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The responses of *Ibalia* species (Hymenoptera : Ibaliidae) to the fungal symbionts of siricid woodwasp hosts

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SYNOPSIS

The oviposition response of *Ibalia drewseni* and *Ibalia leucospoides* is described and compared. Oviposition behaviour is elicited by odours produced by the symbiotic fungus of several species of siricid woodwasps. The responses of the two *Ibalia* species to fungus cultures of different ages and host sources is discussed in relation to their emergence periods and the ecology of their hosts.

Ibalia species locate their hosts by responding to odours emanating from siricid oviposition holes. The host indicator is of fungal origin, derived from the symbiont, *Amylostereum*, which is introduced into the host tree by the siricid during oviposition activity (Madden, 1968). Host material consists of early-stage larvae and embryos but not newly-laid eggs. The parasitoid introduces its ovipositor down the siricid oviposition hole and injects a single egg into the host. Although both *Ibalia drewseni* Borries and *I.leucospoides* (Hochenwarth) utilise host material of similar developmental stages, *I.drewseni* adults emerge in the spring and *I.leucospoides* emerges in late summer, the latter during the flight period of the host (Spradbery, 1970*a*). Because of the different emergence periods of these two *Ibalia* species, there are probably differences in their responses to the host indicator.

In an earlier publication (Spradbery, 1970*a*) the antennal palpating and ovipositor probing response of *I.drewseni* females was described. Typical oviposition behaviour was elicited by cultures of symbiotic fungus from siricid woodwasp hosts but the data were inadequate for analysing the response in relation to the age of the culture. The present communication describes a modified bioassay method, and the results of a comparative study of the responses of *I.drewseni* and *I.leucospoides* to fungal cultures of different ages and siricid host sources.

MATERIALS AND METHOD

Stocks of *Ibalia* adults were reared under outdoor conditions from field-collected timber infested with siricid woodwasps. Adults were maintained on a diet of honey and water.

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The females used in bioassay studies were mated and more than one week old. All observations were made at room temperatures (21 ± 4° C) and humidities (65 ± 5 per cent R.H.) under ordinary laboratory lighting.

Cultures of symbiotic fungus were made weekly by transferring spores from the mycangia of siricid females on to potato dextrose agar plates or subculturing from existing cultures. Cultures were derived from *Sirex noctilio* (F.), *S.juvencus* (L.) and *Urocerus gigas* (L.) host sources and were maintained at 24° C.

The bioassay apparatus consisted of a piece of Perspex (20 cm. × 12 cm. × 1 cm. thick) which had eighteen 1 cm. diameter cavities drilled in it to a depth of 5 mm. Samples of fungus were taken from the centre of culture plates with a 5 mm. diameter cork borer and transferred to the cavities, using 4 discs per cavity. The cavities were covered by a sheet of Perspex (20 cm. × 12 cm. × 2 mm. thick) with 1 mm. holes drilled through it over each cavity. The sheets were covered with paper fixed with cellulose acetate tape and a pin prick made through the paper into each hole to simulate a siricid oviposition hole (fig. 1). A shallow observation box was made by separating the bioassay block from another sheet of Perspex using 2 cm. × 2 cm. pieces of wood.

Eight age classes of fungus were tested, using two cavities per sample. The samples were arranged randomly among the cavities. In each replicate, 10 females were introduced into the bioassay apparatus and kept under observations for two hours. Each antennal palpation or ovipositor probe down the holes in the paper (fig. 1) was recorded.

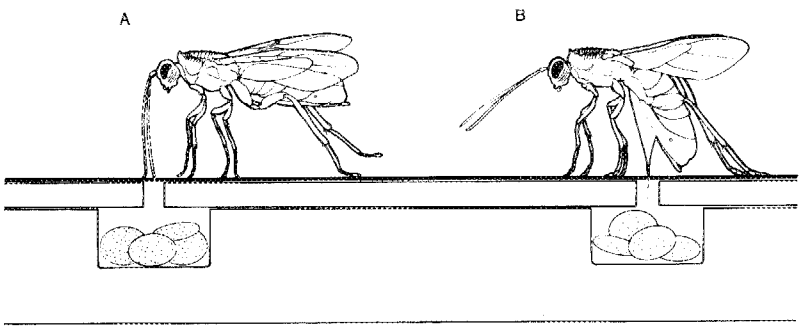

Fig. 1. The antennal palpating (A) and ovipositor probing (B) response of *Ibalia* in response to discs of siricid fungus—impregnated agar in the bioassay situation.

