

POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	46	3	311–326	1998
---	-----------	----------	----------------	-------------

Werner ULRICH

Nicholas Copernicus University in Toruń Department of Animal Ecology
Gagarina 9, 87–100 Toruń; Poland, e-mail: ulrichw @ cc.uni.torun.pl

THE PARASITIC HYMENOPTERA IN A BEECH FOREST ON LIMESTONE III: THE ROLE OF LEAF LITTER FOR THE PARASITOID SPECIES

ABSTRACT: In a mixed beech forest growing on limestone, the effect of an enhanced and a reduced layer of leaf litter on the emergence of parasitic Hymenoptera (as well as their hosts) was studied. A long term increase (4 years with an initially 5-fold value) of the leaf layer and a short term experiment (1 year, factor 5) resulted in a rise of the total density of soil living parasitoids. The abundance of parasitoids which attack hosts in the herb layer or canopy declined. However, in both groups diversity and evenness was lowered. A reduction of the layer of leaf litter resulted in lower densities of the parasitoids of soil living hosts, but higher abundances of the parasitoids of hosts in other strata. The lacking leaf layer caused a reduction in the number of species and lowered both diversity and evenness. The lacking leaf layer also caused changes in the species composition. Experiments with dead snails to attract necrophagous insects and their parasitoids covered by different amounts of leaf litter revealed a species specific reaction to the leaf cover. Total parasitism rates were not reduced under a thick layer of leaf litter. No protective function of the leaf cover could be detected.

KEY WORDS: Hymenoptera, parasitoids, leaf litter, parasitism rates, ground-photo-electors, abundances.

1. INTRODUCTION

In deciduous forests the layer of leaf litter plays an important part for many insect species. Some insect larvae (usually of the orders Coleoptera and Diptera) feed on the fallen leaves (Schaefer 1996). The leaf cover also determines the microclimate of the upper soil. Furthermore, the leaf layer will enhance struc-

tural diversity by providing many microhabitats. Besides these main functions of the leaf litter, for ground and litter dwelling animals it may have a protective or camouflaging role against predators or necrophagous insects which hunt optically or olfactorically: birds, for example, or parasitic Hymenoptera. A thick leaf

layer further provides an extensive habitat that may increase the densities of predators such as spiders or centipedes (Stippich 1986, Poser 1991).

The aim of the present study is to reveal the function of leaf litter for parasitic Hymenoptera. Therefore, I studied the emergence data in long term and short

term experiments in which the amount of leaf litter was manipulated. Some further experiments dealt with carcass (dead *Arion ater*) used by necrophagous Diptera and their parasitoids. The carcass was covered by different amounts of leaf litter.

2. MATERIALS AND METHODS

The studies were done in a mixed beech forest on limestone (420 m altitude) near Göttingen (FRG). The wood is characterized by a rich herb layer of spring geophytes (Melico-Fagetum Subassociation *Lathyrus vernus*) which mainly disappear in the summer, leaving a well exposed layer of leaf litter (for a detailed description of the vegetation see Dierschke and Song 1982). A shrub

layer is not developed. The autumn leaf fall leads to a cover of leaf litter that during the following summer months disappears to a great extent. The dry weight of the fallen leafs is in the order of 400 to 600 mg DW/ m² (Hövmeyer 1992). Species lists of Hymenoptera species and data on abundances, biomass and phenology are provided by Ulrich (1987, 1998a)

2.1 LONG TERM MANIPULATION OF THE AMOUNT OF LEAF LITTER

From 1981 to 1986 every autumn – generally at the beginning of October before the abscission began – 2 experimental plots of 200 m² each were covered with a nylon mesh. In the first weeks of December the meshes with the newly fallen leafs were removed. This procedure resulted in a steady decrease of the amount of leaf litter. After 1983 the plots were nearly free of leaf litter.

In 1981 and in 1982 the leafs fallen at these two plots were removed to two other plots (100 m² each) which then got a 5-fold cover of leaf litter. From 1983 to 1986 the amount of leaf litter dropped to an about twofold layer of leaf litter (Ulrich 1988, Hövmeyer 1992). From 1983 to 1986 all plots were sampled with ground-photo-electors. A detailed description of the program gives Ulrich (1988, 1998a).

The replacement of the fallen leafs may introduce or remove insects or eggs. In the case of the plots with an increased layer of leaf litter this fact will only have affected catches in the year 1983. Indeed, 2 parasitoids of scales emerged in very high numbers from these plots (*Eretmocerus mundus*, *Encarsia* spec.).

From the leaf-free plots, insects might have been removed. But only the parasitoids of beech leaf galls (a few species which attack *Mikiola fagi* and *Hartigiola annulipes* and perhaps some parasitoids of gall mites (*Aceria* spp.) emerged in low numbers. Many miners pupate in the soil (Winter pers. comm.) and only some parasitoids which attack the eggs of Lepidoptera and Rhynchota might have been removed. Parasitoids which attack hosts in the soil or leaf litter will not have been affected.

2.2 SHORT TERM MANIPULATION OF THE AMOUNT OF LEAF LITTER

In April 1986 four 4-m plots were provided with a 5-fold amount of leaf litter. To prevent a transport of animals, the leaves were dried prior to the exposition (1 week at 50 °C). Four other plots of the same size were freed from the undecomposed leaves fallen in the autumn before by hand. From 21 July to 18 December 1986

these plots were sampled by eclectors (1 m² sample area).

All parasitic Hymenoptera sampled were identified to species as far as possible. The sorting of the parasitoids into ecological guilds follows Ulrich (1998a).

2.3. EXPOSITION OF DEAD ARION ATER SNAILS AS A FEEDING SUBSTRATE FOR NECROPHAGOUS DIPTERA AND THEIR PARASITIDS

Large specimens (8 to 17 g fresh weight) of the abundant snail species *Arion ater* were killed by freezing at -30 C. The dead snails were exposed in small (6 × 6 × 6 cm³) boxes of polystyrol (cf. Ulrich 1998b). All sides of these boxes were made of fine nylon nets of 0.06 mm (sides and bottom) or 1 mm (lid) mesh wide. The 0.06 mm mesh did not significantly affect the microclimate inside the boxes, but kept out large predators and necrophages, like Carabidae, Silphidae, and *Arion*. It also prevented the dipterous larvae from leaving the boxes to pupate in the soil. The 1 mm mesh allowed even the larger Anthomyiidae, Fanniidae and Panorpidae to deposit their eggs into the snail. Before the first use, all boxes were kept in water for one week. This proce-

dure cleared the boxes from all remnants of glue.

