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Characterisation of the arrestment responses of *Trichogramma evanescens*

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Summary. Contact kairomones and oviposition in a host egg stimulated arrestment behaviour in *Trichogramma evanescens*, characterised by a reduction in walking speed and increased turning. Previous oviposition experience did not influence a parasitoid's response to contact kairomones, but successive encounters with kairomone patches resulted in parasitoids habituating to the contact chemical. Oviposition on a kairomone patch did not reverse this habituation effect. It was concluded that contact kairomones and host eggs will both contribute independently to the duration of a patch visit. The selection of patches by *T. evanescens* will depend on its response to kairomones. Results from this study indicate that the application of contact kairomones to field crops will not necessarily increase the probability of parasitoids finding hosts.

Host finding in insect parasitoids is generally divided into host-habitat location, host location and host acceptance (eg. Weseloh 1981; Vinson 1984). At each stage, chemical (eg. Read et al. 1970; Sandlan 1980; Sabelis and van de Baan 1983; Vet 1983), acoustic (eg. Cade 1975) or visual (eg. Levinson and Haisch 1983; Glas and Vet 1983) cues derived from the host or host-plant, may be used to assist orientation to host infested areas.

Egg parasitoids of the genus *Trichogramma* are known to respond to several chemical stimuli produced by their Lepidopteran hosts. The sex pheromones of *Heliothis zea* (Boddie) and *Mamestra brassicae* (L), certain excretory producs of *Pieris brassicae* (L) and host-plant materials have been shown to act as long range attractants for *Trichogramma* (Altieri et al. 1981; Lewis et al. 1982; Noldus and van Lenteren 1985 a,b); substances found in the wing scales, frass and fecal material of the host also act as contact kairomones (Jones et al. 1973; Lewis et al. 1976; Smits 1982; Noldus and van Lenteren 1983, 1985).

Following observations of arrestment behaviour by *Trichogramma* spp. to host contact kairomones, extracts of these were applied in the field in an attempt to increase percentage parasitism at low host densities. Results from this work are inconclusive (Lewis et al. 1975; Gross 1981; Gross et al. 1984), with significant increases in parasitism being observed only at high host densities. The distribution of kairomones and pre-release stimulation of parasitoids with kairomones are known to influence the searching efficiency of *Trichogramma* (Gross et al. 1975; Lewis et al. 1979; Beevers et al. 1981), but little information is available on the foraging strategy. Thus suggestions for manipulating parasitoid behaviour to improve their performance in the field, tend to be based on speculation rather than tested hypotheses.

The responses of *Trichogramma evanescens* (Westwood) to the contact kairomones and eggs of one of its hosts, *P. brassicae*, are quantified in this paper and examined with respect to a parasitoid's oviposition experience. Results are reviewed in the context of current foraging theory and criteria suggested by which these parasitoids select patches and determine the duration of a patch visit.

Materials and methods

The parasitoids

The parasitoids used in these experiments originated from a population of *T. evanescens* parasitising *M. brassicae* in cabbage, collected in The Netherlands in 1981 (strain 11 in Pak and van Lenteren 1984). Since then the species has been reared in the laboratory on *Ephestia kuehniella* (Zeller).

Parasitoids were reared at 25° C and were offered honey after emergence. Experiments were carried out at 20° C using 2-day old females; parasitoids were transferred to the experimental room (20° C) one day before the experiment.

In most experiments, females had oviposited in one *P. brassicae* egg (1–2 days old), one hour previously. These females were then regarded as experienced. Inexperienced females had not previously oviposited.

i) *Influence of contact kairomones on the time spent searching by parasitoids on leaves.* Experienced females were released onto Brussels sprout leaves (total surface area 84 cm^2) on the upper surface of which, wing scales of *P. brassicae* had been brushed in three discrete areas (each 0.25 cm^2). The areas were arranged at random. Control experiments were carried out using uncontaminated leaves.

Parasitoids were observed until they flew off the leaf or a period of 60 min had elapsed. The latter period was chosen arbitrarily.

ii) *Characterisation of parasitoid walking behaviour.* The walking behaviour of experienced females was recorded

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using video equipment and traced onto plastic sheets. Tracks were divided into two second intervals (steps) to analyse changes in walking speed and turning behaviour; the direction of turns was also noted – left or right respectively. All experiments were carried out in open Petri dishes (9.0 cm diameter) the base of which was covered with filter paper.

