animal Behaviour*, 33: 155-164.

MACKINTOSH N. J., 1983.- General principles of learning, pp. 149-171. In: *Animal Behaviour 3: Genes, Development and Learning* (HALLIDAY T. R., SLATER P. J. B., Eds).- Blackwell Scientific Publications, Oxford, UK.

NOLDUS L. P. J. J., LENTEREN J.C. VAN, 1983.- Kairomonal effects on host searching of *Trichogramma evanescens* an egg parasite of *Pieris brassicae*.- *Mededelingen van de Faculteit der Landbouwwetenschappen, Rijksuniversiteit Gent*, 48 (2): 183-194.

NOLDUS L. P. J. J., LENTEREN J.C. VAN, 1985a.- Kairomones for the egg parasite *Trichogramma evanescens* Westwood. 1. Effect of volatile substances released by two of its hosts, *Pieris brassicae* L. and *Mamestra brassicae* L.- *Journal of Chemical Ecology*, 11: 781-791.

NOLDUS L. P. J. J., LENTEREN J.C. VAN, 1985b.- Kairomones for the egg parasite *Trichogramma evanescens* Westwood. 2. Effect of contact chemicals produced by two of its hosts, *Pieris brassicae* L. and *Pieris rapae* L.- *Journal of Chemical Ecology*, 11: 793-800.

PAK G. A., LENTEREN J. C. VAN, 1984.- Selection of a candidate *Trichogramma* sp. strain for inundative releases against Lepidopterous pests of cabbage in the Netherlands.- *Mededelingen van de Faculteit der Landbouwwetenschappen, Rijksuniversiteit Gent*, 49 (3a): 827-837.

PROKOPY R. J., AVERILL A. L., COOLEY S. S., ROITBERG C. A., 1982.- Associative learning in egg laying site selection by apple maggot flies.- *Science*, 218: 76-77.

REAL L. A., 1980.- Fitness, uncertainty and the role of diversification in evolution and behaviour.- *American Naturalist*, 115: 623-638.

ROMEIS J., BABENDREIER D., WAECKERS F. L., SHANOWER T. G., 2005.- Habitat and plant specificity of *Trichogramma* egg parasitoids - underlying mechanisms and implications.- *Basic and Applied Ecology*, 6: 215-236.

SCHMIDT J. M., SMITH J. J. B., 1989.- Host examination walk and oviposition site selection of *Trichogramma minutum*: studies on spherical hosts.- *Journal of Insect Behavior*, 2: 143-171.

SHETTLEWORTH S. J., 1984.- Learning and behavioural ecology, pp. 170-194. In: *Behavioural Ecology, an Evolutionary Approach* (KREBS J. R., DAVIES N. B., Eds), 2nd edition.- Blackwell Scientific Publications, Oxford, UK.

SMID H. M., 2006.- Variation in learning of herbivory-induced plant odours by parasitic wasps: From brain to behavior, pp. 89-104. In: *Proceedings of the Frontis Workshop on Chemical Ecology: from Gene to Ecosystem Wageningen* (DICKE M., TAKKEN W., Eds).- Wageningen University, Wageningen, The Netherlands.

STEPHENS D. W., 1981.- The logic of risk-sensitive foraging preferences.- *Animal Behaviour*, 29: 628-629.

VET L. E. M., 1983.- Host-habitat location through olfactory cues by *Leptopilina clavipes* (Hartig) (Hym. Eucoilidae), a parasitoid of fungivorous *Drosophila*: the influence of conditioning.- *Netherlands Journal of Zoology*, 33: 225-249.

VET L. E. M., LEWIS W. J., CARDÉ R. T., 1995.- Parasitoid foraging and learning. pp. 65-101. In: *Chemical Ecology of Insects 2* (CARDÉ R. T., BELL W. J., Eds).- Chapman and Hall, New York, USA.

VET L. E. M., LEWIS W. J., PAPAJ D. R., LENTEREN J. C. VAN, 2003.- A variable-response model for parasitoid foraging behaviour. pp. 25-39. In: *Quality Control and Production of Biological Control Agents: Theory and Testing Procedures* (LENTEREN J. C. VAN, Ed.).- CABI Publishing, Wallingford, UK.

WAAGE J. K., 1979.- Foraging for patchily distributed hosts by the parasitoid *Nemeritis canescens*.- *Journal of Animal Ecology*, 48: 353-371.

Authors' addresses: Joop C. VAN LENTEREN (corresponding author, Joop.vanLenteren@wur.nl), Sara M. GARDNER, Marleen DISSEVELT, Laboratory of Entomology, Wageningen University, P.O. Box 8031, 6700 EH Wageningen, The Netherlands.

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