Each ten of these plastic boxes were placed both under the layer of litter in an experimental area of 100 m² covered with five-fold layer of the normal cover (newly placed in 1987), and in area with no layer of litter (200 m²), as well as in a control area with the normal leaf cover. The boxes were placed at 10 June 1987 and taken away at 07 July. To study the parasitism of the different necrophagous species their pupae were sorted according to species and put aside. This procedure was repeated several times until all the dipterous larvae had pupated. All emerging insects were counted and identified. A detailed account on the procedure is given in Ulrich (1998b).

3. RESULTS AND DISCUSSION

3.1. EFFECTS OF LONG TERM MANIPULATION OF LEAF LITTER

3.1.1. Effects of a reduced amount of leaf litter

On the plots without a cover of leaf litter, densities of parasitic Hymenoptera declined from 1984 to 1986 (Table 1). This is especially evident for parasitoids which find their hosts at the soil. In all of

the years they emerged in lower numbers than in the controls. Species numbers were also reduced. On the other hand, in the species with hosts in the herb layer or the canopy region the opposite trend was

Table 1. Densities (ind. m⁻² a⁻¹) and number of species (S) of major parasitoid guilds on plots with a manipulated amount of leaf litter. Control: plots with normal leaf cover; without: plots with a reduced amount of leaf litter; 5-fold: plots with an initially 5-fold amount of leaf litter. Significant differences between the experimental plots and the control are marked with: ° (p(t) < 0.05); °° (p(t) < 0.01)

Parasitoids of	1983									1984								
	Control			Without			5-fold			Control			Without			5-fold		
	S	Density	S.D	S	Density	S.D	S	Density	S.D	S	Density	S.D	S	Density	S.D	S	Density	S.D
Miners	13	22	5	9	17°	6	17	20	6	3	4	5	5	7	5	6	7	5
Gall-makers	15	86	40	12	190°°	67	15	75	14	13	880	163	12	1048°	214	13	369°°	79
Ectophytophages	15	8	3	14	10°	3	20	11°°	4	3	3	3	2	2	2	3	3	3
Sap-suckers	7	110	43	9	25°°	5	10	823°°	116	5	21	9	6	18	10	5	18	12
Saprophages	14	30	9	11	14°°	11	14	41°°	14	8	50	20	9	74	53	9	34	19
Mycetophages	6	3	2	6	5	3	10	5	3	1	2	4	1	2	4	3	2	3
Predators	14	13	4	12	13	4	11	11	6	6	10	7	3	5	4	6	10	6
Hyperparasitoids	7	8	3	8	11	5	4	4°	2	1	5	5	3	6	4	3	3	3
Egg-parasitoids	12	17	8	12	18	7	12	26°	14	5	65	83	5	14	8	5	14	8
Hosts in the herb layer or canopy	62	234	59	60	258°	68	72	948°°	118	27	920	164	32	1104°°	216	34	411°°	80
Hosts in the soil or leaf litter	38	60	12	29	41°°	13	36	70°°	18	18	113	82	14	82	54	20	52°°	21
Stratum not known	26	26	6	30	26	6	32	22°°	5	15	45	32	11	28	16	14	30	12
All parasitoids	126	319	61	119	324	69	140	1041°°	119	60	1078	186	57	1214°°	223	68	493°°	84

Parasitoids of	1985									1986								
	Control			Without			5-fold			Control			Without			5-fold		
	S	Density	S.D	S	Density	S.D	S	Density	S.D	S	Density	S.D	S	Density	S.D	S	Density	S.D
Miners	8	36	13	5	7°°	5	9	49	13	16	31	6	9	15°°	3	12	25°	8
Gall-makers	17	167	37	10	243°°	46	13	154	28	21	72	12	17	58°°	20	19	67	14
Ectophytophages	8	7	5	0	0	0	2	2	2	23	11	3	12	40°	61	18	8°°	3
Sap-suckers	1	1	2	3	6	5	1	2	4	9	12	6	6	8	3	5	4°	2
Saprophages	7	18	9	5	25	10	12	77°°	31	25	87	19	15	23°°	7	21	91	32
Mycetophages	4	4	3	0	0	0	8	31°	20	18	15	5	10	7°°	3	13	16	9
Predators	4	6	3	2	5	4	5	6	4	17	44	8	9	15°°	4	14	18°°	5
Hyperparasitoids	2	3	3	2	2	2	1	2	4	6	5	2	8	4	2	3	2°	1
Egg-parasitoids	6	24	18	5	8°°	5	4	66	71	16	102	33	10	53°°	23	14	39°°	14
Hosts in the herb layer or canopy	35	217	40	24	265°°	47	26	206	31	80	168	18	53	140°°	65	60	111°°	15
Hosts in the soil or leaf litter	19	34	11	7	27	10	29	173°°	73	65	155	24	38	48°°	10	52	152	37
Stratum not known	14	101	28	10	27°°	10	11	135°	45	44	107	30	25	57°°	25	34	37°°	8
All parasitoids	68	352	50	41	319°°	49	66	514°°	92	189	431	42	116	245°°	70	146	299°°	40

found. They reached higher densities on the plots without leaf cover (with the exception in 1986). But the number of species was reduced.

An exception to this latter trend are the parasitoids of mining insects and their potential hosts (Table 1, 4). Densities and number of species were much lowered in the leaf-free plots. This might have been the result of the experimental removal of leaf litter. Some abundant egg-parasitoids (*Alaptus* spec., *Trichogramma embryo-phagum*) also had low densities in the experimental plots.

