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A comparative functional approach to the host detection behaviour of parasitic wasps. 1. A qualitative study on *Eucoilidae* and *Alysiinae*

Louise E. M. Vet and Jacques J. M. van Alphen

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We studied host detection behaviour in *Alysiinae* (*Braconidae*; *Ichneumonoidea*) and *Eucoilidae* (*Cynipoidea*), the larvae of which are endoparasitoids of fly larvae and investigated whether this behaviour is determined by their descent or can be considered an adaptation to different environments. We compared the searching behaviour of females of 32 *alysiine* and 25 *eucoilid* species from a variety of microhabitats and from different dipteran hosts by using qualitative behavioural variables. Three main modes of searching were detected: vibrotaxis, ovipositor searching and antennal searching, and the species could be classified according to the role these different modes play in the detection of host larvae. The searching modes are largely dependent upon the taxonomic position of the species. In most cases species belonging to one genus show a similar behaviour pattern. However, we also encountered examples of radiation; closely related species that search differently. The function of the three searching modes has not been elucidated so far. Therefore we cannot say that similar searching modes in unrelated species are examples of adaptive convergence. Especially in *Drosophila* parasitoids we encountered great differences in searching behaviour between different species living in the same microhabitat. We believe differences at all levels of searching, including host detection behaviour may contribute to niche segregation and create possibilities for different parasitoid species to coexist in the same microhabitat, even when they attack the same host species.

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Мы изучали поведение при обнаружении хозяев у представителей *Alysiinae* (*Braconidae*, *Ichneumonoidea*) и *Eucoilidae* (*Cynipoidea*), личинки которых – эндопаразиты личинок мух, и исследовали, определяется ли это поведение их наследственностью и может ли рассматриваться как адаптация к различным условиям. Мы сравнивали поисковое поведение самок 32 видов *Alysiinae* и 25 видов *Eucoilidae* из разных микробиотопов и с разных хозяев из числа двукрылых методом использования качественных поведенческих переменных. Выделены 3 основные модуса поиска: вибротаксис, поиск яйцекладом и поиск антеннами, причем, отдельные виды могут быть классифицированы в соответствии с ролью, которую эти три модуса играют в распознавании личинок – хозяев. Модусы поиска в целом зависят от таксономического положения вида. В большинстве случаев виды, принадлежащие к одному роду, обнаруживают сходные особенности поведения. Однако, мы также встречаем и противоположные примеры радиации; когда близкородственные виды ведут поиск разными методами. Функция 3-х модусов поведения разъясняет далеко не все. Поэтому мы не можем сказать, что сходные модусы поиска у неродственных видов – примеры адаптивной конвергенции. Особенно у паразитов *Drosophila* мы встречаем широкие различия поискового поведения у разных видов, обитающих в одних и тех же микробиотопах. Мы предполагаем наличие различий на всех уровнях поиска, в том числе и то, что поведение при обнаружении хозяина может иметь значение при сегрегации ниш и создавать возможности для разных паразитоидных видов к сосуществованию в одном микробиотопе, даже если они используют один и тот же вид хозяина.

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1. Introduction

Lately there has been much debate on the adaptive approach of studying individuals and their characteristics. Especially Lewontin (1978) and Gould and Lewontin (1979) resisted the exclusive focus on adaptation as the only approach to study evolutionary change and strongly supported a more pluralistic approach. Their main arguments against the so-called 'adaptionist programme' are that it would fail to distinguish the current utility of characteristics from the causes of their origin, that it would assume without further proof that all characteristics of organisms are adaptive optimal solutions to problems, that it would rely upon plausibility alone as a criterion for accepting speculative tales and that it would fail to consider alternatives to immediate adaptation for the explanation of characteristics (Gould and Lewontin 1979).

Maynard Smith (1978, 1982) and especially Mayr (1983) clearly refuted Gould and Lewontin's main criticism and we fully agree with them that asking functional questions is a sound scientific approach (See also Bakker 1964). There are, however, evident dangers in the application of this method and these should be well considered. It is obviously misleading to assume that all differences we find between the characteristics of different individuals are adaptive, that each individual or trait is perfectly optimized or that each outcome of natural selection is without any developmental constraint. We may not interpret each minute characteristic of an individual as a separate adaptation (atomistic approach), as differences found could be a result of chance and be selectively neutral. However, we do not need to test whether animals are adapted, but we need to show that possession of a specific characteristic would be favoured by selection. To achieve this goal is through experimental analysis. In the study of animal behaviour this approach has led to the many recent studies on optimal foraging (see for a review Pyke et al. 1977, Krebs 1978). Another method to gain insight into the adaptive value of characteristics is based on comparison, and this is used in this paper. Different species have evolved in relation to different – or the same – environments, and by comparing many different species we may find a correlation between a species characteristic and an environmental factor (e.g. Lack 1971, Schoener 1974).