Parasitoid responses were recorded under three experimental conditions:

a) behaviour on clean filter paper – control,

b) behaviour after contacting wing scales (known to act as a contact kairomone) of *P. brassicae* brushed onto filter paper in two spearate areas, each 30 x 3 mm,

c) behaviour after ovipositing in one *P. brassicae* egg. A parasitoid was released within 2 mm of the egg and recording commenced after she had walked off the egg for the first time.

In each case experiments were terminated after females had walked off the filter paper and had spent 1–2 min walking around the edge of the Petri dish.

iii) *Influence of oviposition experience on a parasitoid's response to host contact kairomones.* The behaviour of experienced and inexperienced parasitoids to the contact kairomones of *P. brassicae* was compared.

Experiments were carried out on discs of white cabbage maximum diameter 3.5 cm. Half of each disc was covered with contact kairomones, wing scales and frass 'deposited' by ovipositing *P. brasssicae* females; the remaining area which had not been exposed to the butterflies formed the control. Each disc was attached to a filter paper and placed in a Petri dish.

A single parasitoid was released into each disc and its walking behaviour observed as in section ii).

iv) *Response at successive visits to host scale areas.* Experienced females were allowed to search in a series of seven Petri dishes, each containing a single area of *P. brassicae* scales (0.78 cm^2) brushed onto filter paper. A single *P. brassicae* egg was also placed in the centre of the scale area of arenas 1 and 6. An interval of 10 min was left between the presentation of each arena. During this period parasitoids were offered clean (control) filter paper. Replacement of filter papers was achieved by removing the base of the Petri dishes when parasitoids were searching on the lid. This method minimised the handling disturbance of a parasitoid.

Parasitoids were observed until they walked off the filter paper.

Results

i) *Effect of contact kairomones on time spent searching on leaves.* The presence of host scales resulted in an increase in time spent searching by experienced parasitoids on Brussels sprout leaves (Table 1). More time was spent searching on the upper surface of kairomone treated leaves when compared to the control, but no difference was observed with respect to the lower leaf surfaces. Since kairomone was only placed on the upper leaf surfaces, these results suggest that it acts solely as a local arrestant, stimulating parasitoids to search intensively within the immediate area of a kairomone patch.

Table 1. Influence of contact kairomones on the time spent searching by experienced parasitoids on different leaf surfaces (time in min, mean ±S.E.)

Treatment	Upper leaf surface	Lower leaf surface
Control	9.7 (±1.8)^a $n=18$	11.6 (±2.2)^a $n=20$
Kairomone	19.3 (±2.3)^b $n=19$	12.1 (±2.3)^a $n=18$

Data followed by different letters are significantly different $P<0.01$ (Mann Whitney *U* test)

