

## Hymenopteran Parasitoids of *Drosophila* Breeding in Decaying Herbage

(Diptera: Drosophilidae)

Monika OFFENBERGER and Albert J. KLARENBERG

### Abstract

*Drosophila* larvae and pupae are used as hosts by many species of parasitoid wasps. During two *Drosophila* breeding seasons eight larval and three pupal hymenopteran parasitoid species of *Drosophila* breeding in decaying herbage and fungi were collected from plant and fungal baits in a temperate woodland in southern Germany. Mean rates of parasitisation in *Drosophila* were 0-13.1%. Studies on host-parasite dynamics in *Drosophila* requires knowledge of exact host-parasite relationships. For this purpose, we developed a new baiting technique by exposing plant and fungal baits with larvae and pupae, raised in the laboratory, of a single *Drosophila* species to hymenopteran parasitoids in nature. Six parasitoid species could be assigned unequivocally to their host(s). Laboratory experiments showed that *Trichopria aequata* Jansson (Diapriidae) could develop in several *Drosophila* species but was most rapid in *D. limbata*. In the field, however, this parasitoid was reared only from *D. limbata* pupae in plant baits. As *T. aequata* was not reared from fungal baits containing *D. limbata* pupae, it is very likely that volatile compounds released by decaying plant material attract this pupal parasitoid.

### Introduction

*Drosophila* larvae and pupae are used as hosts by many species of parasitoid wasps, 22 of which are found in Europe (CARTON et al. 1986, JANSSON et al. 1988). A prerequisite in assigning these hymenopteran parasitoid species to their hosts is a detailed knowledge of the *Drosophila* natural breeding substrates. Although numerous studies have been performed on drosophilids breeding in fruit, fungi or decaying plant material (JAMES et al. 1988; COURTNEY et al. 1990, OFFENBERGER & KLARENBERG 1992a,b), knowledge of *Drosophila*'s parasitic wasps in nature is still limited. Consequently, the host-parasitoid relationships of many *Drosophila* species are obscure and this is one of the main constraints on determining the significance of different mean parasitisation rates in drosophilid communities; these rates range between 0 and 100% (CARTON et al. 1991, JANSSON et al. 1988, DRIESSEN et al. 1990, GRIMALDI & JAENIKE 1983, SEVENSTER 1992). Therefore, it is essential to determine the complete host-spectrum of each species of wasp and establish their preferences within this spectrum. Only with such information will it be possible to investigate the effect of parasitoids on *Drosophila* ecology. Recent studies on the ecology of wild European *Drosophila* species and their parasitoids (JANSSON et al. 1988, DRIESSEN et al. 1990, van ALPHEN et al. 1991) have again demonstrated the importance and value of investigating natural breeding substrates. Both decaying plants and macrofungi proved to be a rich source for various *Drosophila* species (SHORROCKS 1982, BURLA et al. 1991, DAVIS & JENKINSON 1992, OFFENBERGER & KLARENBERG 1992a,b). Within the *quinaria* group *D. phalerata* MEIGEN appears to be predominantly a fungus breeder while *D. limbata* von ROSER seems to be a specialist decaying-herbage breeder (HOFSTETTER 1992, OFFENBERGER 1994).

In the present study, the exact relationship of parasitic wasps to their drosophilid hosts was assessed by testing laboratory-raised larvae and pupae of either *D. limbata* or *D. phalerata* exposed with their substrate to natural populations of parasitoids. We are presenting a checklist of 23 wasp species netted over or reared from baits, of which 11 parasitise *Drosophila*.

## Material and Methods

**Field Observations:** Hymenopteran parasitoids and drosophilids were collected in 1990 and 1991 in Isarauen, a flood plain forest north of Munich in southern Germany (48°N, 11°E; 515 m above sea level; see OFFENBERGER 1994). Collecting was done by netting over baits of fungi or of decaying herbage (OFFENBERGER & KLARENBERGER 1992a,b). Fungus and decaying-herbage baits were exposed for several days in the field and were then brought to the laboratory. They were kept there for two months to sample all eclosing drosophilids and hymenopteran parasitoids. The insects were killed and preserved in 70 % ethanol, dried and pinned. The Hymenoptera were identified to family using van ACHTERBERG (1990) and SCHMIEDEKNECHT (1930), while the genus *Leptopilina* (Eucoilidae) and its constituent species were identified using NORDLANDER (1980). Other Hymenoptera were sent to experienced taxonomists for identification (see acknowledgements). The drosophilids were identified after BÄCHLI & BURLA (1985) immediately after collection.

