Differences in life history traits between isofemale lines of the aphid parasitoid *Aphelinus abdominalis* (Hymenoptera: Aphelinidae)

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Abstract

Six isofemale lines of the aphid parasitoid *Aphelinus abdominalis* (Dalman) were compared for life history traits related to parasitism of three cereal aphid species. The lines differed most in the number of hosts parasitized in 24 h and the developmental times of females and males. Cluster and discriminant analysis showed that these differences were pronounced between line I, line II and lines III-VI, but not between lines III, IV, V and VI. Cross-breeding experiments revealed reproductive barriers between the lines which proved to differ most in life history traits, indicating the possible existence of morphologically similar species. Given the variability in life history traits between lines of *A. abdominalis* recorded in this study, we suggest a careful selection of candidate strains for biological control will be rewarding.

Introduction

Aphelinus abdominalis (Dalman) is a solitary endoparasitoid of aphids during its larval stages, and the adult females are aphid predators. Since 1990, *A. abdominalis* has been released into greenhouses in southern France for the biological control of aphids. With *Macrosiphum euphorbiae* (Thomas) (Homoptera: Aphididae) as the target species, approximately 50 ha of greenhouse crops were treated during 1990 (J.M. Rabasse & J.P. Lafont, unpublished data). *A. abdominalis* successfully controlled *M. euphorbiae* when it was released before the outbreak of the pest. Similarly, control of *M. euphorbiae* was achieved during 1989 and 1990 in an experimental greenhouse in northern Germany after inoculative releases of *A. abdominalis* (H. Wahle & C. Höller, unpublished data). In view of these recent successes, this biological control agent deserves special attention.

Due to intraspecific variability of parasitoid performance, choosing the right strain is of crucial importance for the success of biological control (e.g. González *et al.*, 1979). Intraspecific variation of conspicuous life history traits in hymenopterous parasitoids has been documented for at least 44 species from 11 families (Ruberson *et al.*, 1989). Here we compare life history traits related to parasitism in six *A. abdominalis* isofemale lines (IL; i.e. descendants of one female caught in the wild) from different geographical origins (France and Germany), and from different aphid host species from different plants.

The reason for using IL instead of cultures derived from more than one female was to minimize variability within lines, and to elucidate differences between them. All IL were cross-bred in order to reveal possible reproductive barriers, which were indeed present. The differences between IL documented in this paper allow a glimpse of the variability of what now should be considered a complex of sibling species. We initially suggested that considerable variability, if present, would necessitate the search for strains or lines to fulfill specifically the demands of biological control. Because the differences between IL were important, a careful selection will be rewarding.

Materials and methods

Insect cultures

Cereal aphids were used as hosts for the parasitoids. The cultures of *Metopolophium dirhodum* (Walker), *Rhopalosiphum padi* (Linnaeus) and *Sitobion avenae* (Fabricius) (Homoptera: Aphididae) were derived from single parthenogenetic females collected near Kiel, Schleswig-Holstein (Germany). All aphid clones proved to be

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Table 1. Origins and reproduction modes of six *Aphelinus abominalis* isofemale lines (IL) used in the present study.

IL	Date of collection	Site of collection	Original aphid host	Original plant host	Reproduction mode
I	01.06.1987	Hannover C Germany	*Metopolophium dirhodum*	unknown, greenhouse	uniparental
II	07.12.1987	Antibes S France	*Macrosiphum euphorbiae*	unknown, greenhouse	biparental
III	20.06.1988	Meimersdorf N Germany	*Acyrthosiphon pisum*	*Trifolium* sp	biparental
IV	27.06.1988	Melsdorf N Germany	*Sitobion avenae*	*Triticum aestivum*	biparental
V	08.08.1988	Kiel N Germany	*Macrosiphum rosae*	*Rosa* sp	biparental
VI	31.08.1988	Levansau N Germany	*Metopolophium dirhodum*	*Zea mays*	biparental

holocyclic when exposed to low temperature/short daylight conditions (12°C, L:D 10:14). *S. avenae* was of the green colour form. Oat (cultivar 'Bojar') was used for the aphid rearings.