From 1983 to 1985 some gall-makers and their parasitoids, especially four parasitoids of the gall midge *Contarinia fagi* (*Gastrancistrus walkeri*, *Tetrastichus brachycerus*, *Platygaster* spec. and *Synopeas* spec., cf. Ulrich 1987; Hövemeyer 1985 provided data for the host densities) emerged in exceptionally high densities in the plots without leaf litter. In 1986 the Cecidomyiinae also emerged in very high numbers in the leaf free plots (Table 4). One can speculate that much lowered numbers of predators in these plots caused the low emergence

Table 2. Rank correlations (Spearman's rank) between the rank orders of the parasitoid species of control and experimental plots of the long term manipulation experiment of leaf litter (without and with 5-fold layer of leaf litter). Data from 1983 and 1986.

The species were ranked by their densities.

Parasitoids of	1983				1986			
	without		5-fold		without		5-fold	
	r(S)	p(t)	r(S)	p(t)	r(S)	p(t)	r(S)	p(t)
Miners	0.62	0.001	0.33	0.12	0.82	<0.0001	0.82	<0.0001
Gall-makers	0.51	0.03	0.68	0.001	0.33	0.05	0.47	0.004
Ectophytophages	0.22	0.23	-0.07	0.71	-0.05	0.76	0.25	0.15
Sap-suckers	0.64	0.02	0.64	0.02	0.29	0.45	0.49	0.15
Predators	0.50	0.03	0.29	0.25	0.18	0.43	0.70	0.0004
Mycetophages	0.45	0.15	-0.17	0.60	-0.32	0.10	0.05	0.81
Saprophages	0.32	0.18	0.45	0.04	0.51	0.007	0.74	<0.0001
Eggs	0.19	0.94	0.44	0.06	0.69	0.002	0.86	<0.0001
Parasitoids	0.18	0.60	0.38	0.24	0.02	0.96	0.49	0.10

Table 3. Number of species (S) and densities (ind. m⁻²) of important parasitoid groups and species sampled with ground-photo-electors on experimental areas with 5-fold and without leaf litter layer (emergence of the short-term manipulation experiment from July 1986 to December 1986. Significant differences between the experimental plots and the control plots are marked with °: p(t) < 0.05 or °°: p(t) < 0.01

Guild	Control		Without		5-fold	
	S	Density	S	Density	S	Density
Egg-parasitoids with hosts on the ground	4	26 ± 11	4	22 ± 17	3	55 ± 47
Other egg-parasitoids	10	39 ± 18	6	20 ± 20°	8	8 ± 5°°
Parasitoids of ectophytophages	9	5 ± 1	4	3 ± 2°	4	3 ± 1°°
Parasitoids of miners	9	12 ± 3	8	9 ± 3°	6	5 ± 2°°
Parasitoids of gall-makers	13	35 ± 8	12	18 ± 8°°	10	20 ± 5°°
Parasitoids of ground living predators	6	9 ± 3	8	17 ± 5°°	6	10 ± 3
Other parasitoids of predators	9	26 ± 4	6	12 ± 3°°	7	10 ± 4°°
Parasitoids of sap-suckers	6	4 ± 2	7	5 ± 2	7	2 ± 1°
Hyperparasitoids	4	3 ± 2	6	2 ± 1	7	2 ± 1
Parasitoids of mycetophages	10	7 ± 4	8	5 ± 3	5	6 ± 3
Parasitoids of saprophages	22	53 ± 11	15	54 ± 13	17	28 ± 8°°
Parasitoids with host in canopy or herb-layer	47	95 ± 12	41	56 ± 9°°	42	50 ± 9°°
Parasitoids with host at the ground	48	99 ± 14	37	100 ± 18	36	103 ± 48

rates (cf. Hövemeyer 1985). In the first years, spider densities declined to 1/3 of the usual value, their biomass to less than 20% (Stippich 1986), Lithobiidae nearly vanished (Poser 1991). Although eclectors do not catch spiders quantitatively, the data for 1986 (Table 4) also show the low spider densities in the leaf free plot. Kajak (1978) found that as much as 37% of the emerging Diptera of a meadow were caught by spiders. Assuming that this finding also holds for a beech forest, the lower spider densities might lead to an increase of fly and wasp densities of about 10%. The influence of other predators (especially centipedes and staphylinids) cannot be assessed. Low predator densities may thus account for the higher fly and wasp densities in the experimental plots.

From 1983 to 1986 the parasitoids of soil living saprophagous and mycetophagous Diptera declined. This fact is, of course, attributable to the significantly lower densities of their main hosts in these plots (Table 4, Hövemeyer 1985, 1992).

Egg-parasitoids and the parasitoids of predacious insects (mostly ground living Staphylinidae and Carabidae) also reached markedly lower densities. In the latter case this corresponds to much lowered densities of their hosts in the leaf free areas: the predacious Staphylinidae declined to less than 1/3 of their usual density (judged by the emergences in summer 1986, for the whole year no data are available).

The absence of leaf cover strongly influences microclimatic conditions. The soil of the plots was much drier, and the daily and seasonal temperature fluctuations were more pronounced (Ulrich 1988). Although a clear effect of these abiotic factors on mortality cannot be detected, it is likely that the amount of precipitation and the snow cover in winter will have a strong influence on mortality rates. Therefore, in the parasitoid guilds which change some stratum (from soil to canopy) there may be some compensation of mortality factors in leaf-free areas: more stressful microclimatic conditions and lower host densities at one side, a lowered mortality due to lower densities

Table 4. Eclector densities (ind. m⁻²) of important host groups and predators in 1986. Emergence data on experimental areas with a 5-fold and without a layer of leaf litter. Results of a short term manipulation experiment from July 1986 to December 1986 and results of a long term manipulation 1983 to 1986.