**Experimental analysis:** Plant baits of *Angelica sylvestris* L. or *Heracleum mantegazzianum* SOMM. et LEV., and baits of commercial mushrooms, *Agaricus bisporus* (LANGE) PILÁT, were offered to 20 gravid females, either *D. limbata* or *D. phalerata*. These strains, which originated from Isarauen, had been maintained in the laboratory for 5 to 14 months. The female flies were removed from the baits after sufficient larvae and pupae had developed. The baits – infected with larvae and pupae from a single *Drosophila* species – were then exposed to hymenopteran parasitoids on the forest floor in Isarauen for one day. The baits were subsequently maintained in the laboratory and eclosing hymenopteran parasitoids and drosophilids were collected. The sex ratio and the parasitoid developmental time, were recorded. Laboratory cultures of 13 *Drosophila* species were tested for host acceptance of *Leptopilina heterotoma* (THOMSON) (reared from wild *D. phalerata*) and *Trichopria aequata* (THOMSON) (from *D. limbata*). *Drosophila* larvae and pupae were exposed in malt-food vials (LAKOVAARA 1969) and the parasitoids were left in the vials until they died. Each vial contained at least 50 larvae and/or pupae. “Maximal developmental time” and body size were investigated in *T. aequata*, as no biological information was available on this pupal hymenopteran *Drosophila* parasitoid (GRAHAM 1969). “Maximal developmental time” of the parasitoid was defined as the time between the first contact with the host and the parasitoid’s eclosion. The number of eclosing parasitoids was counted. Body size (length from the head to the tip of the abdomen) of both flies and wasps was measured with a graticule in binocular microscope to an accuracy of  $\pm 0.01$  mm.

**Statistics:** It was not determined which wasp had emerged from which host fly and therefore Kendall’s-Tau B correlation coefficient was calculated from randomly chosen pair combinations of the body size of *Drosophila* adults and eclosed *T. aequata*. This procedure was repeated four times on different pair combinations for each *Drosophila* species. The statistical program SPSS (4.0) was used for the Kendall’s-Tau B correlation.

## Results

**Hymenopteran Parasitoids from Decaying Plants:** A total of 23 wasp species in the families Braconidae, Eulophidae, Eucoilidae, Diapriidae, Pteromalidae and Serphidae was caught or reared from seven different bait types. Table 1 lists 189 wasps of those European parasitoid species known to use *Drosophila* larvae or pupae as a host. In addition the table includes species of *Drosophila* species likely to be the hosts of particular wasp species because both host and parasitoid emerged from the same type of bait. On average, three wasp species eclosed from plant baits. Most parasitoid species were members of the genera *Leptopilina* (Eucoilidae), *Aphaerata* and *Asobara* (both Braconidae). Mashed banana attracted *Asobara tabida* (Nees) in particular. Pupal parasitoids were only collected in low numbers. The *Drosophila* parasitism rate in baits

**Table 1.** A compilation of parasitoid hymenoptera in Germany collected by netting (n) or reared (r) from different baits in 1990 and 1991. Potential host drosophilid species of the larval and pupal parasitoids in Europe, if known (data from CARTON et al., 1986; JANSSEN et al., 1988; DRIESSEN et al., 1990; van ALPHEN et al., 1991; HARDY et al., 1992; OFFENBERGER, 1994; J. J. M. van ALPHEN and M. FISCHER, pers. comm.), are given. Bold faced *Drosophila* species are known hosts. *Drosophila* species which were found in all samples of a given kind of bait in this study are underlined. In addition, the distribution of the parasitoids in Europe is shown. The number of samples are given in parentheses.