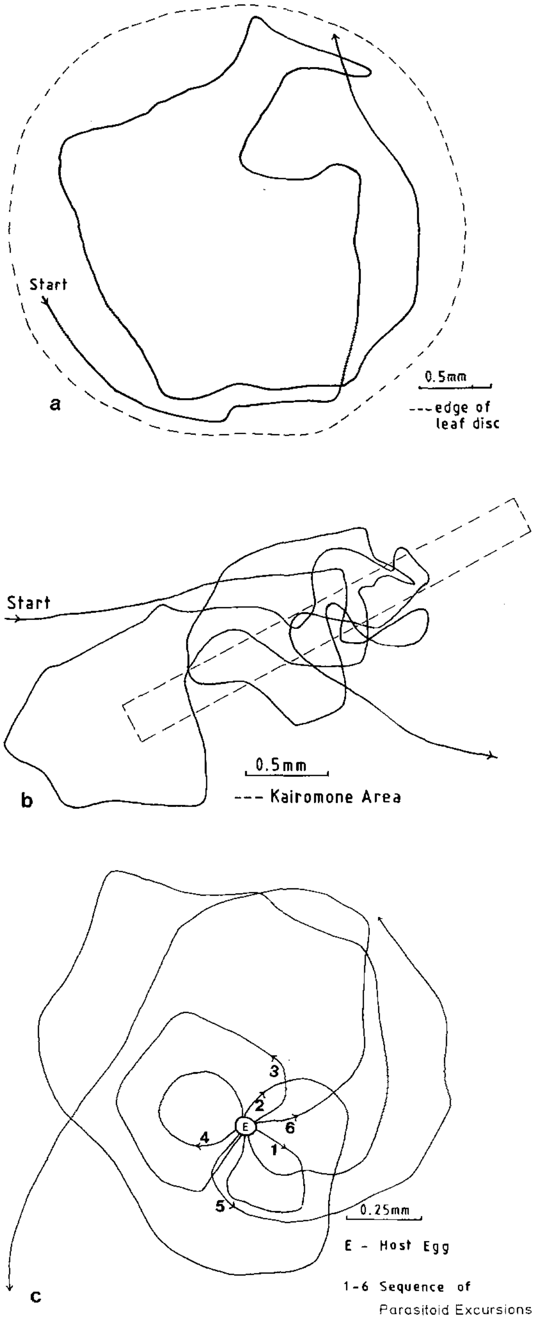

Fig. 1a–c. Walking behaviour of *T. evanescens* **a** on clean cabbage leaf disc – control, **b** after contacting host scales (kairomone) of *P. brassicae*, **c** after oviposition in egg of *P. brassicae*

Table 2. Characteristics of the walking behaviour of *T. evanescens*

Treatment	Walking speed (mm/2 s)	Activity (proportion of time spent searching)	Mean turning angle	Directional changes Percentage of paths in which the proportion of left or right right turns is	
				<0.75	>0.75
Control ($n=20$)	5.8 (±0.1)^{a}	0.96^{a}	$13^{\circ a}$	60^{ab}	40
Inside kairomone area ($n=15$)	2.8 (±0.1)^{b}	0.65^{b}	$25^{\circ b}$	91^{a}	9
Outside kairomone area ($n=15$)	5.1 (±0.1)^{c}	0.93^{a}	$30^{\circ b}$	42^{b}	58
Oviposition ($n=29$)	4.0 (±0.1)^{d}	0.95^{a}	$47^{\circ c}$	15^{c}	85

IS-Initial step

Figures in the same column followed by different letters are significantly different $P<0.01$ (Kolmogorov-Smirnoff test for walking speed and turning angle, chi-squared contingency test for activity and directional changes)

ii) *Characterisation of parasitoid walking behaviour.* Figure 1 presents examples of the walking behaviour of *T. evanescens* on control and kairomone areas and following oviposition. Changes in parasitoid behaviour were determined from comparison of the distribution of walking speed and turning anlges, and the frequency of directional changes. The latter was given by the proportion of left and right turns observed in paths of minimum length of five steps; values greater than 0.75 indicated a bias in one direction.

a) *Control areas:* Parasitoids walked at an average speed of 5.8 mm/2 s (Table 2) and showed little turning movement (Fig. 2a). Turning behaviour did not vary significantly between individuals (median test for left turns: $\chi^2_6=4.04$, p NS; right turns: $\chi^2_7=6.58$, p NS) or according to direction (Kolmogorov-Smirnoff two sample test $D=0.13$, $\chi^2_2=3.83$, p NS). Consequently data from all females were pooled to determine the median turning angle (Table 2). This was 13°. Initial direction was maintained in less than 50% of cases (Table 2).

b) *Kairomone areas:* On entering a kairomone area parasitoids showed a singificant decrease in activity and walking speed (Table 2). Turning behaviour increased significantly (Fig. 2b, comparison with control area $\chi^2_2=24.39$, $p<0.001$) with frequent changes in direction (Table 2).