Significant differences between the experimental plots and the control plots are marked with °: p(t) < 0.05 or °°: p(t) < 0.01

Guild	Short term manipulation			Long term manipulation		
	Control	Without	5-fold	Control	Without	5-fold
Araneida	63 ± 5	53 ± 24	64 ± 47	116 ± 20	67 ± 22 ^{°°}	143 ± 26 ^{°°}
Carabidae	4 ± 3	3 ± 2	2 ± 2	8 ± 6	6 ± 3	9 ± 8
Predatory Staphylinidae	19 ± 2	10 ± 8 [°]	19 ± 9	-	-	-
Curculionidae	33 ± 13	26 ± 7	21 ± 7 [°]	48 ± 20	51 ± 25	32 ± 17 ^{°°}
Microlepidoptera	7 ± 2	5 ± 2	9 ± 3	13 ± 3	7 ± 3 ^{°°}	9 ± 3 [°]
Macrolepidoptera	2 ± 1	3 ± 1	3 ± 3	9 ± 4	4 ± 1 ^{°°}	10 ± 2
Cecidomyiinae	20 ± 6	20 ± 11	20 ± 2	139 ± 73	342 ± 156 ^{°°}	304 ± 131 ^{°°}
Phoridae	265 ± 94	133 ± 50 [°]	124 ± 26 ^{°°}	333 ± 112	95 ± 30 ^{°°}	206 ± 54 ^{°°}
Mycetophilidae	10 ± 7	8 ± 6	2 ± 2 [°]	11 ± 7	3 ± 3 ^{°°}	9 ± 5
Fanniidae	2 ± 2	2 ± 1	5 ± 4	3 ± 2	1 ± 1 [°]	3 ± 2
Sphaeroceridae	13 ± 12	4 ± 3 [°]	4 ± 4 [°]	13 ± 12	< 1 ^{°°}	6 ± 3

of predators at the other side. More stressful microclimatic conditions and lowered host densities should reduce species diversity. In fact, in the leaf free plots the species numbers declined from 1983 to 1986, and this trend holds for almost all of the parasitoid guilds (with the exception of hyperparasitoids). Also reduced were the diversity (as estimated by the index H of Shannon) and the evenness (J): in the soil living species the diversity declined from 3.11 to 0.87, and the evenness declined from 0.76 to 0.24; in the canopy and herb layer living species the index values declined from 3.99 (H) and 0.91 (J) to 2.63 and 0.66, respectively.

To detect, whether differences in the species – abundance rank orders between controls and leaf-free plots occurred I computed the correlation of the rank or-

der of the species of each parasitoid guild using the method of Lawton (1984). High correlation coefficients and significance values below 0.05 indicate similar species rank orders; low coefficients point to rearrangements in the species rank order.

Controls and leaf-free plots differed in species rank order (Table 2). Only 8 of the 18 correlations are significant at the 5% level. Especially in the parasitoids of ectophytophages, sap-suckers, mycetophages, predators and the egg-parasitoids changes in the species composition and their relative abundance occurred. From 1983 to 1986 in most guilds there was also a trend to a rearrangement of the rank order (Table 2): in six out of the nine guilds the correlation coefficients were lower in 1986 than in 1983.

3.1.2. Effects of an increased amount of leaf litter

With regard to population densities, the plots with an increased amount of leaf litter showed a trend reverse of that of the leaf-free plots. The parasitoids of saprophages and mycetophages emerged in higher densities, the parasitoids of gall-makers in (slightly) lower densities. In total, parasitoids which find their hosts in the canopy or the herblayer were less affected by the increased amount of leaf litter than the species living at the soil.

The higher densities of soil living species can be explained by the high densities of their potential hosts. Mycetophilidae, Sciaridae, Heleomyzidae, Sphaeroceridae, Fanniidae and Muscidae rose significantly in density after the manipulation (Hövmeyer 1985, Ulrich 1988). Only the Phoridae were less affected and in 1986 they even reached lower densities in the experimental plots (Table 4). Not surprisingly, their main parasitoids, species out of the subfamilies Alysinae and Diapriinae, did not show

significant reactions to a thicker layer of leaf litter either.

In 1983 two parasitoids of scales, *Eretmocerus mundus* and *Encarsia* spec. emerged in exceptionally high numbers in the plots with a 5-fold amount of leaf litter. This may be an artificial result due to the transport of leaf litter to these areas. In the other years the densities were not higher than in the controls.

The parasitoids of miners, gall-makers, predators and the egg-parasitoids declined towards the last year of the experiment. Especially in 1984, when their total emergences were highest, the parasitoids of gall-makers emerged in very low numbers in the 5-fold plots. Again, predation may in part explain the differences. Both spiders and Lithobiidae rose in abundance under the thick layer of leaf litter. The spider densities increased 50%, their biomass doubled (Table 4 and Stippich 1986). Lithobiidae increased 40% (Poser 1991).

The number of parasitoid species with soil living hosts initially rose in the 5-fold plots, but declined in the last year of the experiment. The same trend is shown by the parasitoids which find their hosts in other strata.

In all of the parasitoid-guilds the rank order of the species of control and experimental plots became more similar from 1983 to 1986 (Table 2). In nearly

every guild the 5-fold areas were also more similar to the control than to the leaf free plots. An exception are the parasitoids of mycetophagous Diptera. In both experimental areas markedly rearrangements of the species rank order occurred (in comparison to the control), indicating that these parasitoids are most susceptible to changes of leaf cover.

3.1.3. Leaf litter and life history

In the year 1986 – when the traps were removed only in mid July – I looked whether species with different life history strategies reacted differently to a manipulation of the layer of leaf litter (Fig. 1). The study was only done with the parasitoids of soil-living hosts because in this guild a sufficient number of species of each life history type occurs. I differentiated between koinobiontic species (those which do not kill their hosts immediately) and idiobiontic species (which kill their hosts shortly after parasitism) (H a e s e l b a r t h 1979). The first group contains mainly larval parasitoids, the latter nearly all of the egg- and pupal-parasitoids. I also differentiated between species which hibernate as adults and those which hibernate as larvae or pupae.