Hymenopteran Species (Family)	N	Bait	Potential Drosophilid Host Species	Distribution (Country)
<b>LARVAL PARASITOIDS</b>				
<i>Leptopilina heterotoma</i> (THS.) (Eucoilidae)	12 <sup>nr</sup>	AS (5)	BUS, <u>FEN</u> , FUN, <u>IMM</u> , <u>KUN</u> , MEL, CH, D, E, F, <u>LIM</u> , OBS, <u>PAL</u> , PHA, SUB, <u>TES</u>	GB, I, NL, S
<i>Leptopilina australis</i> (BELIZIN) (Eucoilidae)	12 <sup>r</sup>	AS (2)	<u>FEN</u> , <u>IMM</u> , <u>KUN</u> , <u>LIM</u> , <u>PAL</u> , PHA, D, NL SUB, <u>TES</u> , TRA	
<i>Leptopilina fimbriata</i> (KIEFFER) (Eucoilidae)	2 <sup>r</sup>	AP* (2)	<u>FEN</u> , <u>LIM</u> , PAL, SUB	D, NL, S
<i>Tanycarpa bicolor</i> (NEES) (Braconidae)	5 <sup>nr</sup> 1 <sup>n</sup>	AS (5) AP (1)	BUS, FEN, IMM, KUN, <u>LIM</u> , <u>PAL</u> , <b>PHA</b> , SUB, TES	D, GB
<i>Tanycarpa graciliformis</i> (NEES) (Braconidae)	1 <sup>n</sup>	AP (2)	?	D
<i>Aphaerata scaptomyzae</i> FISCHER (Braconidae)	24 <sup>r</sup> 1 <sup>r</sup> 1 <sup>r</sup>	AS* (3) HS (1) AP* (1)	FEN, IMM, KUN, <u>LIM</u> , PAL, PHA, D, NL <b>SUB</b> , TES	
<i>Asobara tabida</i> (NEES) (Braconidae)	24 <sup>n</sup> 2 <sup>n</sup>	BA (7) AB (2)	BUS, FUN, KUN, MEL, OBS, SIM SUB	CH, D, F, GB, NL
<i>Asobara rufescens</i> (FÖRSTER) (Braconidae)	4 <sup>n</sup> 1 <sup>n</sup> 8 <sup>r</sup>	BA (2) AU (1) AS* (4)	BUS, <u>FEN</u> , FUN, IMM, KUN, <u>LIM</u> , <u>PAL</u> , PHA, SUB, TES	D, NL
<i>Pentapleura pumilio</i> (NEES) (Braconidae)	1 <sup>n</sup>	SP (2)	BUS, FEN, FUN, IMM, KUN, PHA SUB	D, NL
<b>PUPAL PARASITOIDS</b>				
<i>Trichopria aequata</i> (THOMSON) (Diapriidae)	1 <sup>n</sup> 48 <sup>r</sup>	BA (1) AU (4)	FUN, HYD, IMM, KUN, MEL, <u>LIM</u> , D, NL LIT, PHA, REP, TES, TRA	
<i>Pnigalio soemius</i> (FÖRSTER) (Diapriidae)	2 <sup>n</sup>	HS (1)	?	D
<i>Spalangia erythromera</i> FÖRSTER (Pteromalidae)	2 <sup>r</sup>	AS (10)	BUS, KUN, MEL, <b>PHA</b> , SUB	D, GB, NL
<i>Vrestovia fidenas</i> (WALKER) (Pteromalidae)	37 <sup>r</sup>	AS (11)	FUN, HYD, IMM, KUN, MEL, LIM, D, NL LIT, <b>PHA</b> , REP, TES, TRA	

**Baits:** AB: *Agaricus bisporus* (LANGE) PILÁT; AP: *Aegopodium podagraria* L.; AS: *Angelica sylvestris* L.; AU: *Allium ursinum* L.; BA: Mashed Banana; HM: *Heracleum mantegazzianum* SOMM et LEV.; HS: *Heracleum sphondylium* L.; SP: Spinach. Drosophilids: BUS: *D. busckii* COQUILLET; FEN: *D. fenestrarum* FALLÉN; FUN: *D. funebris* FABRICIUS; HYD: *D. hydei* STURTEVANT; IMM: *D. immigrans* STURTEVANT; KUN: *D. kuntzei* DUDA; LIM: *D. limbata* von ROSER; LIT: *D. littoralis* MEIGEN; MEL: *D. melanogaster* MEIGEN; PAL: *Scaptomyza pallida* ZETTERSTEDT; PHA: *D. phalerata* MEIGEN; REP: *D. repleta* WOLLASTON; SIM: *D. simulans* STURTEVANT; SUB: *D. subobscura* COLLIN; TES: *D. testacea* von ROSER; TRA: *D. transversa* FALLÉN. (\*) Also reared from naturally decaying plant material (see Materials and Methods).

composed of rotting *Angelica sylvestris* was considerably lower in 1991 (2.8 %) than in 1990 (13.1 %). In 1991, no parasitoids were collected from baits made up of *Aegopodium podagraria* L. or commercial mushrooms (*Agaricus bisporus*). In addition the following ten hymenopteran species were attracted to baits (not listed in Table 1), but are not known to use *Drosophila* as their host: Diapriidae – *Idiotype nigriceps* KIEFFER, *Spilomicrus flavipes* THOMSON; Eulophidae – *Chrysocharis viridis* (NEES), *Pedobius acantha* (WALKER); Pteromalidae – *Coruna clavata* WALKER, *Diapara petiolata* WALKER; *Platygerrhus unicolor* GRAHAM; Serphidae – *Brachyserphus parvulus* NEES and *Exallonyx wasmanni* KIEFFER.

**Hymenopteran Parasitoids of *D. limbata* and *D. phalerata*:** Table 2 gives the results for those decaying-herbage baits which produced parasitoids. Six hymenopteran parasitoid species were identified: *Tanycarpa bicolor* (NEES) (Braconidae) and *L. heterotoma*, both larval parasitoids, developed in *D. limbata* and *D. phalerata*; the larval parasitoid *Aphaereta scaptomyza* FISCHER and the pupal parasitoid *Trichopria aequata* (Diapriidae) eclosed from *D. limbata*. Two pupal parasitoids, *Vrestovia fidenas* (WALKER) and *Spalangia erythromera* Förster (Pteromalidae), utilized *D. phalerata* as their host. No hymenopteran wasps emerged from non-infected control baits of either decaying *A. sylvestris* (n=5) or mushrooms, *A. bisporus* (n=10) nor from baits infected with *D. phalerata*, which were composed of either *A. bisporus* (n=10), *H. mantegazzianum* (n=5), or *Impatiens glandulifera* ROYLE (n=2).