After leaving a kairomone area an initial increase in turn angle was observed (Table 2), followed by increased activity and walking speed. Subsequent turning behaviour was similar to that observed within the kairomone area (Fig. 2c). Directionality was maintained in 50% of cases (Table 2) but was not correlated with that of the initial turn.

c) *Oviposition in host egg:* Following oviposition, parasitoids made several excursions from the host egg during which walking speed was reduced (Table 2) and turning behaviour increased (Fig. 2d) compared to that occurring in the control area. Initial turning direction was maintained in 85% of cases until the egg was re-encountered (Table 2), resulting in a characteristic circling pattern (Fig. 1c).

iii) *Effect of oviposition experience on a parasitoid's response to host contact kairomones.* Inexperienced females walked faster than experienced females, but both showed a reduction in walking speed within the kairomone area (Table 3). Individual experienced females spent longer searching in kairomone areas than in control areas (Table 3) but the response of inexperienced females varied considerably. The time spent searching in kairomone and control areas did not differ significantly between the two female types (Mann Whitney U test Time in control areas $U=65.5$, $n_1=11$, $n_2=13$, p NS; time in kairomone area $U=55$, $n_1=11$, $n_2=13$, p NS).

iv) *Effect of successive visits to kairomone areas.* Table 4 presents the time spent searching in and around seven host scale areas, presented to parasitoids at 10 min intervals. The time spent searching decreased significantly between visits 1 and 2 and visits 4 and 5. The first decrease may be attributed to the absence of a host egg in the second arena, since host eggs also elicit significant arrestment behaviour; the second decrease signifies a change in parasitoid response to the contact kairomone. A second oviposition resulted in a temporary increase in time spent searching around the host egg (Visit 6, Table 4) but did not influence a parasitoid's response to host scales (Visit 7, Table 4).

Handling time also decreases significantly between visits 1 and 6 (Table 5). This resulted from a change in time taken to 'recognise' parasitised eggs, which decreased significantly during the course of a first visit (Table 5).

Discussion

Parasitoids searching in control areas walked in relatively straight lines interspersed by erratic turns. Such behaviour has been observed in many motile organisms (eg. Jander 1975), and would seem to form the most efficient strategy for moving between patches of hosts or orientating along a chemical gradient (Bell and Tobin 1982).

Oviposition or contact with host scales stimulated a change in walking behaviour characterised by a reduction in walking speed and increase in turning frequency. The pattern of each response differed with respect to frequency in directional changes. Following oviposition initial direction was maintained, resulting in a circling pattern which increases the chance of *T. evanescens* finding other eggs laid within the vicinity (Laing 1938; Yano 1978; van Lenteren et al. 1982). Similar behaviour has been demonstrated in insects after feeding (Dethier 1957; Carter and Dixon 1982) and during mate-finding (Schal et al. 1983).

Parasitoids searching inside a host scale area showed frequent changes in direction, resulting in an intensive scan-