In some cases the correlation found can have a high predictive value for further comparisons between species (Krebs and Davies 1981, Mayr 1983). In particular, comparative research on related and less related species ('outgroup comparison') can reveal to what extent differences have an historical and/or a functional explanation, e.g. which characteristics can be considered apomorphic and which plesiomorphic (Ridley 1982, Wannertorp 1983). The distinction made here is of course relative, since differences viewed as having an historical explanation today, will often have arisen as a result of adaptation to different environments in the past. We

must also keep in mind that the same ecological pressures may have induced different adaptations in different species i.e. there may exist different solutions for survival.

In this paper we are using behavioural traits of parasitic Hymenoptera as comparative characteristics. Parasitoids have to search for hosts to produce their offspring and they do so by performing a fairly set pattern of behavioural steps as a reaction to many different stimuli. Because of the direct link between successful searching and the production of offspring we can expect especially searching behaviour to be a trait under direct influence of natural selection.

Searching females first have to orientate themselves towards a potential host habitat e.g. through olfaction (Vet 1983, Vet et al. 1983, 1984) and secondly (the subject of the present paper) towards a potential host. Small interspecific differences at all levels of searching may lead to niche segregation (see e.g. Vet et al. 1984), especially under conditions of strong interspecific competition.

When comparing the searching behaviour of species we may encounter four extreme situations as shown in Fig. 1. Situation 1 we would expect, for example, when comparing the searching behaviour of closely related allopatric species that fill a similar niche in different geographic areas. If species in situation 2 show differences in their ecology we may be dealing with adaptive radiation of the searching behaviour. If the species in situation 3 show great similarity in their ecology and if the behaviour has developed independently (i.e. is an apomorphic trait) we may be dealing with adaptive convergence of the behaviour and we may call it a case of analogy (in contrast with homology in situation 1). This is not the case if the behavioural trait represents an an-

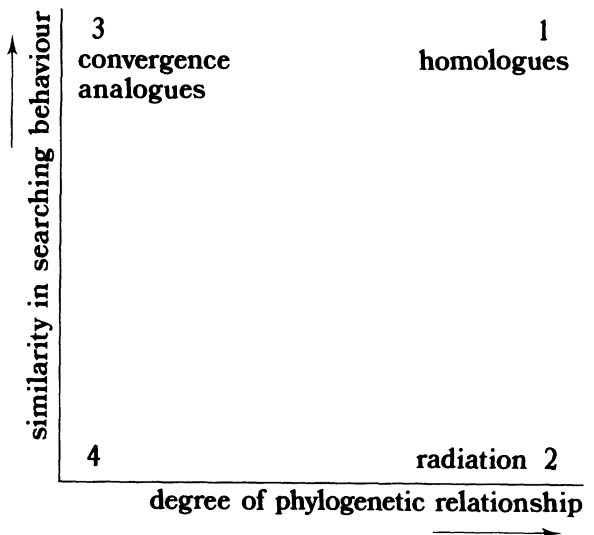


Fig. 1. The possible relationships between the degree of phylogenetic relationship and the degree of similarity in searching behaviour in parasitic Hymenoptera.

cestral condition, i.e. is plesiomorphic. It is obvious that to answer functional question about behavioural differences and to make any statement whether behavioural traits are homologous or analogous outgroup comparison is necessary and we must consider species sets that occur in both situations 2 and 3. Situation 4 remains: which is perhaps for our comparative purposes less interesting. Obviously several behavioural traits of these species will still be functional but from this kind of comparison we can never deduce which traits are and which are not functional. Other comparisons with more related species will then be necessary.

Two species that are in situation 4 led to the comparative study as presented in this paper. Two unrelated endoparasitoids of frugivorous *Drosophila* larvae that attack the same host species in the same fruits showed a totally different host detection behaviour after having entered a potential microhabitat. *Asobara tabida* (Nees) detects larvae by sensing their movement (vibrotaxis). Searching females show a typical walk-stop behaviour pattern while walking over the substrate. Only after having located the position of a larva do they use their ovipositor to try and probe the host (van Alphen and Drijver 1982). *Leptopilina heterotoma* (Thomson) does not react to host movement at all. Searching females almost continuously walk over the substrate while rhythmically probing the surface with their partly extended ovipositor (van Lenteren 1976). No regular motionless stops are made as in *A. tabida*. These two species are in different superfamilies. *Asobara tabida* belongs to the Alysiinae, a subfamily of the Braconidae (Ichneumonoidea), while *L. heterotoma* belongs to the Eucoilidae (Cynipoidea). This raised the question whether this systematic difference was the explanation for the behavioural differences. Both eucoilid and alysiine species attack larvae of all kinds of Diptera, which live in a variety of microhabitats (substrates). We investigated whether the host detection behaviour of Alysiinae and Eucoilidae parasitoids is determined by their descent and can be considered a more recent adaptation to different environments. We therefore compared the host detection behaviour of 32 Alysiinae and 25 Eucoilidae species by using several qualitative behavioural parameters.