**Host Specificity of *Trichopria aequata*:** Both *L. heterotoma* and *Trichopria aequata* developed in all *Drosophila* species offered (Table 3). With some exceptions, e.g. *D. funebris*, female biased sex ratios were observed for the wasps. In all the *Drosophila* species tested, *T. aequata* males developed more quickly than females. The difference in maximal developmental time between the sexes ranged from 2.5 days in *D. limbata* to 7 days in *D. funebris* FABRICIUS. Developmental time of *T. aequata* in *D. limbata* was significantly shorter than in *D. innuigrans* STURTEVANT (U-Test;  $p < 0.001$ ) and also shorter than in the three other *quinaria* species (*D. kuutzei* DUDA, *D. phalerata* and *D. transversa* FALLÉN: U-Test,  $p < 0.05$ ). *T. aequata* had a significantly shorter development in host species which produced more than 20 females than in those host species which produced fewer than 20 females (U-Test,  $p < 0.05$ ). *T. aequata* body size showed a weak, but significantly positive correlation with *Drosophila* body size (Fig. 1.; Kendall's Tau B=0.35,  $p < 0.01$ ).

**Table 2.** Parasitoid hymenoptera that eclosed from different baits, exposed in Isarauen, with larvae and pupae from a single *Drosophila* species. Maximal developmental times (mean  $\pm$  s.e.; days) of the parasitoids in the different *Drosophila* species are shown. For abbreviations, see Table 1. The number of samples of a given bait is shown in parentheses.

Bait	Hymenopteran Species	Males		Females	
		n	Max.Dev.Time	n	Max.Dev.Time
<i>D. limbata</i> + AB (5)	–	–	–	–	–
<i>D. limbata</i> + AU (4)	<i>Trichopria aequata</i>	22	39.2 $\pm$ 0.1	26	39.7 $\pm$ 0.3
<i>D. limbata</i> + HM (10)	<i>Aphaereta scaptomyza</i>	–	–	1	22
	<i>Leptopilina heterotoma</i>	1	27	3	28
	<i>Tanycarpa bicolor</i>	1	18	2	21
<i>D. phalerata</i> + AB (5)	–	–	–	–	–
<i>D. phalerata</i> + AU (10)	–	–	–	–	–
<i>D. phalerata</i> + HM (10)	<i>Leptopilina heterotoma</i>	2	23	3	24.7
	<i>Spalangia erythromera</i>	–	–	2	23
	<i>Tanycarpa bicolor</i>	–	–	1	25
	<i>Vrestovia fidenas</i>	6	19.3 $\pm$ 0.3	17	19.6 $\pm$ 0.4

## Discussion

Twenty-three hymenopteran species were recorded in Isarauen, southern Germany, of which eleven species are *Drosophila* parasitoids, eight of them attacking larvae and three pupae. The number of hymenopteran species is of the same order of magnitude as in southern England and Holland respectively, where, nine and twelve species have been recovered (BAKER 1979, JANSSEN et al. 1988). However, more recently van ALPHEN (1992) estimated at least nineteen larval and seven pupal parasitoid Hymenoptera for drosophilids in the Netherlands. In contrast, hymenopteran parasitoids of *Drosophila* are rare in the north of England, Scotland and Sweden (A. J. DAVIS and G. NORDLANDER, pers. comm.). The interpretation of these data is hampered by differences in the intensities of parasitoid sampling and the methods used. Therefore such comparisons need rigid standardization.

Assigning hymenopteran parasitoid species to their hosts can be approached using different techniques. A straightforward technique is to net them over, or rear them out of, baits or natural substrates infected with *Drosophila* larvae or pupae (CARTON et al. 1986, DRIESSEN et al. 1990, OFFENBERGER 1994). This method, however, may not always be very efficient when the hosts, the wasps or both are present at low densities. But it could be very productive at locations with high parasitism rates (see JANSSEN et al. 1988). The disadvantage of collecting parasitoids in this way is that it gives no information on parasite-host relationships; it only gives an indication as to the number of *Drosophila* species that can potentially be parasitized (HARDY et al. 1992,

**Table 3.** Breeding success of *Leptopilina heterotoma* and *Trichopria aequata* in different *Drosophila* species. The number of female parasitoids given to a culture of each fly species is shown in parentheses. For *Trichopria aequata*, the maximal developmental time (mean  $\pm$  s.e.; days) after the first contact with their host is shown.