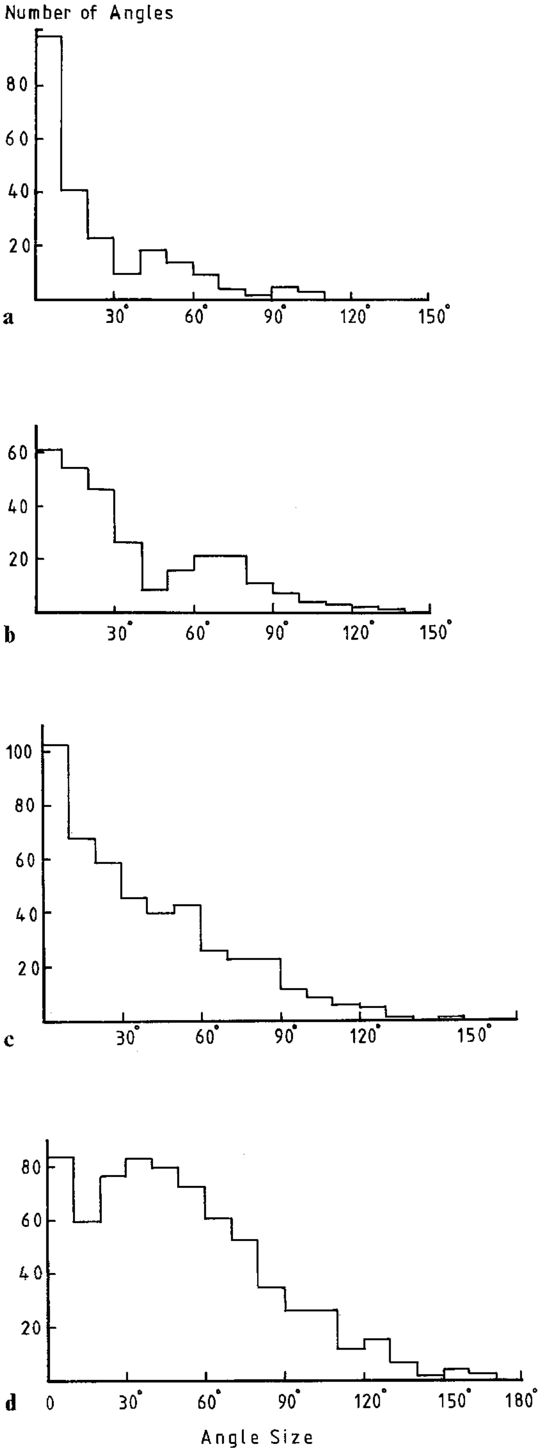

Fig. 2a–d. Distribution of turning angles of parasitoids walking in **a** Control area, **b** within kairomone area, **c** after leaving kairomone area, **d** after oviposition

ning of the area. On leaving the area, an initial increase in turn angles was observed, following which turning tended to be unidirectional. This 'boundary response' is common to many searching insects (eg. Nelson 1977; Waage 1978; Havukkala 1980), and will assist *T. evanescens* to re-enter a patch and to follow trails of contact kairomones deposited by hosts searching for suitable oviposition sites (Smits 1982).

Table 3a, b. Parasitoid responses to the contact kairomones of *P. brassicae* (mean ±S.E.)

	Control	Kairomone
a Experienced females $n=13$		
Walking speed (mm/s)	1.8^{a} (±0.1)	1.4^{b} (±0.1)
Time spent searching in each area (s)	63.1^{g} (±16.1)	99.2^{h} (±19.6)
b Inexperienced females $n=11$		
Walking speed (mm/s)	2.5^{c} (±0.2)	2.0^{d} (±0.1)
Time spent searching in each area (s)	90.9^{gh} (±34.4)	102.3^{gh} (±40.4)

Figures followed by different letters are significantly different $P<0.05$ (Mann Whitney *U* test)

Table 4. Response of experienced parasitoids to the contact kairomones of *P. brassicae* over a sequence of seven visits (time in s, mean ±S.E.)

Visit number	*n*	Time spent searching in kairomone area	Time spent searching around kairomone area
1*	23	156.7 (±29.3)^{a}	62.6 (±16.3)^{a}
2	24	50.7 (±9.4)^{b}	32.2 (±7.5)^{b}
3	24	38.3 (±6.6)^{b}	31.2 (±8.0)^{b}
4	24	43.7 (±7.9)^{b}	23.2 (±7.7)^{b}
5	22	28.2 (±10.9)^{c}	0.0^{c}
6*	20	55.4 (±11.7)^{b}	46.5 (±13.6)^{b}
7	19	21.3 (±3.6)^{c}	4.8 (±3.0)^{c}

* Parasitoids oviposited in one host egg placed in kairomone area. Data followed by different letters are significantly different $P<0.01$ (tested within columns only, Kruskal Wallis and Mann Whitney *U* tests)

Foraging experience is known to influence the behaviour of many insects, although the processes responsible for observed behavioural changes are frequently difficult to separate (see Papaj and Rausher 1983; for review). Previous oviposition in a host did not influence the time spent searching by *T. evanescens* in the kairomone area of the encountered species. Oviposition experience does however influence the response of *T. evanescens* to kairomones of hosts in which they have not oviposited (Gardner et al. 1985).

T. evanescens is known to mark host eggs following oviposition (Salt 1937), although the response of females towards parasitised hosts is dependent upon their oviposition experience (Klomp et al. 1980). Results from this study indicated that successive contacts with parasitised hosts resulted in a reduction in time spent examining them on subsequent encounters. Such behaviour is common in insect parasitoids and may arise from an increased sensitivity towards chemical markers associated with parasitised hosts (van Lenteren 1981).