Both, idiobiontic and koinobiontic species declined in the leaf-free plots (Fig. 1). But the idiobionts, the pupal- or egg-parasitoids, were less affected by this manipulation. There was also a relatively higher number of species in the leaf-free plots. The opposite trend is seen in the 5-fold plots. Koinobiontic species reached higher abundances, idiobionts declined in density. Especially the abundant diapiids *Basalys pedisequa* and *Trichopria evanescens* and the egg-parasitoids *Litus cynipseus* and *Eustochus atripennis* declined to half of their usual density. All these differences are statistically signifi-

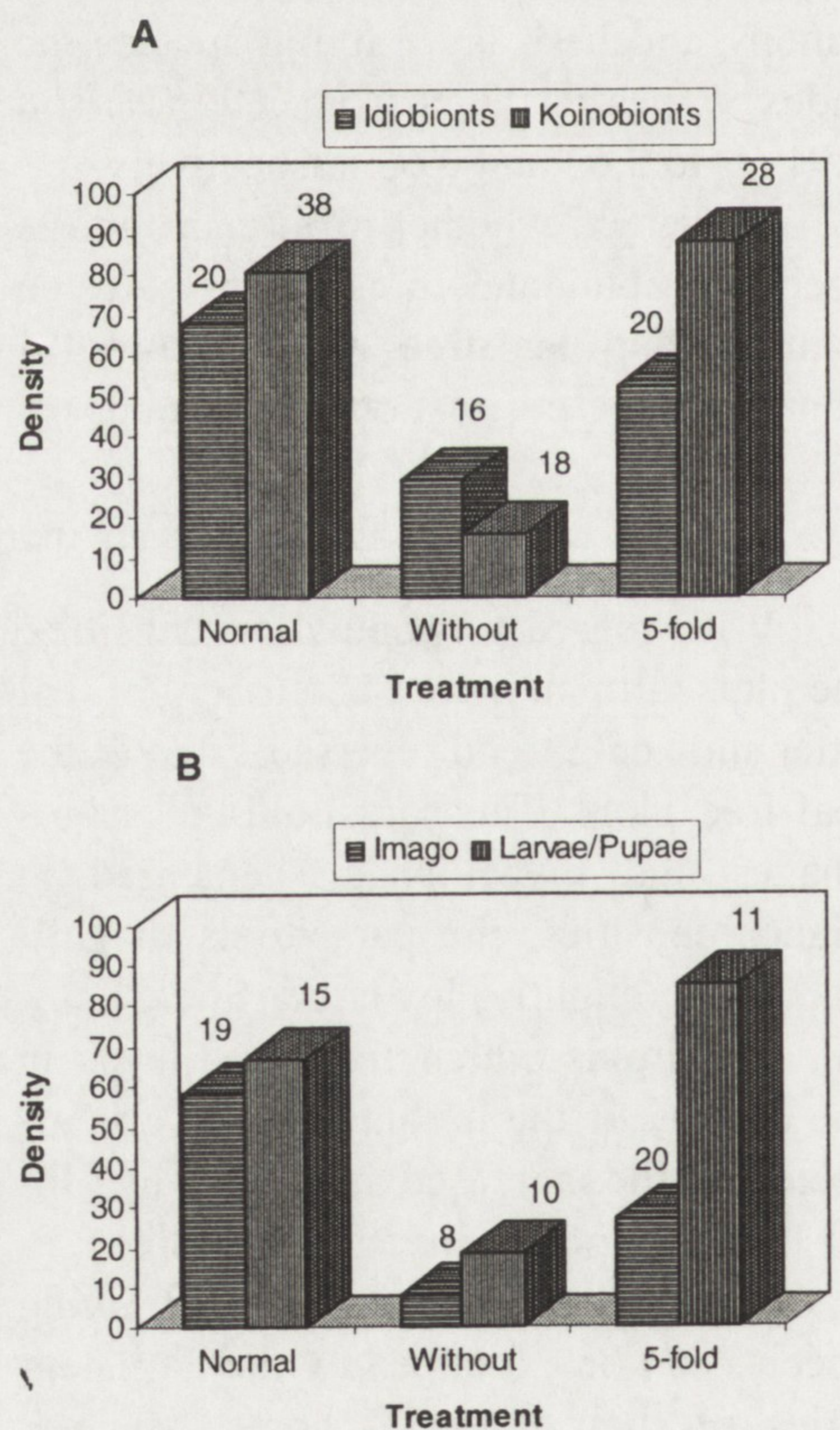


Fig. 1. Densities (ind. m⁻² a⁻¹) of the parasitic Hymenoptera in plots with different amounts of leaf litter. A) Parasitoid type: idiobiontic – koinobiontic; B) Mode of hibernation: imago – larvae/pupae. Given are also the numbers of species in each of the treatments

cant at the 5%-level. One can speculate that the pupal- and egg-parasitoids are less affected by the harsher microclimatic conditions in the leaf-free plots and that,

on the other hand, the larval parasitoids and their hosts find better conditions under a pronounced leaf cover.

Species which hibernate as imago or as larva/pupa both declined in the leaf-free plots. However, the species of the first group were more affected. The same trend holds for the 5-fold plots. Although the mean densities at control and 5-fold

plots were the same (124 ± 21 and 112 ± 33 respectively), the species which hibernate as larvae/pupae rose and the parasitoids which hibernate as imago declined markedly. It seems that a thicker layer of leaf litter is less suited for overwintering as imago.

3.2. SHORT TERM EFFECTS OF AN INCREASED AND A DECREASED AMOUNT OF LEAF LITTER

3.2.1. Reduction of leaf litter

The removal of the leaves at 4 experimental plots in April 1986 had strong negative effects, particularly on parasitoids which find their hosts in the herb layer or canopy region (Table 3). Parasitoids of ectophytophages, gall-makers, miners and egg-parasitoids decreased in abundance and number of species. This result is only partly accounted for by the experimental removal of the leaves and a possible transport of animals. As already mentioned, most mining insects pupate in the soil and probably were not removed. Furthermore, nearly all parasitoids of miners, the egg-parasitoids and 20% of the parasitoids of gall-makers produce two generations per year. Therefore, trapping from July to December samples the second generation which could not have been removed. This is clearly seen in the

emergence data of the possible hosts: Micro- and Macrolepidoptera, Cecidomyiinae and Curculionidae did not decline significantly in density (Table 4).

The parasitoids of soil-living saprophagous hosts did not react to a short term manipulation of leaf litter, but their main host groups, the Phoridae and Sphaeroceridae, declined. The parasitoids of soil-living Staphylinidae even rose in density, but their potential hosts declined. The last two results may indicate that parasitic Hymenoptera are better adapted to harsh microclimatic conditions than their potential hosts and this supports the view of Ulrich (1998b), who found that *Megaselia* spp. (Phoridae) strongly react on the desiccation of their feeding substrates, but that their parasitoids are less affected.