<i>Leptopilina heterotoma</i>						
Species	Males	Females	Total	Sex Ratio		
<i>D. kuntzei</i> (3)	11	30	41	0.27		
<i>D. limbata</i> (3)	34	40	74	0.46		
<i>D. phalerata</i> (3)	34	60	94	0.36		
<i>D. transversa</i> (3)	40	53	93	0.43		
<i>D. funebris</i> (3)	243	9	252	0.96		
<i>D. immigrans</i> (3)	5	–	5	1.00		
<i>D. repleta</i> (3)	30	–	30	1.00		

<i>Trichopria aequata</i>						
Species	Males		Females		Total	Sex Ratio
	Max.Dev.Time	No.	Max.Dev.Time	No.		
<i>D. kuntzei</i> (8)	52.0 $\pm$ 2.3	4	56.9 $\pm$ 1.0	15	19	0.21
<i>D. limbata</i> (8)	51.3 $\pm$ 0.9	18	53.9 $\pm$ 0.5	54	72	0.25
<i>D. phalerata</i> (6)	55.1 $\pm$ 1.1	22	57.7 $\pm$ 1.1	20	42	0.52
<i>D. transversa</i> (3)	49.0 $\pm$ 1.0	13	55.5 $\pm$ 0.6	38	51	0.25
<i>D. funebris</i> (3)	48.2 $\pm$ 0.1	9	55.2 $\pm$ 0.9	28	32	0.32
<i>D. hydei</i> (3)	61.0 $\pm$ 0.0	2	64.0 $\pm$ 1.2	5	7	0.28
<i>D. immigrans</i> (3)	53.5 $\pm$ 4.1	15	57.5 $\pm$ 0.7	20	35	0.43
<i>D. littoralis</i> (3)	63.3 $\pm$ 0.7	3	–	–	3	1.00
<i>D. repleta</i> (3)	49.0 $\pm$ 0.8	6	57.0	1	7	0.86
<i>D. busckii</i> (3)	–	–	–	–	–	–
<i>D. melanogaster</i> (8)	69.0	1	69.5 $\pm$ 0.5	2	3	0.33
<i>D. simulans</i> (3)	–	–	–	–	–	–
<i>D. testacea</i> (7)	52.0 $\pm$ 1.6	6	56.2 $\pm$ 1.2	12	18	0.33

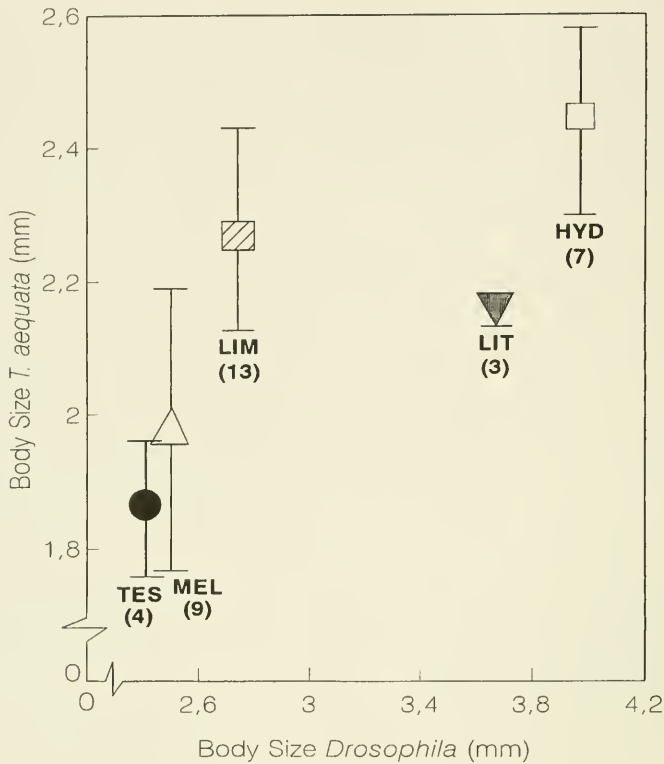


Fig. 1. Body sizes (mean  $\pm$  s.d.) of *Trichopria aequata*, a pupal parasitoid, which eclosed in the laboratory from five different *Drosophila* species (mean of N=7 individuals). The number of eclosed *T. aequata* is given in parentheses.

OFFENBERGER 1994). Parasitized species may be identified by their pupae (Baker 1979, HOFFMEISTER 1992). However, not all drosophilid species have yet been described in this way. Assessing parasite-host relationships in the laboratory by measuring the survival of parasitoid species in a series of potential drosophilid hosts (Table 3) may be indicative. However, there is still the chance for artefacts. Only field observations give certainty.