The parasitoid cultures were derived from single mated (if biparental) and unmated (if uniparental) females. In table 1, the origins and the reproduction modes of the parasitoid IL are listed. The females which were used to establish an IL and all further generations produced from these females in the laboratory were allowed to parasitize *S. avenae* exclusively. All IL were kept for at least five months or were cultured for at least seven generations on *S. avenae* before being used in the experiments. IL were maintained by transferring 2-8 females to clean rearing units containing 200-300 unparasitized *S. avenae*. Their offspring (again 2-8 females) were collected after 3-4 weeks and transferred to clean rearing units. A few specimens of all lines were sent to a specialist in taxonomy of *Aphelinus*, Dr M.W.R. de V. Graham (Oxford). He regarded all material as being *A. abdominalis*. Voucher specimens of all lines are deposited in the collection of the first author (H.H.). All aphid and parasitoid cultures were maintained in a climatic chamber at 20 ± 1.5°C and a L:D 16:8 regime.

Experimental set-up

All experiments, from the standardization of the initial plant, aphid and parasitoid material to the emergence of the parasitoid offspring, were carried out at 20°C in the climatic chamber also used for the cultures. Experimental units consisted of three potted oat seedlings (ca. 10 cm tall) which were enclosed in a plexiglas tube (diameter 10 cm, height 20 cm). The tube's upper end and a ventilation hole on its' side were sealed with gauze. Plaster was applied on the soil surface inside the plexiglas tubes in order to avoid possible losses of parasitized aphids.

Rate of parasitism and parasitoid development studies

Wasps were standardized as follows; parasitized and mummified aphids (referred to as mummies) were taken from the cultures and were confined individually in 1 cm^3 gelatine capsules. One female and one male parasitoid were transferred, within 24 h after emergence, to a petri dish to allow mating and feeding on 15% sucrose solution. The parasitoids were kept in the petri dish for five days before being used in experiments because at average temperatures, age-specific fecundity of *Aphelinus* is highest during days 5-15 after emergence (Monadjemi, 1972a; Wahab, 1985; H. Haardt, unpublished data). All parasitoids were naive (had no contact to hosts) before being used in the experiments.

Ten second instar *M. dirhodum*, *R. padi* and *S. avenae* were offered simultaneously to single standardized females for 24 h. The aphids were allowed to settle on the plants 1 h before the start of the experiment. After 15 days, all mummies were carefully detached from the substrate, identified to aphid species, and confined in gelatine capsules. Determination of aphid species was based on the shape and colour of siphunculi and antennae. Numbers of aphids parasitized, emergence rates, times required for parasitoid development and sex ratios were calculated. Each of the six IL was replicated 20 times.

Cross-breeding experiments

Males and females from different lines which emerged individually in gelatine capsules were confined in couples in petri dishes with 15% sucrose food for 1 h, to allow copulation. Their behaviour was watched during this time and any matings were noted. Subsequently, both partners were transferred to experimental units (as described above) containing approximately 100 *S. avenae* larvae and adults. Males of the uniparental IL I were produced by using old females (>30 days) as mothers (Haardt, unpublished data). Because these males failed to fertilize females from other lines, ten of them were dissected in Ringer's saline to check for the presence of viable sperm. A few males from other IL were also dissected to allow comparison. Combinations of partners from different IL which yielded at least one F_1 female were considered successful (i.e., not totally reproductively isolated) and were therefore not replicated further. Ten replicates were carried out when no F_1

females emerged. Crossing experiments were performed for evaluation of strain differences exclusively, not for an in-depth assessment of reproductive barriers (backcrosses were not carried out).

Data analysis

For the most part, data were not normally distributed; therefore we used distribution-free statistics. If the Kruskal-Wallis test suggested that differences between IL existed, means of parasitism rates and developmental times were compared pairwise using the Mann-Whitney test. Differences between IL were tested separately with regard to aphid host species. The relative performance of IL on different aphid hosts was not tested as the study of host switching behaviour was beyond the scope of the experimental design (performance on a new host in *Aphelinus* can be very low in the first generation after transfer and increase considerably in later generations; see Michel, 1970).

Rates of parasitism and parasitoid developmental times were transformed into binary codes for cluster analysis using the single linkage Euclidian distance (Schuchard-Ficher *et al.*, 1980). The three IL for which the most data were available were subsequently separated by means of discriminant analysis, using sets of four life history variables (Hawkins, 1982).

Results

Rate of parasitism

IL I-III produced more offspring on all three host species than IL IV-VI (table 2). This difference was significant on *M. dirhodum* (Kruskal-Wallis test: H = 46.95, $P_{K\text{-}W} < 0.001$) and on *S. avenae* (H = 56.46, $P_{K\text{-}W} < 0.001$). In addition, IL II parasitized significantly (two-tailed Mann-Whitney test: $P_{M\text{-}W} < 0.05$) more *S. avenae* than IL I and III. *R. padi* was clearly less often parasitized than *M. dirhodum* and *S. avenae*, with IL I performing significantly better (H = 83.43, $P_{K\text{-}W} < 0.001$; $P_{M\text{-}W} < 0.05$) on *R. padi* than IL II-VI.