Some females were used for two or more replicates but they were replaced with more recently emerged adults during the course of the flight period. Small differences in the age classes of fungal cultures offered to the two *Ibalia* species were necessitated by their different emergence periods which also prevented simultaneous comparison of their responses.

To compare the response of *Ibalia* species to different symbionts, three age classes of *S.noctilio*, *S.juvencus* and *U.gigas* symbiont cultures were used. *I.drewseni* was offered 5-, 11- and 13-week-old cultures and *I.leucospoides* was offered 2-, 3- and 4-week-old cultures, using two samples of each per replicate.

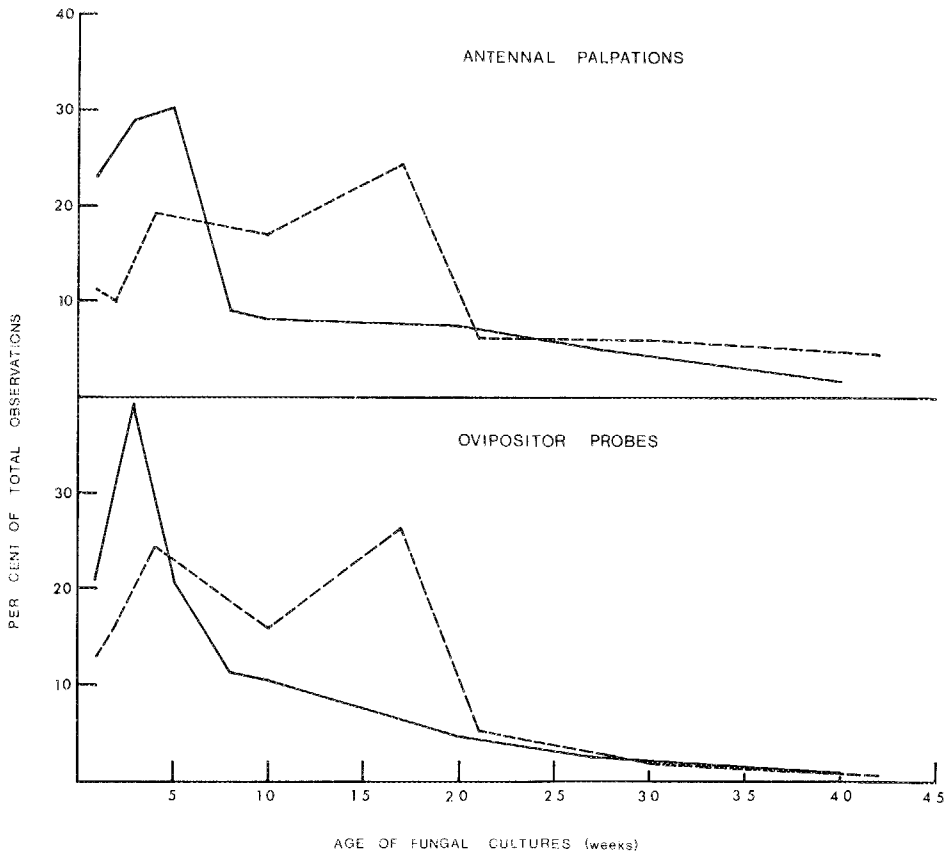

Fig. 2. Responses of *Ibalia leucospoides* (———) and *Ibalia drewseni* (— — —) females to siricid fungus cultures of different ages.

RESULTS

The results of the bioassay of different-aged fungal cultures are given in figure 2. There were 1338 antennal palpations and 153 ovipositor probings recorded for *I.drewseni* in 16 replicates and 2286 palpations and 95 probings for *I.leucospoides* in 26 replicates.

The results of the bioassay of *S.noctilio*, *S.juvencus* and *U.gigas* symbionts are given in Table 1. The data were transformed by $\ln(x + 1)$, where x = number of palpations or probings respectively, and a one-way classification analysis of variance carried out on each response for each species. In *I.drewseni* both palpations and probings to *U.gigas* symbiont were significantly less ($p < 0{\cdot}01$) than to *S.noctilio* and *S.juvencus* symbionts which were indistinguishable. In *I.leucospoides*, there were no significant differences in responses to the three symbiotic fungi.