We have shown that with a new technique, i.e. baiting with decaying-herbage or mushrooms which were infected with a single *Drosophila* species, the disadvantages of the methods described above can be overcome. The parasitoid wasps could only use larvae and pupae from the *Drosophila* species in the bait which had been inoculated in the laboratory and then set out for not longer than one day in nature. Other insect species which are attracted to the baits in the field may, however, lay eggs on it; they can be excluded as hosts, since the wasps parasitize only larvae or pupae, (which do not eclose from eggs before one day time). Using this procedure, two parasitoid hymenopteran species, *V. fidenas* and *T. aequata*, could be assigned unequivocally to their host(s) (Table 2). Four additional species, *L. heterotoma*, *T. bicolor*, *A. scaptomyzae* and *S. erythromera*, have been recorded earlier using *Drosophila* as host (CARTON et al. 1986, van ALPHEN et al. 1991, HARDY et al. 1992). *T. bicolor* and *A. scaptomyzae* were previously unknown as *D. limbata* parasitoids. *T. aequata* was only reared from *Allium ursinum* L./*D. limbata* baits that were set out in Isarauen. In spring, *Allium ursinum* is found in large patches in woodlands and is a natural breeding substrate for *D. limbata*, which concentrates on decaying plants (OFFENBERGER & KLARENBERG 1992a, OFFENBERGER 1994). *T. aequata* was reared

in the laboratory from a total of twelve *Drosophila* species. Maximal developmental time of *T. aequata* in *D. limbata* was shorter than in any other potential host species including the other European *quinaria* group species *D. kuntzei*, *D. phalerata* and *D. transversa*. Moreover, the body size of *T. aequata* reared in *D. limbata* was larger than in *D. littoralis* MEIGEN (Fig. 1). These data also suggest that *D. limbata* is the principal host of *T. aequata*. *L. heterotoma* and *T. aequata* showed female biased sex ratios in most drosophilid hosts (Table 3), which is the rule for many hymenopteran parasitoids (HARDY 1994). However there was one exception, *D. funebris*, where *L. heterotoma* breaks the rule by producing an excess of males. Tests with *L. heterotoma* showed that all four European *quinaria* species were suited for development. This is in contrast to van ALPHEN et al. (1991) who reported that *L. heterotoma* did not successfully reproduce in *D. limbata*. The causes for this discrepancy are unknown. However, our results agree with those of van ALPHEN et al. (1991) and HARDY et al. (1992) that *L. australis* (BELIZIN), *L. fimbriata* (KIEFFER) and *L. heterotoma* attack hosts in decaying plants.

*Agaricus bisporus* attracted only two individuals of *Asobara tabida*, whereas not a single individual was reared. Further tests will have to be performed to determine whether this substrate attracts parasitoid Hymenoptera. In the Netherlands fungus-breeding *Drosophila* are parasitized by *L. clavipes* (HARTIG) (DRIESSEN et al. 1990). This parasitoid was, however, not attracted to commercial mushrooms but to stinkhorns (*Phallus impudicus* PERSSON). The absence of stinkhorns in Isarauen may be the cause for the missing of this parasitoid from our collections. VET et al. (1984) have demonstrated that female *Asobara* and *Leptopilina* species are attracted by substances released from the host breeding substrate. WISKERKE et al. (1993) showed that *L. heterotoma* uses the *Drosophila* adult aggregation pheromone. The experiments with the fungus and decaying plant baits inoculated with *Drosophila* larvae and pupae indicate that the type of substrate may be more important in attracting parasitoids than the host larvae and pupae themselves. This suggests that volatile compounds released by the substrate are involved in attracting the parasitoids.

We believe that the baiting method with fixed numbers of *Drosophila* larvae or pupae could be used to monitor parasitization rates of given host-parasitoid combinations and to estimate the relative population density of parasitoids in different habitats. Moreover, different strains of a single *Drosophila* species or mixtures of different *Drosophila* species could be tested under field conditions with respect to their suitability as hosts for hymenopteran parasitoids. However, for testing the relationship between host distributions and parasitoid distributions (MAY & SOUTHWOOD 1990, PACALA & HASSEL 1991, GODFRAY 1994), our data are not suited. Such an analysis could be very successful when large numbers of baits containing small amounts of substrate, which mimic the size of the natural patches used by *Drosophila*, are set out in the field. These data should be compared with collections of natural patches used by the hosts.

The data for the known versus potential drosophilid host species (Table 1) demonstrate how scanty our knowledge of host-parasitoid relationships in temperate woodlands of Europe still is. It stresses once again the need for more field observations, in particular with respect to the pupal hymenopteran *Drosophila* parasitoids.