2. Materials and techniques

2.1. Collections

Parasitoids were collected as adults in the field, while they were searching for hosts in a particular microhabitat and/or were reared in the laboratory from material collected from the field (see for techniques Vet 1983, Vet et al. 1984). In some cases we exposed traps with fruit medium or decaying plant material in the field. We obtained alysiine and eucoilid parasitoid species from fermenting fruits, decaying plant material such as rotten

tomatoes and vegetables, decaying beet leaves, and reed detritus from the edges of fresh water lakes, mushrooms (collected after their caps had opened), cowdung and carrion. We were not always successful in identifying the host species of the collected parasitoids. All Alysiinae were identified by C. van Achterberg, Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands. All Eucoilidae were identified by G. Nordlander, Swedish University of Agricultural Sciences, Uppsala, Sweden.

2.2. Observations

We observed several species in the field and all of them in the laboratory. In the laboratory females were allowed to search on host food material (e.g. a piece of mushroom, fermenting fruit material, a small amount of cow-dung). Often this was the same material from which the females were collected as adults in the field. The medium contained larvae of the identified host or of a host species which was accepted for oviposition. The searching and oviposition behaviour of the females was observed through a binocular microscope and was recorded on video tape. From some species we could observe only a few individuals. From others we observed many different individuals, originating from several collection sites.

3. Results

Tab. 1 lists the observed species, together with their hosts, the microhabitat from which they were collected, and the country or state of origin. Several species belonging to the genera *Asobara* and *Leptopilina* were included in the studies. The other species belong to related genera. Some new species have not yet been described and are only assigned to a genus or merely numbered. At the start of our studies limited ecological information was available and for several species this is the first record on host and microhabitat identity. Many species attack Drosophilidae and are specific in their choice of microhabitat (Vet 1983, Vet et al. 1983, 1984, van Alphen and Vet, unpubl.). In general only a few Alysiinae and Eucoilidae species are found to inhabit more than one microhabitat and most species appear to restrict their host range to one family only (For Alysiinae see also Wharton, in press).

After having observed many individuals of different species we chose several behavioural variables to characterize host detection behaviour. We selected those variables which did not show any significant intraspecific variation, when measured under different environmental circumstances such as high or low host densities, the presence of hosts of different preference, the presence of substrates of different preference and different microclimatic conditions.

Tab. 1. Observed parasitoid species, their hosts, their microhabitat and their country or state of origin.