Habituation to chemical odours has been demonstrated in several insect species (eg. Thorpe 1938; Bartell and Lawrence 1977; Kuenen and Baker 1981), and has been suggested as a basic mechanism by which parasitoids determine

Table 5. Parasitoid response to host eggs during visits 1 and 6 (mean values ±S.E.)

	Visit 1 ($n=23$)	Visit 6 ($n=20$)
Oviposition time (s)	882.6 (±76.9)^a	836.8 (±72.5)^a
Number revisits to egg	5.5 (±0.8)^a	3.9 (±0.6)^a
Time spent on parasitised egg		
– Visits 1&2 (s)	215.1 (±18.2)^a ($n=42$)	142.4 (±24.9)^b ($n=27$)
– Subsequent visits	139.9 (±13.1)^b ($n=61$)	124.2 (±17.4)^b ($n=30$)
Time spent in kairomone area (s)	156.7 (±30.0)^a	55.4 (±11.7)^b
Time spent searching around kairomone area (s)	62.6 (±16.3)^a	46.5 (±13.6)^a

Data followed by different letters are significantly different $P<0.01$ (Mann Whitney *U* test between columns)

the duration of a patch visit (Waage 1979). Successive encounters with 'empty' kairomone patches resulted in a significant decrease in time spent searching by *T. evanescens*. Oviposition in a host egg did not however increase a parasitoid's response to contact kairomone (see also Gardner et al. 1985). Unlike *Nemeritis canescens* (Grav.), the insect studied by Waage (1978, 1979), both contact kairomones and oviposition elecited significant arrestment behaviour in *T. evanescens*. Both factors will therefore contribute independently to the time spent searching on a patch, the duration of which would seem to depend on a parasitoid's initial response to kairomone and the number and/or rate of ovipositions (Gardner and van Zoest in prep.).

Parasitoids searching in a patchy environment must determine which areas are the most profitable in order to maximise their chances for survival and reproduction (Hubbard and Cook 1978). Patch selection by *T. evanescens* will depend on its response to host kairomones. This response is not influenced by the number of ovipositions (Gardner et al. 1985) but apparently on the frequency of oviposition in a particular patch type. Caraco (1980, 1981) has suggested that a strategy in which patches are ranked according to 'reward' probability rather than mean benefit, may be a better solution for animals searching within a stochastic environment. Such a strategy will reduce the risk of an individual accumulating a large energy deficit while searching for patches with the highest mean reward (Real 1980; Caraco and Chasin 1984).

Results from this work have important implications for the use of contact kairomones in the field. Contact kairomones have been shown to induce arrestment behaviour in *T. evanescens*, but do not stimulate parasitoids to search outside the treated area. Their application will not therefore increase the probability of parasitoids finding hosts, unless applied to the actual oviposition sites of hosts. Parasitoids will be retained initially in the crop, but the effect of searching in unprofitable areas will reduce their expectation of finding hosts and subsequently their response to kairomones. The consequences of this behaviour for the control of the host will depend on the size and distribution of both the host and parasitoid populations (Waage and Hassell 1982).

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References

Altieri MA, Lewis WJ, Nordlund DA, Gueldner RC, Todd JW (1981) Chemical interactions between plants and *Trichogramma* spp. wasps in soybean fields. Prot Ecol 3:259–273

Bartell RJ, Lawrence LA (1977) Reduction in responsiveness of male apple moths, *Epiphyas postvittana*, to sex pheromone following pulsed pheromonal exposure. Phys Ent 2:1–6

Beevers M, Lewis WJ, Gross HR, Nordlund DA (1981) Kairomones and their use for management of entomophagous insects: X Laboratory studies on manipulation of host-finding behaviour of *Trichogramma pretiosum* Riley with a kairomone extracted from *Heliothis zea* (Boddie) moth scales. J Chem Ecol 7:635–648

Bell WJ, Tobin TR (1982) Chemo-orientation. Biol Rev Camb Phil Soc 57:219–260

Cade W (1975) Acoustically orientating parasitoids: fly phonotaxis to cricket song. Science 190:1312–1313

Caraco T (1980) On foraging time allocation in a stochastic environment. Ecology 6:119–128

