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 II: STUDY OF THE SEX RATIOS AND THEIR DEPENDENCE ON ECOLOGICAL FACTORS

ABSTRACT: The sex ratio of the parasitic Hymenoptera of a beech forest on limestone near Göttingen (FRG) was studied using ground-photo-eclectors. Judged from the mean sex ratios the parasitoids could be separated into 4 groups. Parasitoids of miners and gall-makers had the highest sex ratios (30 to 40% males) and less than 5% of the species were thelytokous. The species which attack soil-living sapro- or mycetophagous Diptera as well as the parasitoids of ectophytophages had (on average) 20 to 30% males and only 1.5% of them were thelytokous. Parasitoids of sap-suckers and egg-parasitoids usually had sex ratios below 20% males and 29% of them were thelytokous. The lowest sex ratios (below 10% males) and the highest number of thelytokous species (30%) were found among hyperparasitoids and parasitoids of soil-living Staphylinidae. No clear trend was detectable between the sex ratio and the density of the species. The density fluctuations and the degree of aggregation of the species influenced the sex ratio. The data are consistent with the hypothesis that K-selected parasitoid species have higher sex ratios on average. Koinobiontic species (mostly parasitoids of gall-makers and miners) had (on average) significantly higher sex ratios if their host lives in the herb or crown layer (32% versus 21%). They also produced more males if they are univoltine (32% versus 22%) and hibernate as larvae or pupae (30% versus 17%). After a MANOVA-analysis the voltinism turned out to be the main influencing factor. There was a trend towards higher percentages of males in the summer generation.
KEY WORDS: sex ratio, local mate competition, parasitoids, ground-photo-eclectors, Hymenoptera.

1. INTRODUCTION

Parasitic Hymenoptera are haplo-diploid organisms. That means (normally) males develop from unfertilized eggs, females from fertilized ones. Exceptions are thelytokous species in which only females are produced. Due to this mode of sex allocation the sex ratios are very variable. Ecological and evolutionary theory

predict (Hamilton 1967, Charnov 1982, Waage 1986, King 1987) that sex-ratios should be adjusted to values that allow an optimal reproductive success. Several ecological factors may influence the sex ratio of parasitic Hymenoptera:

• The number of males: Low numbers may possibly lower the fertilization rate and hence lower sex ratio.

• The generation: Some parasitoids of mining insects produce a higher number of males in the second generation (Askew and Ruse 1974, Godfray and Shaw 1987).

• The host size, constitution and age (Sandlan 1979, Van Alphen and Thunnissen 1983, King 1987, Mayhew and Godfray 1997).

• The host density: Several studies demonstrated a relationship between host density and sex ratio, but there is no evident dependence, though different mechanisms have been proposed (Jackson 1958, Waage and Ng 1984).

• The density of the female parasitoids: A high female density should favor the production of males because it lowers the chance of egg deposition for the females but enhances the probability and the frequency for males to mate. This argument is reversed at high male densities (Strand 1988, King 1987). Very low parasitoid densities may lead a species to become thelytokous because of the difficulties to find mates.

• The degree of aggregation of the parasitoids: The theory of local mate competition (LMC) (Hamilton 1967) predicts that highly aggregated species with a low dispersal of males should only produce the number of males necessary to fertilize the females of the local patch.

• The host quality: Females may discriminate between small and or less suited host patches and larger and/or better ones, choosing the less suited patches for depositing only male eggs and the better ones for laying female and a few male eggs (Mayhew and Godfray 1997).

• Low resource availability also should result in investment in the cheaper sex (the males). In the case of *Philanthus triangulum* this has been shown experimentally by Strohm and Linsenmair (1997).

Besides these factors there are others that may affect the sex ratio, for example the age of the females, their constitution, the amount of sperm, and climatic factors like temperature, sunshine and humidity (King 1987, Ode *et al.* 1997).

The aim of this study is to give an overview of the sex ratios of the parasitic Hymenoptera of a beech forest on limestone in northern Germany. When possible it tests the above-mentioned suppositions concerning the adjustment of sex ratios in parasitoids. The samplings were undertaken with ground-photo-eclectors that were used during 1981 to 1987 (see Ulrich 1998a for a detailed description of the eclector program and the hymenopterous fauna of this forest). During this period a total of 720 species of Hymenoptera were found in the forest. 669 of them were parasitoids. For the present study the 148 most abundant of them (of which more than 20 individuals were collected) were selected.