Alysiinae ¹			
<i>Alysia manducator</i> Panzer	Calliphoridae	carrion	the Netherlands
<i>Aphaereta minuta</i> (Nees)	Muscidae	decaying plants	the Netherlands; Greece
<i>A. cf. oscinidis</i> Ashmead ³	Muscidae	decaying plants	California
<i>A. pallipes</i> (Say) ³	Sarcophagidae	cowdung	Texas
<i>A. cf. pallipes</i> (Say) ⁴	Drosophilidae	decaying fruits mushrooms	New York ⁵ ; California
<i>A. scaptomyzae</i> Fischer	Drosophilidae	decaying plants fermenting fruits	the Netherlands
<i>A. tenuicornis</i> Nixon	Drosophilidae	decaying plants	the Netherlands
<i>Asobara</i> sp. nov. C van Achterberg	Drosophilidae	fermenting fruits	Australia ⁵
<i>A. citri</i> Fischer	Drosophilidae	fermenting fruits	South Africa
<i>A. gahani</i> (Papp)	Drosophilidae	fermenting fruits	Puerto Rico ⁵
<i>A. persimilis</i> (Papp)	Drosophilidae	fermenting fruits	Australia ⁵
<i>A. rufescens</i> (Foerster)	Drosophilidae	decaying plants	the Netherlands
<i>A. tabida</i> (Nees)	<i>Drosophila</i>	fermenting fruits	the Netherlands
<i>Atopandrium debilitatum</i> (Morley)	?	decaying plants	the Netherlands
<i>Dinotrema</i> sp. "nr. <i>hirticornis</i> (Thomson)"	Phoridae	decaying fruits	the Netherlands
<i>Dinotrema</i> cf. <i>hodiensis</i> (Fischer)	Phoridae	mushrooms	the Netherlands
<i>Dinotrema</i> sp. nov. L van Achterberg	Phoridae	mushrooms	the Netherlands
<i>Dinotrema</i> sp. nov. M van Achterberg	Phoridae	mushrooms	the Netherlands
<i>Dinotrema</i> sp. nov. S van Achterberg	Phoridae	mushrooms	the Netherlands
<i>D. taurica</i> (Telenga)	Phoridae	mushrooms	the Netherlands
<i>Orthostigma</i> sp. "nr. <i>laticeps</i> (Thomson)"	Phoridae	mushrooms	the Netherlands
<i>O. sculpturatum</i> Tobias	Phoridae	mushrooms	the Netherlands
<i>Pentapleura fuliginosa</i> (Haliday)	Anthomyiidae	decaying plants	the Netherlands
<i>P. angustula</i> (Haliday)	?	decaying plants	the Netherlands
<i>Phaenocarpa breviflagellum</i> van Achterberg & Zaykov	Sepsidae (?)	cowdung	France
<i>P. canaliculata</i> Stelfox	<i>Fannia</i> spp.	decaying mushrooms decaying plants	the Netherlands
<i>P. conspurcator</i> (Haliday)	Anthomyiidae	cowdung rotten vegetables	the Netherlands
<i>P.</i> sp. "nr. <i>galatea</i> (Haliday)"	?	reed detritus	the Netherlands
<i>P. ruficeps</i> (Nees)	<i>Pegomyia</i> spp.	mushrooms	the Netherlands
<i>P. tacita</i> Stelfox	Drosophilidae	mushrooms	the Netherlands
<i>Tanycarpa bicolor</i> (Nees)	Drosophilidae	mushrooms	the Netherlands
<i>T. punctata</i> van Achterberg	<i>Drosophila</i>	decaying plants fermenting fruits	the Netherlands
Eucolidae ²			
<i>Chrestosema</i> sp. "PBP 24-3"	<i>Drosophila</i>	fermenting fruits	Guadeloupe ⁵
<i>Ganaspis</i> sp. "d"	<i>Drosophila</i>	fermenting fruits	Australia ⁵
<i>Ganaspis</i> sp. "2"	<i>Drosophila</i>	fermenting fruits	Florida; Puerto Rico ⁵
<i>Ganaspis</i> sp. "G-365"	<i>Drosophila</i>	fermenting fruits	Guadeloupe ⁵
<i>G. xanthopoda</i> (Ashmead)	<i>Drosophila</i>	fermenting fruits	Tanzania; Florida; Puerto Rico ⁵
<i>Kleidotoma bicolor</i> (Giraud)	<i>Drosophila</i>	decaying mushrooms	the Netherlands
<i>K.</i> sp. "nr. <i>bicolor</i> (Giraud)"	<i>Drosophila</i> (?)	fermenting fruits	Canada
<i>K. brevicornis</i> Thomson	?	decaying plants	the Netherlands
<i>K. dolichocera</i> Thomson	Drosophilidae	decaying plants	the Netherlands
<i>K.</i> sp. "nr. <i>flicornis</i> Cameron"	?	reed detritus	the Netherlands
<i>K.</i> sp. "nr. <i>psiloides</i> Westwood"	?	decaying plants	the Netherlands
<i>K.</i> sp. "nr. <i>psiloides</i> Westwood"	?	reed detritus	the Netherlands
<i>Leptopilina bouardi</i> (Barbotin et al.)	<i>Drosophila</i>	fermenting fruits	California; Greece; South Africa
<i>L. clavipes</i> (Hartig)	<i>Drosophila</i>	decaying mushrooms	the Netherlands
<i>L. fimbriata</i> (Kieffer)	Drosophilidae	decaying plants	the Netherlands
<i>L. heterotoma</i> (Thomson)	Drosophilidae	fermenting fruits trap with decaying plant materials	the Netherlands
<i>L. victoriae</i> Nordlander	<i>Drosophila</i>	fermenting fruits	Seychelles
<i>L.</i> sp. "nr. <i>victoriae</i> Nordlander"	<i>Drosophila</i>	fermenting fruits	Madras ⁵

<i>Leptopilina</i> sp. "PB 10-5"	<i>Drosophila</i>	fermenting fruits	Guadeloupe ⁵
<i>Leptopilina</i> sp. "PR 222-2"	<i>Drosophila</i>	fermenting fruits	Puerto Rico ⁵
<i>Trybliographa agaricola</i> (Thomson)	<i>Pegomyia</i> spp.	mushrooms	the Netherlands
<i>T. diaphana</i> (Hartig)	<i>Delia</i> spp.	decaying plants	the Netherlands
<i>T. rapae</i> (Westwood)	<i>Delia brassicae</i>	decaying cabbages	the Netherlands
Species not assigned to a genus ⁶			
PB 26-4	<i>Drosophila</i>	fermenting fruits	Guadeloupe ⁵ ; Florida
PB 26-7	<i>Drosophila</i>	fermenting fruits	Florida

1. Reference collections deposited in the Rijksmuseum van Natuurlijke Historie at Leiden, the Netherlands.
2. Reference collections with G. Nordlander, Swedish University of Agricultural Sciences, Uppsala, Sweden.
3. Gregarious species.
4. Solitary species.
5. Collected by P. Chabora, Queens College, Flushing, New York.
6. Numbering according to species references system of Carton, Chabora and Nordlander (unpublished).

The variables used were:

- 1) *Reaction to host movement*. Movement in the close vicinity of the parasitoid elicits a change in the latter's searching behaviour. The position of the female is abruptly directed towards the source of movement, followed by a motionless period (after which probing attempts towards the source of movement are often made, see 5). The source of movement can be an active larva or an imitation of such induced by moving the tip of a small paint brush on or slightly under the surface of the host medium.
- 2) *Ovipositor searching*. Rhythmic probing of the substrate with the ovipositor while walking.
- 3) *Regular stops*. Walking (with or without probing) is regularly alternated with motionless stops.
- 4) *Stand and probe*. Intensive probing of the substrate directly upon stopping.
- 5) *Probe at host*. Probes directly at host after a motionless period.
- 6) *Probes backwards*. The ovipositor is probed in backward direction between the hind legs.
- 7) *Antennal searching*. Females rhythmically drum the substrate with the tips of their antennae, or they non-rhythmically palpate irregularities in the substrate.