The associated siricid fauna and geographical origins of *I.drewseni* are given in Table 2. *I.leucospoides* was obtained from 114 localities, the dominant siricid host species being *S.noctilio* (in 36 localities), *S.juvencus* (25), *Sirex cyaneus* (F.) (17) and *Urocerus* species (26). Of the *Urocerus* localities, *Sirex* species were absent in 17 of them.

Table 1. The response of *Ibalia* females to fungal symbionts from different siricid species.

Source of symbiotic fungus	Antennal palpations		Ovipositor probes	
	Number	Per cent of total	Number	Per cent of total
Ibalia drewseni (11 replicates)				
Sirex noctilio	422	42·1	59	43·7
Sirex juvencus	411	41·0	61	45·2
Urocerus gigas	169	16·9	15	11·1
Total	1002	100·0	135	100·0
Ibalia leucospoides (15 replicates)				
Sirex noctilio	412	43·9	73	51·4
Sirex juvencus	262	27·9	31	21·8
Urocerus gigas	265	28·2	38	26·8
Total	939	100·0	142	100·0

Table 2. Associated siricid species and geographical origins of *Ibalia drewseni*.

Origin		Number of *I.drewseni*	Siricid species: Number emerged					
			S.noctilio	*S.cyaneus*	*S.juvencus*	*U.gigas*	*U.augur*	*X.spectrum*
England:	Thetford	24	33	0	0	40	0	0
Scotland:	Finglack	1	0	1	0	230	0	0
Belgium:	Rochefort	22	24	0	2	0	0	1
	Ave et Auffe	2	866	0	0	0	0	0
	Eupen	1	0	0	206	5	0	188
Germany:	Fallingbostel	7	27	0	0	0	0	0
Norway:	Nordmarker	2	0	0	181	25	0	0
Sweden:	Skokloster	6	0	0	71	18	0	6
France:	Le Boreon	32	0	4	1159	0	14	16
	Tend	3	0	0	140	67	0	376
	Turini	17	0	9	0	144	0	208
Switzerland:	Ablandschen (1)	22	0	0	279	0	0	55
	Ablandschen (2)	63	0	19	464	25	0	7
	Le Devin	1	0	0	9	0	0	0
	Lucelle	15	0	366	25	14	40	47
	Chatillon	3	0	134	30	5	0	64
	Jaun pass	48	0	60	13	0	0	43
Spain:	Castro Urdiales	1	9	0	0	0	0	0
Italy:	Carnia	4	0	0	85	0	0	9
Czechoslovakia:	Banska Stiavnica	66	0	277	100	0	0	5
Turkey:	Meryamana	5	0	0	45	0	0	0
	Grhaneli	9	3	0	0	0	0	0
	Namrun	4	0	0	0	35	53	49
Total		358	962	870	2809	608	107	1074

ferent siricid species.

positor probes	
nber	Per cent of total
	43·7
	45·2
	11·1
	100·0
	51·4
	21·8
	26·8
	100·0

Ibalia drewseni.

U.gigas	*U.augur*	*X.spectrum*
40	0	0
230	0	0
0	0	1
0	0	0
5	0	188
0	0	0
25	0	0
18	0	6
0	14	16
67	0	376
144	0	208
0	0	55
25	0	7
0	0	0
14	40	47
5	0	64
0	0	43
0	0	0
0	0	9
0	0	5
0	0	0
0	0	0
35	53	49
608	107	1074

DISCUSSION

European species of siricid woodwasps emerge throughout the summer and autumn. *Xeris spectrum* (L.) emerges first (early June to mid-August) followed by the *Urocerus* species (July), *Sirex cyaneus* (F.) and *S. juvencus* (July and August), and *S.noctilio* which begins to emerge in August and continues until late autumn. *X.spectrum*, which is the only species without a symbiotic fungus, oviposits in timber inoculated by *Urocerus* or *Sirex* species during the previous year (unpublished observations). Depending on temperature and the moisture content of the timber, siricid eggs can hatch within 10 days although overwintering in the egg or embryonic stage also occurs.