### Acknowledgements

We would like to thank C. van ACHTERBERG (Rijksmuseum voor Natuurlijke Historie, Leiden, The Netherlands), I. WALL (Mühlingen, Germany), G. NORDLANDER (Swedish University of Agricultural Sciences, Uppsala, Sweden) and M. DOGANLAR, (Cumhuriyet Üniversitesi, Tokat, Turkey) for their kind support in identifying hymenopteran parasitoid species. We are grateful to J. van ALPHEN (Dept. of Population Biology, Rijksuniversiteit Leiden, The Netherlands) for hospitality to M. OFFENBERGER, to E. DILLER (Zoologische Staatssammlung München) for mediation and to L. KERSTEN for baiting *Trichopria aequata*. Mrs. A. CLARK-OTT kindly corrected the English. For commenting earlier versions of the manuscript we thank A. DAVIS (Leeds), J. JACOBS (München), I. HARDY and J. van ALPHEN (Leiden). Most of the identified wasps are given to Zoologische Staatssammlung München.

## Zusammenfassung

Larven und Puppen von Drosophiliden werden von einer Vielzahl von Hymenopteren-Arten parasitiert. Das Artenspektrum parasitischer Wespen wurde in zwei aufeinanderfolgenden Jahren durch regelmäßige Netzfänge über Ködern aus verrottenden Früchten, Kräutern und Pilzen bestimmt. In den Isaraunen bei München exponierte Köder und natürliche Brutsubstrate wurden im Labor nach ausschließlichen Taufliiegen und Wespen abgesucht; die daraus ermittelten Parasitierungsraten lagen bei 0 bis 13,1 %. Über den Einfluß parasitoider Hymenopteren auf die Populationsstruktur und -entwicklung einzelner *Drosophila*-Spezies sagen solche Daten allerdings wenig aus. Vielmehr müssen die exakten Zuordnungen von Wirts- und Parasitenspezies geklärt werden. Daher wurde eine Methode entwickelt, die eindeutige Brutnachweise im Freiland ermöglicht. Mit der neuen Technik gelangen bei sechs Wespenarten Brutnachweise aus *D. limbata* bzw. aus der nah verwandten *D. phalerata*. Anschließende Laborversuche bestätigten die Tauglichkeit dieser und weiterer Arten als Wirte für vier Wespenarten. *Vrestovia fidenas* (Pteromalidae), deren Biologie bisher unbekannt war, schlüpfte aus Puppen von *D. phalerata*; *Trichopria aequata* (Diapriidae) konnte sich in zahlreichen *Drosophila*-Arten, am schnellsten aber in *D. limbata* entwickeln. Im Freiland lockten nur mit *D. limbata* besetzte Köder aus verrottenden Pflanzen, nicht jedoch solche aus Pilzen *T. aequata* an. Daraus läßt sich schließen, daß Duftstoffe der *Drosophila*-Brutsubstrate bei der Wirtsfindung maßgeblich beteiligt sind.

## References

- ACHTERBERG, C. van 1990: Illustrated key to subfamilies of the Holarctic Braconidae (Hymenoptera: Ichneumonoidea). – Zool. Med. Leiden **64**, 1-26.
- ALPHEN, J. J. M. van, 1992: De levensgemeenschap van fruitvliegjes (*Drosophila*) en hun parasieten in Meijndel. – Meijndel Mededelingen **24**, 91-98.
- ALPHEN, J. J. M. van, NORDLANDER, G. & EIJS, I. 1991: Host habitat finding and host selection of the *Drosophila* parasitoid *Leptopilina australis* (Hymenoptera, Eucoilidae), with a comparison of the niches of European *Leptopilina* species. – Oecologia **87**, 325-329.
- BÄCHLI, G. & BURLA, H. 1985: Diptera Drosophilidae. – Insecta Helvetica 7. Schweizerischen Entomologischen Gesellschaft. Zürich.
- BAKER, R. H. A., 1979: Studies on the interactions of *Drosophila* parasites. Ph.D. Thesis, Oxford University.
- BURLA, H. & BÄCHLI, G. 1991: A search for pattern in faunistical records of drosophilid species in Switzerland. – Z. Syst. Evolutionsforschung **29**, 176-200.
- CARTON, Y., BOULETREAU, M., van ALPHEN, J. J. M. & van LENTEREN, J. C. 1986: The *Drosophila* parasitic wasps. In: ASHBURNER, M., CARSON, H. L., THOMPSON, J. N. (eds.), The Genetics and Biology of *Drosophila* 3e. Academic Press, London, 347-394.
- CARTON, Y., HAOUAS, S., MARRAKCHI, M. & HOCHBERG, M. 1991: Two competing parasitoid species coexist in sympatry. – Oikos **60**, 222-230.
- COURTNEY, S. P., KIBOTA, T. T. & SINGLETON, T. A., 1990: Ecology of mushroom-feeding Drosophilidae. – Adv. Ecol. Res. **20**, 225-274.
- DAVIS, A. J. & JENKINSON, L. S., 1992: *Drosophila fenestrarum* from Leeds, Yorkshire, a new record for northern England, with notes on larval feeding sites. – Naturalist **117**, 28-30.
- DRIESSEN, G., HEMERIK, L. & van ALPHEN, J. J. M., 1990: *Drosophila* species, breeding in the stinkhorn (*Phallus impudicus* PERS.) and their larval parasitoids. – Neth. J. Zool. **40**, 409-427.
- GRAHAM, V. 1969: The Pteromalidae of North-Western Europe (Hymenoptera: Chalcidoidea). – Bull. Brit. Mus. Nat. Hist. Ent. Suppl. **16**, London.
- GRIMALDI, D. & JAENIKE, J. 1983: The Diptera breeding on skunk cabbage, *Symplocarpus foetidus* (Araceae). – J. NY. Ent. Soc. **91**, 83-89.
- GODFRAY, H. C. J. 1994: Parasitoids: behavioural and evolutionary ecology. – Princeton University Press. Princeton, New Jersey.
- HARDY, I. C. W., van ALPHEN, J. J. M. & van DIJKEN, M. J. 1992: First record of *Leptopilina longipes* (Hymenoptera: Eucoilidae) in the Netherlands, and its hosts identified. – Ent. Ber., AMST. **52**, 128-130.