3.2.2. Enhancement of leaf litter

A 5-fold amount of leaf cover had also a negative effect on the emergences of the parasitic Hymenoptera (Table 3). Species with hosts in the canopy or the herb layer declined markedly in density, but the emergences of their potential hosts, especially the Cecidomyiinae were higher (Table 4).

The parasitoids of saprophagous Diptera reached lower densities. Of course, this fact is explained by the lower emergences of their potential hosts, the Phoridae and the Sphaeroceridae. The Staphylinidae and their potential parasitoids did not react to the manipulation of leaf litter.

Of course, the emergences of parasitoids and hosts depend on several factors:

the amount of leaf layer, densities of hosts or feeding substrates, macro- and microclimatic conditions, the abundance of predators, depth of the soil or its microstructure. The leaf layer greatly influences microstructure and microclimatic conditions. These factors together with

soil parameters affect predator and host densities.

Is it possible to separate these factors? Table 5 shows the results of a MANCOVA, computed with the emergence data (1986) of all experimental and control plots of the long and the short

Table 5. MANCOVA (regression approach) to detect the dependence of host and parasitoid species on the amount of leaf litter. Study of the most abundant parasitoid species of the Göttingen forest. The depth of the soil and (in the case of the parasitoids) the density of species were used as covariates. Data from the experimental plots of a short and long term manipulation of leaf litter: 8 plots without cover, 4 plots with a 5-fold cover, 4 plots with a 2-fold cover and 4 control areas. Densities in 1986. The species numbers are the same as in Ulrich (1998a). Depth of soil refers to the depth of the humus layer without leaf layer; the values are given in Ulrich (1988)

Independent variable	Covariate	R ²	p(F)	Variance explanation of leaf layer	
				%	p(F)
<i>Aspilota</i> 2	Depth of soil Density of Phoridae	0.73	0.004	21	0.09
<i>Aspilota</i> 23	Depth of soil Density of Phoridae	0.49	0.12	44	n.s.
<i>Aspilota</i> 5	Depth of soil Density of Phoridae	0.37	0.33	15	n.s.
<i>Aspilota</i> spp.	Depth of soil Density of Phoridae	0.45	0.18	30	n.s.
<i>Glauraspidia microptera</i>	Depth of soil Density of Phoridae	0.44	0.2	30	n.s.
<i>Basalys abrupta</i>	Depth of soil Density of Phoridae, Fanniidae, Sphaeroceridae	0.76	0.01	63	0.004
<i>Basalys pedisequa</i>	Depth of soil Density of Phoridae, Sphaeroceridae	0.62	0.03	48	0.03
<i>Trichopria evanescens</i>	Depth of soil Density of Phoridae	0.71	0.005	7	n.s.
All parasitoids of saprophages	Depth of soil Density of saproph. Brachycera	0.57	0.18	19	n.s.
All parasitoids of mycetophages	Depth of soil Density of Mycetophilidae	0.32	0.46	12	n.s.
<i>Exallonyx quadriceps</i>	Depth of soil Density of pred. Staphylinidae	0.5	0.12	5	n.s.
All parasitoids of Staphylinidae	Depth of soil Density of pred. Staphylinidae	0.6	0.03	31	0.09
Mycetophilidae	Depth of soil	0.55	0.03	20	n.s.
Phoridae	Depth of soil	0.66	0.003	17	n.s.
Sphaeroceridae	Depth of soil	0.58	0.02	34	0.07
Fanniidae	Depth of soil	0.67	0.003	66	0.01
Predatous Staphylinidae	Depth of soil	0.69	0.002	31	0.03

term leaf litter experiment. The analysis was done only with the soil-living species, because potential parasitoids can better be attributed to hosts and the soil-living hosts should be more affected by a manipulated amount of leaf litter than their canopy-living counterparts. For the parasitoids I used the density of the potential hosts and, as an abiotic factor, the depth of the soil, as covariates. For the hosts only the depth of the soil run as covariate. The soil depth varies in the part of the forest under study between 0 and more than 60 cm. The values for all experimental and control plots are given in Ulrich (1988). The soil depth greatly affects the density of major predator groups, such as Lithobiidae and Carabidae (Poser 1991). A deeper soil layer also leads to a more humid microclimate. Table 5 shows that especially for the hosts but also for the parasitoids these factors explain a high percentage of the density variance. In the case of the hosts all R^2 -values are significant. However,

the variance explanation is largely caused by the covariates. In the case of the parasitoids this is of course the expected result. The main factor for parasitoids should be the density of hosts.

A pronounced effect of the leaf layer can only be seen in the Sphaeroceridae, Fanniidae and the predacious Staphylinidae. In the case of the parasitoids in only two species, *Basalys abrupta* and *B. pedisequa*, the leaf layer significantly influenced the density. (Out of 11 computations 1 significant result is expected just by chance.) Especially in the case of the parasitoids of Phoridae, I could not detect a pronounced effect of the amount of leaf litter. This result might mean that the leaf layer does not decrease parasitism. The Hymenoptera seem to be well adapted for host searching under a cover of leaf litter. Furthermore, the density differences, listed in Table 1, 3 and 4, are probably caused by other factors, which are not depended on the leaf cover.

3.3. REACTION OF NECROPHAGOUS DIPTERA AND THEIR POTENTIAL PARASITIDS TO A MANIPULATED AMOUNT OF LEAF LITTER

3.3.1 Number of species and trophic structure

In breeding experiments from dead *Arion ater* snails 3 species of *Megaselia* (Phoridae: *M. ruficornis*, *M. ?pulicaria* and *M. ?angusta*) and one unidentified species of *Pegomya* (Anthomyiidae) emerged. The larvae of *Megaselia* spp. were parasitized by 3 oligophagous species of *Aspilota* (Braconidae) and the pu-

pal parasitoid *Idiotype nigriceps* (Diapriidae). *Aspilota* spp. reached parasitism rates between 1 and 26%, with *Aspilota* spec. 3 the most abundant species (Table 6). The diapriid was only bred twice. *Pegomya* spec. was attacked by *Atractodes* spec. (Ichneumonidae, two parasitoid specimens out of four *Pegomya*).