The emergence of *I.leucospoides* takes place during August–October in temperate Europe (although adult *Ibalia* have been taken as late as December in southern Spain, unpublished observation) which coincides with the availability of host material. *I. drewseni* emerges during late May and June, several weeks before host material of the current season becomes available and parasitises hosts derived from overwintered eggs (Spradbery 1970*a*).

Madden (1968) established that *I.leucospoides* prefer oviposition holes or symbiotic fungal cultures 2–3 weeks old, which coincided with a reduction in moisture content and the incubation period of host eggs. My data for *I.leucospoides* confirm Madden's results, the preference being for young cultures 1–7 weeks old with a maximal ovipositor probing response elicited by 3-week old cultures (fig. 2). By contrast, the *I.drewseni* response was more protracted with maximal attraction to 17-week-old cultures. The ichneumonid parasitoid of siricids, *Rhyssa persuasoria* (L.), which emerges at the same time as *I.drewseni*, also responds to fungal cultures of a similar age with a maximal response to 12–16-week-old samples (Spradbery 1970*b*). The *I.drewseni* response to cultured fungus corresponds approximately with field conditions for symbiont inoculations by the host species are made 7–10 months earlier compared to one month or less for *I.leucospoides* host material.

The specific fungal metabolite(s) responsible for parasitoid attraction is not known although acetaldehyde and paraldehyde present in young fungal cultures elicit the antennal response in *I.leucospoides* (Madden, 1968). Differences in the behaviour of the two *Ibalia* species may result from changes, during fungal maturation, in the relative concentrations of a specific attractant or proportion of metabolites if more than one component is involved.

The symbiotic fungi associated with conifer-inhabitating siricids are *Amylostereum areolatum* (Fr.) Boid. from *S.noctilio* and *S. juvencus* and *A.chailletii* (Pers.) Fr. from *Urocerus* species (P. Gautt, personal communication). *S.cyaneus* is generally associated with *A.areolatum* (R. A. Bedding, personal communication). These taxonomic affinities were confirmed during bioassay, for *I.drewseni* females did not distinguish between symbiont cultures derived from *S.noctilio* and *S. juvencus* although their response to *U.gigas* symbiont was significantly lower. Because of the early emergence of *U.gigas* adults and their preference for dead trees or cut timber with a low moisture content (unpublished observations) it is unlikely that their eggs would overwinter and thus be exposed to parasitism by *I.drewseni*. This ecological feature is supported by the emergence data (Table 2) for, of the 23 localities where *I.drewseni* was found, *U.gigas* was the dominant siricid species in only three and *Sirex* species were absent in only one of them.

Under experimental conditions, *I.leucospoides* did not distinguish between cultures of *S.noctilio*, *S.juvencus* and *U.gigas* symbionts and the emergence data demonstrate that both *Sirex* and *Urocerus* species are parasitised. *I.leucospoides* emerges at a time when *Urocerus* and *Sirex* host material is available and it is probable that it responds equally to both species of symbiotic fungus under natural conditions.

In spite of similarities in the life history and mode of parasitism of the two *Ibalia* species, they may be distinguished by differences in their responses to symbiotic fungal cultures of different ages and the two species of *Amylostereum* symbiont. These differences are correlated with emergence patterns and the availability of host material at different times of the year.

SUMMARY

Ibalia drewseni Borries females, which emerge during the spring and parasitise overwintered embryos and larvae of siricid woodwasps, exhibited positive oviposition responses to a wide age-range of the cultured symbiotic fungus of its host. Maximal response was stimulated by 17-week-old cultures. *Ibalia leucospoides* (Hochenwarth) emerges during mid to late summer, parasitises hosts produced during the current year and responds to a narrow age-range of cultured symbiont with a maximal response to three-week-old cultures. Host detection is dependent on attraction to symbiotic fungus and the results indicate a temporal response difference which is correlated with the emergence of the parasitoids and their hosts.

Emergence data, host records and ecological observations suggest that *Urocerus* species are rarely parasitised by *I.drewseni* which responds at a significantly lower level to the *Urocerus gigas* (L.) symbiont, *Amylostereum chailletii* (Pers.) Fr., compared to the *Sirex* species symbiont, *A.areolatum* (Fr.) Boid. *I.leucospoides* parasitises both *Urocerus* and *Sirex* species and responded equally to cultured symbiotic fungus derived from *Urocerus* and *Sirex* sources.

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