Caraco T (1981) Risk-sensitivity and foraging groups. Ecology 62:527–531

Caraco T, Chasin M (1984) Foraging preferences: response to reward skew. Anim Behav 32:76–85

Carter MC, Dixon AFG (1982) Habitat quality and the foraging behaviour of coccinellid larvae. J Anim Ecol 51:865–878

Dethier VG (1957) Communication by insects: physiology of dancing. Science 125:331–336

Gardner SM, Dissevelt M, Lenteren JC van (1985) Behavioural adaptations in host finding by *Trichogramma evanescens* (Westwood): the influence of oviposition experience on the response to host contact kairomones. (submitted)

Glas PCG, Vet LEM (1983) Host-habitat location and host location by *Diachasma alloeum* Muesebeck (Hym. Braconidae) a parasitoid of *Rhagoletis pomonella* Walsh (Dipt. Tephritidae). Neth J Zool 33:41–54

Gross HR Jr (1981) Employment of kairomones in the management of parasitoids. In: Nordlund DA, Jones RL, Lewis WJ (eds) Semiochemicals, their role in pest control. John Wiley & Sons, New York, pp 79–95

Gross HR Jr, Lewis WJ, Jones RL, Nordlund DA (1975) Kairomones and their use for management of entomophagous insects: III Stimulation of *Trichogramma achaeae, T. pretiosum* and *Micropletis croceipes* with host seeking stimuli at time of release to improve their efficiency. J Chem Ecol 1:431–438

Gross HR Jr, Lewis WJ, Beevers M, Nordlund DA (1984) *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae): Effects of augmented densities and distribution of *Heliothis zea* (Lepidoptera: Noctuidae) host eggs and kairomones on field performance. Env Ent 13:981–985

Havukkala I (1980) Klinokinetic and klinotactic humidity reactions of beetles *Hylobius abietis* and *Tenebrio molitor*. Phys Ent 5:133–140

Hubbard SF, Cook RM (1978) Optimal foraging by parasitoid wasps. J Anim Ecol 47:593–604

Jander R (1975) Ecological aspects of spatial orientation. A Rev Ecol Syst 6:171–188

Jones RL, Lewis WJ, Beroza M, Bierl BA, Sparks AN (1973) Host seeking stimulants (kairomones) for the egg parasite *Trichogramma evanescens*. Env Ent 2:593–596

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

Kuenen LPS, Baker TC (1981) Habituation versus sensory adaptation as the cause of reduced attraction following pulsed and constant sex pheromone pre-exposure in *Trichoplusia ni.* J Insect Physiol 27:721–726

Laing J (1938) Host finding by insect parasites. II The chance of *Trichogramma evanescens* finding its hosts. J Exp Biol 15:281–302

Lenteren JC van (1981) Host discrimination by parasitoids. In Nordlund DA, Jones RL, Lewis WJ (eds) Semiochemicals: their role in pest control. John Wiley&Sons, New York, pp 153–179

Lenteren JC van, Glas PCG, Smits PH (1982) Evaluation of control capabilities of *Trichogramma* and results of laboratory and field research on *Trichogramma* in The Netherlands. Proc 1er Symp Intern Trichogrammes 257–268

Levinson HZ, Haisch A (1983) Optical and chemosensory stimuli involved in host recognition and oviposition of the cherry fruit fly *Rhagoletis cerasi* L. In: Cavalloro R (ed) Fruit flies of economic importance. AA Balkema, Rotterdam, Netherlands, pp 268–275

Lewis WJ, Jones RL, Nordlund DA, Sparks AN (1975) Kairomones and their use for management of entomophagous insects: I Evaluation for increasing rates of parasitization by *Trichogramma spp.* in the field. J Chem Ecol 1:343–347

Lewis WJ, Jones RL, Gross HR Jr, Nordlund DA (1976) The role of kairomones and other behavioural chemicals in host finding by parasitic insects. Behav Biol 16:267–289

Lewis WJ, Beevers M, Nordlund DA, Gross HR Jr, Hagen KS (1979) Kairomones and their use for management of entomophagous insects: IX Investigations of various kairomone-treatment patterns for *Trichogramma* spp. J Chem Ecol 5:673–680