Table 2. Host parasitism. Means and ranges of the numbers of hosts parasitized in 20 replicates are given. Ten hosts of each species were offered simultaneously per replicate. Different letters within rows indicate statistical differences between IL on a given host species (two-tailed Mann-Whitney test, P <0.05).

	Aphelinus abdominalis IL					
Aphid host	I	II	III	IV	V	VI
Metopolophium dirhodum	2 3 0-5 *a*	2 9 0-8 *a*	1 9 0-5 *a*	0 4 0-3 *b*	0 4 0-3 *b*	0.5 0-2 *b*
Rhopalosiphum padi	1.1 0-3 *a*	0 4 0-2 *b*	0.2 0-2 *b*	0.0	0.1 0-1 *b*	0.0
Sitobion avenae	3.3 1-7 *b*	4 6 0-9 *a*	2.7 0-6 *b*	0.5 0-3 *c*	0 9 0-4 *c*	0.9 0-7 *c*

Parasitoid development

Females required more time for development at 20°C from egg to adult (21.2-27.0 days) than males (19.6-25.3 days) in IL II-V (table 3). Differences in developmental times between IL of both sexes were recorded from parasitoids developing in *M. dirhodum* and *S. avenae* (H = 31.78-93.78, $P_{K\text{-}W} < 0.001$). IL I, II and V needed generally less time to develop than IL III, IV and VI (see table 3 for statistical differences).

Emergence rates ranged from 84.6 to 100% and were not statistically different between IL irrespective of the host species consumed (chi-squared contingency table, $P_{\chi^2} > 0.1$; data not shown). Sex ratios were also not

Table 3. Duration of development. Means of the numbers of days required for development from egg to adult at 20°C and N-values of the numbers of females or males emerged from mummies produced in 20 replicates are given. Aphid host:IL:sex combinations with $N < 5$ females or males are not considered. Different letters within rows indicate statistical differences between IL on a given host species (two-tailed Mann-Whitney test, $P < 0.05$).

	Aphelinus abdominalis IL					
Aphid host	I	II	III	IV	V	VI
	Females					
Metopolophium dirhodum	22.8 45 *b*	21.4 7 *c*	27.0 10 *a*	23.7 6 *b*		
Rhopalosiphum padi	22.8 20					
Sitobion avenae	23.1 62 *b*	21.2 34 *c*	26.4 23 *a*	26.6 5 *a*	23.4 13 *b*	25.9 12 *ab*
	Males					
Metopolophium dirhodum		20.5 48 *b*	24.8 23 a			25.3 6 *a*
Rhopalosiphum padi		20.4 5				
Sitobion avenae		20.4 41 *c*	25.2 28 *a*	22.8 5 *b*	19.6 5 *c*	

Table 4. Sex ratio. Percentages parasitoid females and N-values of the numbers of parasitoids emerged from mummies produced in 20 replicates are given. Aphid host:IL combinations with $N < 10$ parasitoids emerged and replicates yielding males exclusively (mother possibly not fertilized) are not considered.

	Aphelinus abdominalis IL					
	I	II	III	IV	V	VI
Metopolophium dirhodum	100 45	33.3 21	37.0 27			40.0 10
Rhopalosiphum padi	100 20					
Sitobion avenae	100 62	72.3 47	52.3 44	60.0 10	81.3 16	75.0 16

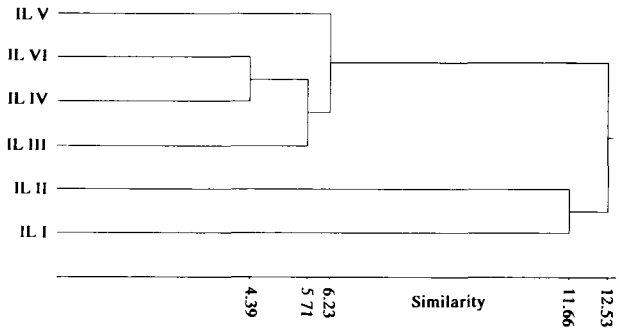

Fig. 1. Dendrogramm depicting the degrees of similarity between *Aphelinus abdominalis* IL I-VI. Similarity values were calculated using the single linkage Euclidian distance for cluster analysis.