3.3.2. Dependence of *Megaselia* spp. on the cover of leaf litter

To study the effect of different covers of leaf litter I performed analyses of variance on the number of *Megaselia* in the experimental plots and the controls (Table 7). The weight of the dead snails

was introduced as a covariate to eliminate their possible effect on the attack rate. Although in the control experiment the highest number of *Megaselia* emerged, there are no significant differences be-

Table 6. Number of *Megaselia* spp. and *Aspilota* spec. bred out of boxes with dead *Arion ater* exposed without cover of leaf litter, under 5-fold cover of leaf-litter and with normal cover. There had been 10 boxes in each experiment

Treatment	No. of		<i>Aspilota</i> 1		<i>Aspilota</i> 2		<i>Aspilota</i> 3		All species of <i>Aspilota</i>	
	<i>Megaselia ruficornis</i>	<i>Megaselia ?pul./?ang.</i>	N	% para-sitation	N	% para-sitation	N	% para-sitation	N	% para-sitation
Control	93	201	15	4	25	7	18	5	58	16
without cover of leaf litter	108	148	29	9	42	13	9	3	80	24
5-fold cover of leaf litter	150	62	2	1	18	6	82	26	102	32

Table 7. Analysis of variance: Response of *Megaselia* spp. upon different layers of leaf litter (normal, without and 5-fold). The weight of the dead snails was introduced as a covariate to eliminate the response of *Megaselia* to different amounts of substrate

Effect	<i>M. ?angusta/?pulicaria</i>					Effect	<i>M. ruficornis</i>				
	SS	dF	MS	F	p		SS	dF	MS	F	p
Weight of <i>A. ater</i>	109.1	1	109.1	0.71	0.415	Weight of <i>A. ater</i>	1154.7	1	1154.7	1.9	0.178
Normal versus without layer	15.3	1	15.3	0.1	0.75	Normal versus without layer	44.3	1	44.3	0.08	0.778
Within	2600.6	17	153			Within	10094.1	17	593.8		
Effect	<i>M. ?angusta/?pulicaria</i>					Effect	<i>M. ruficornis</i>				
	SS	dF	MS	F	p		SS	dF	MS	F	p
Weight of <i>A. ater</i>	234.8	1	234.8	1.32	0.266	Weight of <i>A. ater</i>	33.7	1	33.7	0.07	0.76
Normal versus 5-fold layer	639.4	1	639.4	3.6	0.072	Normal versus 5-fold layer	369.8	1	369.8	0.75	0.402
Within	3031.7	17	178.3			Within	8350.3	17	491.2		

tween the variants. Only *M. ?angusta* / *?pulicaria* (because their pupae were not clearly separable both species were treated together) showed a slight tendency to avoid the variant with 5-fold cover.

To eliminate a further possible influence due to competitive exclusions of the three phorids, I run a multiple regression

with one species as the dependent and the other species, the weight of the dead snail, and the cover of leaf litter as the independent variables (Table 8). It appeared that the number of *Megaselia* was not significantly dependent on each of the three factors (total variance explanation: 0 and 14%). Neither species was affected by the amount of leaf litter.

Table 8: Results of 2 runs of a multiple regression:

Dependent variable: One of the two *Megaselia* spec.

Independent variables: The other *Megaselia* spec., the weight of the dead snails and the amount of leaf cover (normal: value 1; without: value 0; 5-fold: value 5)

Dependent variable: <i>Megaselia ?angusta/?pulicaria</i>				
Independent variable: Amount of leaf litter, weight of <i>A. ater</i> , Number of <i>M. ruficornis</i> bred.				
Multiple correlation:	0.476		F (3;26): 2.53	p: 0.078
Adjusted R ² :	0.137			
R ² :	0.23			
Variable	β	B	S.E. of B	p
Leaf litter	-0.25	-1.81	-1.39	0.17
Weight of <i>A. ater</i>	0.35	2.2	1.94	0.06
No. of <i>M. ruficornis</i>	0.2	0.24	1.1	0.28
Dependent variable: <i>Megaselia ruficornis</i>				
Independent variable: Amount of leaf litter, weight of <i>A. ater</i> , Number of <i>M. ?ang./?pul.</i> bred.				
Multiple correlation:	0.301		F (3;26): 0.89	p: 0.461
Adjusted R ² :	-0.01			
R ² :	0.09			
Variable	β	B	S.E. of B	p
Leaf litter	0.18	1.08	0.93	0.37
Weight of <i>A. ater</i>	-0.22	-1.14	-1.1	0.28
No. of <i>M. ?angusta/?pulicaria</i>	0.23	0.18	1.1	0.28

3.3.3. Dependence of the parasitoids on the cover of leaf litter

In an analysis of variance the species of *Aspilota* showed no clear reaction to a different amount of leaf litter (Table 9). As expected, they reacted positively to the number of host larvae present, but only *Aspilota* spec. 3 emerged significantly more abundant under the 5-fold cover. Under the higher cover the species reached a parasitism rate of 26%, under the normal cover only a rate of 5% (Table 6). The two other species did not react to a different amount of leaf litter.

Competitive effects between the three *Aspilota* spp. may conceal the influ-

ence of the leaf cover. As a test I also performed a regression analysis with one species as the dependent and the other species as well as the amount of leaf litter and the number of hosts present as independent variables. As in the case of the analysis of variance, only *Aspilota* 3 reacted significantly positively to the amount of leaf cover. However, the total variance explanation for this species was only 23% (p = 0.03).

Three conclusions emerge from the previous discussion:

Table 9. Analysis of variance: response of *Aspilota* spp. upon different layers of leaf litter (normal, without and 5-fold).
The Number of hosts was introduced as a covariate to eliminate the response of *Aspilota* to different host numbers

<i>Aspilota 1</i>						<i>Aspilota 3</i>					
Effect	SS	dF	MS	F	p	Effect	SS	dF	MS	F	p
No.of <i>Megaselia</i> spp.	106.4	1.0	106.4	5.4	0.03	No.of <i>Megaselia</i> spp.	118.9	1.0	118.9	3.3	0.08
Leaf cover	28.8	2.0	14.4	0.7	0.5	Leaf cover	365.0	2.0	182.5	5.1	0.014
Within	516.6	26.0	19.9			Within	939.2	26.0	36.1		
<i>Aspilota 2</i>						<i>All Aspilota spp.</i>					
Effect	SS	dF	MS	F	p	Effect	SS	dF	MS	F	p
No.of <i>Megaselia</i> spp.	93.9	1.0	93.9	3.8	0.06	No.of <i>Megaselia</i> spp.	955.4	1.0	955.4	16.9	0.0004
Leaf cover	27.3	2.0	13.7	0.6	0.59	Leaf cover	214.3	2.0	107.1	0.3	0.169
Within	637.8	26.0	24.5			Within	1469.8	26.0	56.5		

1. Parasitoids and their dipterous hosts react species-specific upon experimentally manipulated amounts of leaf litter.

2. A protective effect of the leaf litter could not be detected. A markedly higher layer of leaf litter had only a small effect on substrate and host finding of necrophagous Diptera and their parasitoids. Both groups are well adapted to search for feeding substrates or hosts and to deposit eggs between the leaves.