The host detection behaviour of *A. tabida* is characterized by variables 1, 3 and 5, that of *L. heterotoma* by variable 2 only. We now present how the variables are distributed over the other observed species.

1) The total absence of a behavioural response to host movement was only found in three other species besides *L. heterotoma*, viz. *L. victoriae*, *L. "sp. near victoriae"* and *L. clavipes*, all of which are closely related to *L. heterotoma*. All other species reacted to host movement to some extent, so the use of this stimulus in host detection was certainly not restricted to *Asobara* or the Alysiinae, but is probably generally present in larval parasitoids. There was, however, great interspecific variation in the importance of this stimulus in the detection of larvae. It was the most important – and perhaps the only direct – stimulus in the host detection be-

haviour of all *Aphaereta*, *Asobara*, *Atopandrium*, *Pentapleura*, *Phaenocarpa* (except *P. breviflagellum*) species and in *Tanycarpa bicolor*. In other Alysiinae it was not the only mode of searching but still an important one. In the Eucilidae it was also present and the most important stimulus for species belonging to the genus *Ganaspis* and *Chrestosema* sp., whose host detection behaviour is, in many ways, comparable to that of the *A. tabida* type. In other eucoilid species it was much less important.

2) Ovipositor searching as found in *L. heterotoma* was the most important mode of detecting hosts in all *Leptopilina* species. This rhythmic use of the ovipositor while walking was however not restricted to this genus but it was also present in all *Kleidotoma* species and in species PB 26-4. It was absent in all Eucilidae that strongly reacted to host movement (*Ganaspis* spp., *Chrestosema* sp.), and in *Trybliographa* species who mainly search while standing still with their ovipositor deep in the substrate (see 4). Ovipositor searching was, however, not restricted to Eucilidae only as we also discovered a group of Alysiinae who searched in this way: members of the genus *Dinotrema* and *Orthostigma*. *Alysia manducator* and *P. breviflagellum* also frequently used their ovipositor while walking. The same was reported for *Alysia ridibunda* Say by Burgess and Wingo (1968). However, in these last three species reaction to host movement was also important in host finding.

3) There is a correlation between the amount of time spent standing still and the use of host movement as a stimulus while searching. All species that strongly reacted to host movement regularly stood motionless while searching. Like *A. tabida* all alysiines with strong vibrotaxis showed a characteristic sequence of walks (a few steps) and stops (a few seconds). (See also van Alphen and Drijver 1982, Wharton, in press). This sequence was also present in the eucoilid genus *Ganaspis*, in *Chrestosema* sp. and in the genus *Trybliographa*, although in these species pauses are much longer and to-

tal velocity is lower. In *Leptopilina* only those species that were reacting to host movement made regular motionless stops.

4) Several species seemed to be specialized in searching for hosts that live in deeper layers or hidden spaces. Their most typical host detection behaviour consists of little walking and intensive probing of the substrate directly upon stopping. This kind of behaviour was most distinct in the eucoilid *Trybliographa* and *Kleidotoma* species. It was also shown by the alysiines *Phaenocarpa ruficeps* and *Dinotrema taurica* who use their long ovipositors to probe for hosts through the caps of mushrooms, and to a lesser extent by the other *Dinotrema* and *Orthostigma* species who search for Phoridae larvae between the gills of mushrooms (except for *D. "sp. nr. hirticornis"*).

In these species reaction to a source of movement on top of the substrate (e.g. with the tip of a small brush) often resulted in the females probing deep into the substrate, rather than probing directly towards the source of movement.

5) Like in *A. tabida* all species that mainly locate their hosts by detecting host movement probed directly at the host after a motionless stop. In these species the use of the ovipositor was generally limited to this kind of probing.

6) Backward probes were only detected in *A. manducator* and in the *Dinotrema* and *Orthostigma* species (except *D. taurica*).

7) Within the alysiines *Tanycarpa punctata* was the only species that showed real antennal searching. Females rhythmically drummed the substrate with their antennal

tips. *Aphaereta* females kept the tips of their antennae slightly bent towards the substrate, but did not show real antennal investigation. A eucoilid species with antennal searching like *T. punctata* was PB 26-7, a species not assignable to a recognized genus. The tips of its antennae have an aberrant shape compared with that of other eucoilid *Drosophila* parasitoids (Nordlander pers.comm.). *Leptopilina fimbriata* and especially all *Trybliographa* species also make regular use of their antennae in host detection. They palpate irregularities in the substrate in a non-rhythmic way.