- HARDY, I. C. W. 1994: Sex ratio and mating structure in the parasitoid Hymenoptera. – *Oikos* 69, 3-20.
- HOFFMEISTER, T. 1992: Factors determining the structure and diversity of parasitoid complexes in tephritid fruit flies. – *Oecologia* 89, 288-297.
- HOFSTETTER, A. 1992: Eiablage- und Futterpräferenz bei *Drosophila limbata* und *Drosophila phalerata*. – Diplomarbeit an der Fakultät Biologie der Ludwig-Maximilians-Universität München.
- JAMES, A. C., JAKUBCZAK, J., RILEY, M. P., & JAENIKE, J. 1988: On the causes of monophagy in *Drosophila quinaria*. – *Evolution* 42, 741-748.
- JANSSEN, A., DRIESSEN, G., de HAAN, M. & ROODBOL, N. 1988: The impact of parasitoids on natural populations of temperate woodland *Drosophila*. – *Neth. J. Zool.* 38, 61-73.
- LANKOVAARA, S., 1969: Malt as a culture medium for *Drosophila* species. – *Dros. Inf. Serv.* 44, 128.
- MAY, R. M. & SOUTHWOOD, T. R. E. 1990: Introduction. In: SHORROCKS, B. and SWINGLAND, I. R. (eds.), *Living in a Patchy Environment*. – Oxford University Press, Oxford, 1-22.
- NORDLANDER, G. 1980: Revision of the genus *Leptopilina* FÖRSTER, 1869, with notes on the status of some other genera (Hymenoptera, Cynipoidea: Eucoilidae). – *Ent. Scan.* 11, 428-453.
- OFFENBERGER, M. 1994: Ökologische Studien an Drosophiliden, die verrottenden Pflanzen als Brutsubstrate nutzen. Doktorarbeit an der Fakultät Biologie der Ludwig-Maximilians-Universität München. – Shaker Verlag, Aachen.
- OFFENBERGER, M. & KLARENBERG, A. J. 1992a: Baiting of *Drosophila* with plants in which decay was artificially induced. – *Dros. Inf. Serv.* 71, 234-235.
- OFFENBERGER, M. & KLARENBERG, A. J., 1992b: Attractiveness and exploitation of decaying herbage by *Drosophila* in temperate woodland. – *Oecologia* 92, 183-187.
- PACALA, S. W. & HASSEL, M. P. 1991: The persistence of host-parasitoid associations in patchy environments. II. Evaluation of the field data. – *Am. Nat.* 138, 548-605.
- SEVENSTER, J. G. 1992: The Community Ecology of Frugivorous *Drosophila* in a Neotropical Forest. – Ph.D. thesis, Rijksuniversiteit Leiden.
- SHORROCKS, B. 1982: The breeding sites of temperate woodland *Drosophila*. In: ASHBURNER, M., CARSON, H. L., THOMPSON, J. N. (eds.), *The Genetics and Biology of Drosophila* 3b. – Academic Press, London, 385-428.
- SCHMIEDEKNECHT, O. 1930: Die Hymenopteren Mitteleuropas. – Gustav Fischer Verlag, Jena.
- WISKERKE, J. S. C., DICKE, M. & VET, L. E. M. 1993: Larval parasitoid uses aggregation pheromone of adult hosts in foraging behaviour: a solution to the reliability-detectability problem. – *Oecologia* 93, 145-148.

Anschrift der Verfasser:

Monika OFFENBERGER  
Isartalstraße 24  
D-80469 München

Albert J. KLARENBERG  
Zoologisches Institut  
Karlstr. 23  
D-80333 München