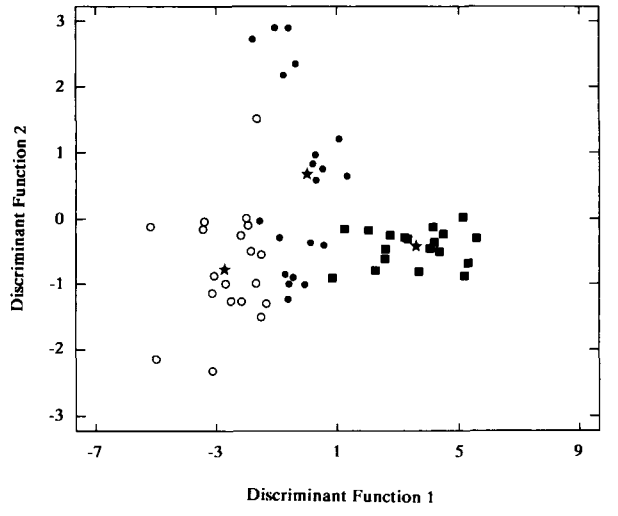

Fig. 2. Scatterplot of *Aphelinus abdominalis* IL I (closed circles), IL II (open circles) and IL III (squares) projected onto discriminant function 1 versus discriminant function 2. Centroids are marked by asterisks.

significantly different between the biparental IL (P_{χ^2} = 0.141; table 4).

Cluster analysis was performed using the following data (aphid hosts in parentheses): rates of parasitism (*M. dirhodum*, *R. padi* and *S. avenae*), developmental time (*S. avenae*), hatching rate (*S. avenae*) and sex ratio (*S. avenae*). The variables were selected according to the number of data available. The dendrogram in fig. 1 shows the degrees of similarity between lines. IL I and II were separated by a distance of 5.43 from IL III-VI. In contrast, the distance between IL V vs. IL VI and VI was only 1.84.

Only IL I, II and III were compared by means of discriminant analysis since not enough data were available for IL IV-VI (see tables 2-4). The following data were used (aphid hosts in parentheses); rates of parasitism (*M. dirhodum*, *R. padi* and *S. avenae*), and developmental times of females (*S. avenae*). Discriminant analysis showed that IL I and II were not very different from each other, but were separated clearly from IL III (fig. 2). Discriminant function 1 was more powerful than discriminant function 2 (relative percentage of eigenvalues 95.6 and 4.4, respectively), but both functions indicated significant differences between IL (Wilks' Lambda 0.096 and 0.759, χ^2 = 130.2 and 15.3, df = 8 and 3, $P_{\chi^2} < 0.001$ and P_{χ^2} =0.002, respectively). Weighted standardized discriminant function coefficients were (absolute values sorted in descending order): developmental time in *S. avenae* 0.960, parasitism rate of *S. avenae* 0.354, of *R. padi* 0.300, and of *M. dirhodum* 0.169. Hence, developmental time of females in *S. avenae* contributed most to discriminant function, whereas the rates of parasitism had comparatively little discriminative power.

Cross-breeding experiments

IL I and II males proved to be unsuccessful in fertilizing females from non-kin IL (table 5), even though all dissected males contained apparently viable sperm and matings readily occurred when IL I and II males were confined with non-kin IL females. In IL I, the males also mounted kin females. The barriers to crossing were symetric in IL II, since females were apparently not fertilized by non-kin males. In contrast, partners of IL III-VI freely hybridized in both directions.

Discussion

We compared life history traits of six *A. abdominalis* inbred lines from different geographical origins, different aphid host species, different plants, and from either greenhouses or the field. Lines III-VI proved to be similar to each other. However, considerable differences were recorded between lines III-VI, line II and line I. Comparable differences in life history traits between strains are known from braconid aphid parasitoids (Flint, 1980; Kambhampati & Mackauer, 1989) and from aphelinids of the genus *Aphytis* (Rössler & DeBach, 1972; Khasimuddin & DeBach, 1976), but, to our knowledge, have not been reported from the genus *Aphelinus*. However, the occurrence of brachypterous and macropterous forms (Monadjemi, 1972b) and the sympatric coexistence of uniparental and biparental strains in *A. abdominalis* (Botto, 1980; Wahab, 1985) and *Aphelinus asychis* Walker (Wilbert, 1964; Mackauer, 1968) suggest that such differences may exist in *Aphelinus* spp.

The differences between lines reported herein were

Table 5. Cross-breeding YES, combinations resulting in the production of at least one F_1 female; NO, combinations yielding no female offspring in 10 replicates; ?, fertilization uncertain.