Lewis WJ, Nordlund DA, Gueldner RC, Teal PEA, Tumlinson JH (1982) Kairomones and their use for management of entomophagous insects. XIII Kairomonal activity for *Trichogramma* spp. of abdominal tips, excretion and a synthetic sex pheromone blend of *Heliothis zea* (Boddie) moths. J Chem Ecol 8:1323–1331

Nelson MC (1977) The blowflies dance: role in regulation of food intake. J Insect Physiol 23:603–612

Noldus LPJJ, Lenteren JC van (1983) Kairomonal effects on host searching of *Trichogramma evanescens* an egg parasite of *Pieris brassicae.* Med Fac Landbouw Rijks Univ Gent 48/2:183–194

Noldus LPJJ, Lenteren JC van (1985 a) Kairomones for the egg parasite *Trichogramma evanescens* Westwood. I Effect of volatile substances released by two of its hosts, *Pieris brassicae* L. and *Mamestra brassicae* L. J Chem Ecol (in press)

Noldus LPJJ, Lenteren JC 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 *Mamestra brassicae* L. J Chem Ecol (in press)

Pak GA, Lenteren JC van (1984) Selection of a candidate *Trichogramma* sp. strain for inundative releases against Lepidopterous pests of cabbage in The Netherlands. Med Fac Landbouw Rijksuniv Gent 49/3:827–837

Papaj DR, Rausher MD (1983) Individual variation in host location by photophagous insects. In: Ahmad S (ed) Herbivorous insects: Host seeking behaviour and mechanisms. Academic Press, New York

Read DP, Feeney PP, Root RB (1970) Habitat selection by the aphid parasite *Diaretiella rapae* (Hymenoptera: Braconidae) and hyperparasite *Charips brassicae* (Hymenoptera: Cynipidae). Can Ent 102:1567–1578

Real LA (1980) Fitness, uncertainty and the role of diversification in evolution and behaviour. Am Nat 115:623–638

Sabelis MW, Baan HE van de (1983) Location of distant spider mite colonies by phytoseiid predators: demonstration of specific kairomones emitted by *Tetranychus urticae* and *Panonychus ulmi.* Ent exp appl 33:303–314

Salt G (1937) The sense used by *Trichogramma* to distinguish between parasitised and unparasitised hosts. Proc R Soc series B 122:57–75

Sandlan K (1980) Host location by *Coccygomimus turionellae* (Hymenoptera: Ichneumonidae). Ent exp appl 27:233–245

Schal C, Surbel JL, Vogel G, Todin TR, Tourtellot MK, Leban RA, Bell WJ (1983) Search strategy of sex pheromone stimulated male German cockroaches. J Insect Physiol 29:575–579

Smits PH (1982) The influence of kairomones of *Mamestra brassicae* L. on the searching behaviour of *Trichogramma evanescens* Westwood. Proc 1er Symp Intern Trichogrammes 139–150

Thorpe WH (1938) Further experiments on olfactory conditioning in a parasitic insect. The nature of the conditioning process. Proc R Soc London Series B 126:370–397

Vet LEM (1983) Host habitat location through olfactory cues by *Leptopilina clavipes* (Hartig) (Hym: Eucoilidae), a parasitoid of fungivorous *Drosophila*: the influence of conditioning. Neth J Zool 33:225–248

Vinson SB (1984) Parasitoid-host relationships. In: Bell WJ, Cardé (eds) Chemical ecology of insects. Chapman&Hall, London, pp 205–236

Waage JK (1978) Arrestment responses of the parasitoid *Nemeritis canescens* to a contact chemical produced by its host *Plodia interpunctella.* Phys Ent 3:135–146

Waage JK (1979) Foraging for patchily distributed hosts by the parasitoid *Nemeritis canescens.* J Anim Ecol 48:353–371

Waage JK, Hassell MP (1982) Parasitoids as biological control agents: a fundamental approach, Parasitology 84:241–268

Weseloh RM (1981) Host location by parasitoids. In: Nordlund DA, Jones RL, Lewis WJ (eds) Semiochemicals: their role in pest control. John Wiley&Sons, New York, pp 79–95

Yano E (1978) A simulation model of searching behaviour of a parasite. Res Popul Ecol 20:105–122

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