3. It is not clear whether small effects upon host finding reflect negative reac-

tions to cover and microclimate or if the animals are relatively unaffected by both.

ACKNOWLEDGMENTS: For helpful comments on early versions of the manuscript I thank Prof. M. Schaefer. For valuable comments on the manuscript I also thank Prof. J. Buszko. Dr. K. Hövemeyer kindly determined the Diptera bred out of the carcasses and H. Hilpert checked the determination of *Trichopria evanescens*. Miss H. Pearson kindly improved the English text.

This work was in part supported by a grant from the Deutsche Forschungsgemeinschaft. The author received a scholarship from the Friedrich-Ebert-Foundation.

4. SUMMARY

In a mixed beech forest growing on limestone (FRG), the effect of an enhanced and a reduced layer of leaf litter on the emergence of parasitic Hymenoptera (as well as their hosts) was studied. A long term increase (4 years with an initially 5-fold value) of the leaf layer and a short term experiment (1 year, factor 5) resulted in a rise of the total density of soil living parasitoids (Table 1). The abundance of parasitoids which attack hosts in the herb layer or canopy declined. However, in both groups diversity and evenness was lowered. A reduction of the layer of leaf litter resulted in lower densities of the parasitoids of soil living hosts, but higher

abundances of the parasitoids of hosts in other strata (Table 1). The lacking leaf layer caused a reduction in the number of species and lowered both diversity and evenness. The lacking leaf layer also caused changes in the species composition (Figure 1). Markedly changes in the species rank order occurred (Table 2). Experiments with dead snails to attract necrophagous insects and their parasitoids covered by different amounts of leaf litter revealed a species specific reaction to the leaf cover (Table 6, 7, 8). Total parasitism rates were not reduced under a thick layer of leaf litter. No protective function of the leaf cover could be detected (Table 5).

5. REFERENCES

- Dierschke H., Song J. 1982 – Die Vegetation der Untersuchungsfläche des SFB 135 und ihrer Umgebung im Göttinger Wald – Kurzmitt. aus dem SFB 135 – Ökosysteme auf Kalkgestein 1: 3–8.
- Haeselbarth E. 1979 – Zur Parasitierung der Puppen von Foreule (*Panolis flammea* (Schiff.)), Kiefernspanner (*Bupalus piniarius* (L.)) und Heidelbeerspanner (*Boarmia bistortana* (Goeze)) in bayerischen Kiefernwäldern – Z. Ang. Entomol. 87: 186–202; 311–322.
- Kajak A. 1978 – Analysis of consumption by spiders under laboratory and field conditions – Ekol. Pol. 26: 409–428.
- Haeselbarth E. 1979 – Zur Parasitierung der Puppen von Foreule (*Panolis flammea* (Schiff.)), Kiefernspanner (*Bupalus piniarius* (L.)) und Heidelbeerspanner (*Boarmia bistortana* (Goeze)) in bayerischen Kiefernwäldern – Z. Ang. Entomol. 87: 186–202; 311–322.
- Hövemeyer K. 1985 – Die Zweiflügler (Diptera) eines Kalkbuchenwaldes: Le-

- benszyklen, Raum-Zeit-Muster und Nahrungsbiologie – Thesis Univ. Göttingen.
- Hövmeyer K. 1992 – Response of Diptera populations to experimentally modified leaf litter input in a beech forest on limestone – *Pedobiologia* 36: 35–49.
- Lawton J.H. 1984 – Herbivore community organization: general models and specific tests with phytophagous insects – In: P.W. Price, C.N. Slobodchikoff and W.S. Gaud 1984: *A New Ecology. Novel Approaches To Interactive Systems* – New York (Wiley).
- Pielou E.C. 1977 – *Mathematical Ecology* – New York (Wiley).
- Poser G. 1991 – Die Hundertfüßer (Myriopoda: Chilopoda) eines Kalkbuchenwaldes: Populationsökologie, Nahrungsbiologie und Gemeinschaftsstrukturen – *Berichte des Forschungszentrums Waldökosysteme Göttingen A* 71: 1–211.
- Schaefer M (1996) – Die Bodenfauna von Wäldern: Biodiversität in einem ökologischen System – *Abh. Math.-Naturw. Klasse Akad. Wiss. Lit. Mainz* 1996: 1–81.
- Stippich G. 1986 – Die Spinnenfauna (Arachnida: Araneida) eines Kalkbuchenwaldes: Bedeutung von Habitatstruktur und Nahrung – Thesis Univ. Göttingen.
- Ulrich W. 1987 – Wirtsbeziehungen der parasitoiden Hautflügler in einem Kalkbuchenwald (Hymenoptera) – *Zool. Jb. Syst.* 114: 303–342.
- Ulrich W. 1988 – Welche Faktoren beeinflussen die Populationen und die Strukturen der Gemeinschaften von bodenlebenden parasitoiden Hymenopteren in einem Buchenwald – Thesis Univ. Göttingen (FRG).
- Ulrich W. 1998a – The parasitic Hymenoptera in a beech forest on limestone I: Species composition, species turnover, abundance and biomass – *Pol. J. Ecol.* 46: 261–289.
- Ulrich W. 1998b – Species composition, coexistence and mortality factors in a carrion exploiting community composed of necrophagous Diptera and their parasitoids – *Pol. J. Ecol.* (in press)

Received after revising April 1998