All *Kleidotoma* species showed a typical behaviour which was not discovered in any other species. After having searched the substrate for about one minute females pause and fold their wings closely around the abdomen. They do this by stroking the wings with their hind legs so that the wings are bent at a hyaline patch at the inner part of the radial cell. This wing-folding behaviour is correlated with searching motivation as it is significantly more prominent when kairomones are present in the substrate (Vet 1984). It seems an adaptation to search for host larvae in small holes and crevices in the substrate. The type of radial cell where wing folding occurs is unique for the genus *Kleidotoma* within the family Eucoilidae (Nordlander pers. comm.). The searching behaviour of *Kleidotoma* seemed very complex in general, as these species used different searching modes alternatively: walking while probing, stand and probe, and vibrotaxis. We concluded that their behaviour can be considered intermediate between *Ganaspis* species (vibrotaxis) and most *Leptopilina* species (ovipositor searching). This is further substantiated by Vet and Bakker (1984). Another species with such intermediate behaviour was *Leptopilina* sp. "PR 222-2".

Summarizing we could detect three main modes of searching in these larval parasitoids: Vibrotaxis (VT),

A		B		C	
	VT +++ OS - AS -		VT ++ OS + AS -		VT ++ OS +++ AS -
Alysiinae	Eucoilidae	Alysiinae	Eucoilidae	Alysiinae	Eucoilidae
Aphaereta (6) Asobara (6) Atopandrium (1) Pentapleura (2) Phaenocarpa (5) T. bicolor	Ganaspis (4) Chrestosema sp. "PBP 24-3"	A. manducator P. breviflagellum		Dinotrema (6) Orthostigma (2)	Kleidotoma (7) L. sp. "PR 222-2"
D		E		F	
	VT + OS - AS +++		VT + OS +++ AS ++		VT + OS +++ AS -
Alysiinae	Eucoilidae	Alysiinae	Eucoilidae	Alysiinae	Eucoilidae
T. punctata	PB 26-7		L. fimbriata		L. bouhardi L. sp. "PB 10-5" PB 26-4
G		H			
	VT + OS ++ AS ++		VT - OS +++ AS -		
Alysiinae	Eucoilidae	Alysiinae	Eucoilidae		
	Trybliographa (3)		L.clavipes L. heterotoma L.victoriae L.sp."nr. victoriae"		

Searching mode :

- not present
- + present
- ++ important
- +++ most important

Fig. 2. Classification of Alysiinae and Eucoilidae species according to the role different searching modes play in host detection behaviour. VT = vibrotaxis, OS = ovipositor searching, AS = antennal searching. Between parentheses number of species in genus studied in each group.

ovipositor searching (OS) (which also included the use of the ovipositor in a different way than that of *L. heterotoma*), and antennal searching (AS). According to the role these different modes played in the host detection behaviour of each species (which is based on the amount of searching time they allocate to this behaviour) we could distinguish eight different groups as shown in Fig. 2. Going from left to right in this figure ovipositor searching becomes increasingly more important, and at the bottom right it is the only mode. At the top left of the figure vibrotaxis is the only mode of searching. No noticeable use is made of ovipositor or antennae and probing occurs only after detection of a moving host. The three lower left groups consist of species with antennal searching. They differ mainly in the importance of their ovipositor searching.

4. Discussion

Having classified the different species according to their searching modes we will now try to relate this classification to differences in their ecology and their phylogenetic relationship (see Fig. 1, Introduction). Is it possible to give genuine adaptive explanations for some of the differences in searching modes we have observed and to what extent can the observed variation be explained by historical factors as opposed to ecological factors?

It seems obvious that the searching modes are largely dependent upon the taxonomic position of the species. In most cases species that belong to one genus show a similar behaviour pattern. In the Eucolidae all *Leptopilina* species use their ovipositor while walking, all *Kleidotoma* species show the typical wing folding, all *Trybliographa* species stand and probe and all *Ganaspis* species detect hosts by vibrotaxis. In the Alysiinae many species, even belonging to different genera (but belonging to the same generic group) search like *A. tabida*: All *Asobara*, *Aphaereta* etc. (group A, Fig. 2) species. All *Dinotrema* and *Orthostigma* species studied (belonging to a different generic group) use their ovipositor (group C, Fig. 2). The predictive value of such characteristics and their importance in biosystematic studies are obvious. During our studies we could frequently classify species to genus level by looking at their searching behaviour only, identifications which were independently confirmed by morphological examinations by the taxonomists. In these cases we were dealing with situation 1 in Fig. 1: Related species show great similarity in searching behaviour.

However, in many of these cases species within one genus are also similar in their ecology and we may be dealing with synapomorphic or shared derived behavioural traits. All *Ganaspis* we studied attack *Drosophila* species in fermenting fruits. All, but one, *Dinotrema* spp. and all *Orthostigma* spp. – with very similar searching behaviour – attack Phoridae in mushrooms (see also Wharton, in press).

When we compare genera it is tempting to assume that all differences in searching modes we discover are adaptive because they are selected for through differences in their ecology. For example, it seems functional for the fungivorous *Dinotrema* and *Orthostigma* species to search for their phorid hosts that are hidden between the gills of mushrooms by regularly probing deep in between these gills with their ovipositor and part of their laterally compressed abdomen. A pure vibrotaxis searching behaviour may be much less functional in these alysiines.