	♂ IL					
♀ IL	I	II	III	IV	V	VI
I		?	?	?	?	?
II	NO		NO	NO	NO	NO
III	NO	NO		YES	YES	YES
IV	NO	NO	YES		YES	YES
V	NO	NO	YES	YES		YES
VI	NO	NO	YES	YES	YES	

confirmed by means of crossing experiments. Even though we did not back-cross the F_1 offspring in order to elucidate more subtle reproductive barriers, our data clearly show that IL I, II and III-VI represent three reproductively isolated groups (at least under laboratory conditions). Possibly, allopatric speciation processes lead to the formation of morphologically similar species. Breeuwer & Werren (1990) and Stouthamer *et al.* (1990) documented recently the role of microorganisms in cytoplasmic incompatibility, and hence reproductive isolation, in parasitic wasps. The bacteria were found near the posterior pole of the egg (Breeuwer & Werren, 1990), a phenomenon also observed in *A. abdominalis* (D. Gritzka-Stoeβel & C. Höller, unpublished data). Since matings readily occurred between all IL, the microorganisms found in the eggs possibly mediated reproductive isolation in *A. abdominalis*. In addition, the microorganisms could be responsible for the occurrence of uniparental forms, as has been reported from *Trichogramma* spp. Stouthamer *et al.* (1990) found that if females of uniparental *Trichogramma* species or strains were fed antibiotics or kept at temperatures above 30°C, they began to produce males and females similar to biparental lines. Likewise, an uniparental *A. asychis* strain produced males at high temperatures (Schlinger & Hall, 1959), perhaps because microorganisms were inactivated by heat.

Old females of the uniparental IL I also produced males which contained viable sperm. These males were, however, unable to fertilize non-kin females. Furthermore, IL I females were mounted by non-kin males and possibly used their sperm. The utilization of sperm by uniparental females for offspring production has been demonstrated in *Aphytis mytilaspidis* (LeBaron) (Rössler & DeBach, 1972) and *Trichogramma* spp. (Stouthamer *et al.*, 1990). However, because genetic markers are not at hand for *Aphelinus abdominalis*, we have no conclusive evidence for sperm utilization by IL I females. Regarding the inability of IL I males to reproduce with non-kin females, we may suspect also an inability of IL I females to cross-breed with IL II-VI males.

Two different kinds of reproductive strategies can be distinguished in the genus *Aphelinus*: specialists such as *A. mali* (Haldeman) and *A. thomsoni* Graham have very narrow host ranges, low fecundities and are usually well synchronized with their hosts (Evenhuis, 1961; Hamilton, 1973; Graham, 1976). On the other hand, the bulk of the 11 known European *Aphelinus* spp. are generalists, which parasitize a variety of host species, have high fecundities and are poorly synchronized with their hosts (e.g. Hartley, 1922; Ferrière, 1965; Mackauer, 1982). *A. abdominalis* belongs to the latter group, but the possible allopatric existence of sibling species gives reason to reexamine host records and other life history data published so far (Flanders, 1953; Ferrière, 1965; Michel, 1969; Botto, 1980; Wahab, 1985).

Cluster analysis of life history data clearly reflected the results of the crossing-experiments. Even though cluster analysis has its drawbacks (Everitt, 1977), it is a useful method for a preliminary classification of groups. Preliminary classification is a necessary step to precede discriminant analysis (Schuchard-Ficher *et al.*, 1980). Given the limited amount of data available for IL IV-VI, we subjected only IL I, II and III to discriminant analysis, assuming that IL III would represent its counterparts from northern Germany. We used this method to quantify differences between IL and to evaluate the discriminative power of variables (Hawkins, 1982). The results indicate that IL III is separated to a greater extent from IL I and II than the latter are from each other.

Developmental time of females of *S. avenae* proved to be the most powerful life history trait variable used for separation of IL by means of discriminant analysis. Hence, this variable seems to be most suited for a quick screening of *A. abdominalis* lines. Even though varying between lines, the comparatively long times required for development by all *A. abdominalis* IL (compare results of this study with developmental times of other aphelinid aphid parasitoids: Finney *et al.*, 1960; Zhodi, 1976; Höller, 1989) will be crucial in determining the performance of the species as a biological control agent. However, the 24 h/single temperature approach used in this study permits just a glimpse of the performance criteria which should be evaluated before selecting a line or strain for biological control (for instance, see Kambhampati & Mackauer, 1989). Our data do, however, show that considerable variability in life history traits exists in *A. abdominalis*, which will reward the careful selection of a candidate strain.

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