We must be careful, however, not to give plausible answers, merely thought up to fit the facts. A more extensive outgroup comparison is needed to give such general explanations. Unfortunately it is nearly impossible to make a sister group analysis at the genus level as the genealogical relationships are still far from known, especially in the Eucolidae (Nordlander 1982).

We feel more confident in explaining the adaptive value of considerable differences in searching modes we find in more closely related species. Then we are dealing with situation 2 from Fig. 1: Related species have a different searching behaviour. If we can explain their differences as obvious adaptations to different ecological circumstances we are focussing on autapomorphic traits and we may speak of adaptive radiation of this behaviour. We will discuss two such examples.

Tanycarpa bicolor and *T. punctata*

We observed totally different searching behaviours in these closely related species. *Tanycarpa bicolor* that attacks young Drosophilidae larvae in decaying plant materials and mushrooms shows a typical vibrotaxis searching behaviour, very similar to that of many other Alysiinae (group A, Fig. 2). *Tanycarpa punctata* attacks *Drosophila* in fermenting fruits. This species however is one of the exceptional species that searches with their antennae, which may be considered a derived trait, based on outgroup comparison with the other alysiine genera. Females rhythmically drum the substrate with their antennal tips to detect the hind spiraculi of older *Drosophila* larvae which, at this stage, dig vertically into the medium with their spiraculi protruding from the surface. *T. punctata* also uses host movement as host detection stimulus but to a lesser extent and in a different way from *T. bicolor*. There is no probing reaction to young larvae that crawl over the surface, but vibrations from the older larvae seem to evoke a behavioural reaction. This finely tuned behavioural radiation is clearly correlated with differences in preferred host stages of the two species, and is analogous to two opiine parasitoids reported by Glas and Vet (1983).

Leptopilina fimbriata

All *Leptopilina* species attack Drosophilidae. *Leptopilina heterotoma*, *L. boulandi*, *L. victoriae*, *L. sp.* “PB

10-5", *L. sp.* "nr. *victoriae*" and *L. sp.* "PR 222-2" attack *Drosophila* in fermenting fruits, and *L. clavipes* in decaying mushrooms. Although there are some differences in searching between these species (especially in the importance of vibrotaxis) (Vet and Bakker 1984) their behaviour is very similar, especially when compared with *L. fimbriata* that attacks *Scaptomyza pallida* in decaying plant materials. *L. fimbriata* is the only *Leptopilina* species studied with significant antennal searching. Its antennae are morphologically unique for the genus (Nordlander 1980). Also the behavioural reaction to larval kairomones is different in *L. fimbriata* (Vet and Bakker 1984, Vet and van der Hoeven 1984).

We think differences in host distribution and perhaps in absolute host densities between the different microhabitats to be factors which have influenced this searching behaviour. Rich fermenting fruits and decaying mushrooms usually contain high density clusters of host larvae, whereas in decaying leaves hosts seem to have a more dispersed distribution with low density patches. In decaying beet leaves we often found single larvae of *S. pallida* – a species closely related to real leaf miners – feeding in a small area of decaying tissue. These larvae were still covered by the cuticle of the leaf. In this, for *Leptopilina*, aberrant situation we might expect different searching methods with regard to the use of antennae and ovipositor, the use of kairomones and the use of host movement stimuli. Further experimental research and comparison with the – still – ecologically unknown and unobserved species *L. longipes* is certainly needed.

We are uncertain whether antennal searching in *L. fimbriata* is a derived or a primitive trait. The "primitive" genus *Trybliographa* searches with the antennae which may suggest that antennal searching is a plesiomorphic trait. It may however, be a secondarily derived trait in *L. fimbriata* (autapomorphy).

It is more difficult to deduce examples of ecological convergence (situation 3, Fig. 1) from our studies.

As all species studied are larval parasitoids we cannot conclude that the more or less general reaction to host movement is an example of adaptive convergence related to the host stage attacked. We would have to compare with related species that attack eggs or pupae of the host, but no such alysiines or eucoilids are known.

In both families we do find examples of ovipositor searching but they are not clearly attributable to similarities in ecology. Neither can we speak of an ecological analogy between alysiine and eucoilid species that search with their antennae. In fact, in one fermenting fruit, containing only *Drosophila* larvae we may find several parasitoid species, even from one family, all searching in a different way: a *Leptopilina* species (ovipositor searching), a *Ganaspis* species (vibrotaxis) and a species that searches with its antennae (PB 26-7). Each searching mode is likely to be optimal under a certain very specific set of conditions present in the same fruit.

There may be a link with host stage or host species selection.

In previous papers (Vet et al. 1984, Vet and Janse 1984) we reported on the importance of differences in microhabitat odour responses in relation to the coexistence of some *Asobara* species. But differences at all levels of searching may contribute to niche segregation, also differences in host detection behaviour. Such differences show yet another example of creating possibilities for different, potentially competing species to coexist in the same microhabitat, even when they attack the same host species.

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References

- Alphen, J. J. M. van and Drijver, R. A. B. 1982. Host selection by *Asobara tabida* Nees (Braconidae: Alysiinae) a larval parasitoid of fruit inhabiting *Drosophila* species. I Host stage selection with *Drosophila melanogaster* as host species. – Neth. J. Zool. 32: 215–231.
- Bakker, K. 1964. Background of controversies about population theories and their terminologies. – Z. angew. Ent. 53: 187–208.
- Burgess, L. P. and Wingo, C. W. 1968. The host and present status of *Alysia ridibunda* Say in Missouri. – Proc. Ent. Soc. Wash. 70: 204–208.
- Glas, P. C. G. and Vet, L. E. M. 1983. Host-habitat location and host location by *Diachasma alloem* Muesebeck (Hym.: Braconidae) a parasitoid of *Rhagoletis pomonella* Walsh (Dipt. Tephritidae). – Neth. J. Zool. 33: 41–54.
- Gould, S. J. and Lewontin, R. C. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. – Proc. R. Soc. Lond. B 205: 581–598.
- Krebs, J. R. 1978. Optimal foraging: decision rules for predators. – In: Krebs, J. R. and Davies, N. B. (eds.) Behavioural ecology: an evolutionary approach. Blackwell Sci. Publ., Oxford, pp. 23–63.
- and Davies, N. B. 1981. An introduction to behavioural ecology. – Blackwell Sci. Publ., Oxford.
- Lack, D. 1971. Ecological isolation in birds. – Blackwell Sci. Publ., Oxford.
- Lenteren, J. C. van. 1976. The development of host discrimination and the prevention of superparasitism in the parasite *Pseudeucoila bochei* (Hym: Cynipidae). – Neth. J. Zool. 26: 1–83.

- Lewontin, R. C. 1978. Adaptation. – *Sci. Am.* 239: 156–169.
- Maynard Smith, J. 1978. Optimization theory in evolution. – *Ann. Rev. Ecol. Syst.* 9: 31–56.
- 1982. Evolution and the theory of games. – Cambridge Univ. Press.
- Mayr, E. 1983. How to carry out the adaptationist program. – *Am. Nat.* 121: 324–334.
- Nordlander, G. 1980. Revision of the genus *Leptopilina* Förster, 1869 with notes on the status of some other genera (Hymenoptera, Cynipoidea: Eucoilidae). – *Ent. Scand.* 11: 428–453.
- 1982. Systematics and phylogeny of an interrelated group of genera within the family Eucoilidae (Insecta: Hymenoptera, Cynipoidea). – Ph. D. thesis, Univ. of Stockholm.
- Prokopy, R. J. and Webster, R. P. 1978. Oviposition deterring pheromone of *Rhagoletis pomonella*, a kairomone for its parasitoid *Opius lectus*. – *J. Chem. Ecol.* 4: 481–494.
- Pyke, G. H., Pulliam, H. R. and Charnov, E. L. 1977. Optimal foraging a selective review of theory and tests. – *Quart. Rev. Biol.* 52: 137–154.
- Ridley, M. 1982. How to explain organic diversity. – In: Chermas, J. (ed.), Darwin up to date. JPC Magazines, London.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. – *Science* 185: 27–39.
- 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. – *Neth. J. Zool.* 33: 225–248.
- 1984. Response to kairomones by some alysiine and eucoilid parasitoid species (Hymenoptera). – In: Vet, L. E. M. Comparative ecology of hymenopterous parasitoids. Ph. D. thesis, State Univ. of Leiden, Chapter 9.
- and Bakker, K. 1985. A comparative functional approach to the host detection behaviour of parasitic wasps. 2. A quantitative study on eight eucoilid species. – *Oikos* 44: 487–498.
- and Hoeven, R. van der. 1984. Comparison of the behavioural response of two *Leptopilina* species (Hymenoptera: Eucoilidae), living in different microhabitats, to kairomone of their host (Drosophilidae). – *Neth. J. Zool.* 34: 220–227.
- and Janse, C. J. 1984. Fitness of two sibling species of *Asobara* (Braconidae: Alysiinae), larval parasitoids of Drosophilidae in different microhabitats. – *Ecol. Ent.* 9: 345–354.
- , Janse, C., Achterberg, C. van and Alphen, J. J. M. van. 1984. Microhabitat location and niche segregation in two sibling species of drosophilid parasitoids: *Asobara tabida* (Nees) and *A. rufescens* (Foerster) (Braconidae: Alysiinae). – *Oecologia (Berl.)* 61: 182–188.
- , Lenteren, J. C. van, Heymans, M. and Meelis, E. 1983. An airflow olfactometer for measuring olfactory responses of hymenopterous parasitoids and other small insects. – *Physiol. Ent.* 8: 97–106.
- Wanntorp, H.-E. 1983. Historical constraints in adaptation theory: traits and non-traits. *Oikos* 41: 157–160.
- Wharton, R. A. 1984. Biology of the Alysiinae (Hymenoptera: Braconidae), parasitoids of cyclorrhaphous Diptera. – *Beitr. Ent.* (in press).