2. MATERIALS AND METHODS

The studies were done in a mixed beech forest (*Fagus sylvatica*) on limestone (~ 420 m above sea level) near Göttingen (northern FRG). D i e r s c h k e and S o n g (1982), S c h a e f e r (1990) and S c h a e f e r and S c h a u e r m a n n (1990) describe the vegetation and the soil of the study area in detail. The sampling methods are given in U l r i c h (1988, 1998a).

Most of the forest insects pupate or hibernate in the leaf litter or the soil. Only a few species stay in the crown layer (some Lepidoptera and Neuroptera, Winter pers. comm.) or hibernate as adults under the bark of dead trees (like some Ichneumonidae). Therefore, the majority of the pterygote insects should be caught with emerging traps like photo-eclectors (see T h i e d e 1975 and U l - r i c h 1988 for a detailed discussion). Emerging traps further minimize the bias in sampling of the sexes. Other methods like sweep net sampling or pyrethrum knocking usually overestimate the number of females because they are more active and live longer.

Of the species listed in the Appendix the females of *Basalys parva, B. pedisequa, Diaeretellus ephippium, Glauraspidia microptera, Lagynodes pallidus*, and probably the males of *Eustochus atripennis* are brachypterous or apterous (*L. pallidus, D. ephippium*). However, problems arise only in the case of *G. microptera* and *L. pallidus* due to the high number of males caught. Their sex-ratios may be overestimated.

Table 1 compares the sex ratios of some soil-living parasitoids which could be bred with the ratios obtained by ground-photo-eclectors. Both ratios are sufficiently similar. Only from one spe-

Table 1. Sex ratios (proportion of males) of some parasitiod species or grup. Comparison between breeding and elector sampling. Ratios of breeding and sampling were obtained in the same year

Taxon	Sex ratio	
	eclector sampling	breeding
All Oxytorinae	0.10	0.06
Aspilota 1	0.20	0.23
Aspilota 2	0.26	0.38
Aspilota 3	0.44	0.41
Basalys parva	0.13	0.24
Kleidotoma psiloides	0.20	0.27
Orthostigma 1	0.48	0.60
Pentapleura spec.	0.26	0.28

cies of *Aspilota* (Braconidae) a higher number of males were bred than caught and (surprisingly) the (in the female sex) brachypterous diapriid *Basalys parva* even had a lower sex ratio (that means more females) in the eclector sampling than from breeding. Therefore, the sex ratios of most parasitoid species which emerge from the soil to the herb and crown layer could correctly be estimated.

All specimen were sorted according to species and, if possible, identified. A list of all species together with data on the abundance, biomass and notes on the biology are given in U l r i c h (1987, 1998a). Most of the species were caught only in small numbers and, especially in the orthocentrine and geline ichneumonids and the Ceraphronoidea, it is very difficult to link the sexes. For the present study only those species are treated which allow a reliable estimation of the sex ratios, i.e. from which more than 20 individuals were caught. The resulting 148 parasitoid species (from a total of 669) are listed in the Appendix. In the present study sex ratios always refer to the proportion of males.

3. RESULTS AND DISCUSSION

3.1. SEX RATIOS OF DIFFERENT PARASITOID GUILDS

The parasitoids can be classified into guilds according to the biology of their hosts. Such a classification is provided in Table 2 and follows the grouping of U l - r i c h (1987, 1998a). If one compares the mean sex ratio of the species of these guilds, marked differences appear:

out of 65 species (= 1.5%) was thelytokous (*Copidosoma* spec., parasitoid of ectophytophagous hosts). The dominant *Acropiesta rufiventris* had 48% males, *Basalys pedisequa* 7%, *Entomacis perplexa* 15%, and *Trichopria aequata* 31%. In the case of the parasitoids of ectophy-

Table 2. Mean values of the sexual index of the parasitoid guilds in the Göttingen forest-
Values of the most abundant (more than 20 individuals found) species

Guild	Mean sex-ratio	Standard deviation of mean sex-ratio	No. of species	No. of thelytokous species
Hyperparasitoids	0.05	0.08	4	2
Parasitoids of ground living predators	0.09	0.11	6	1
Egg-parasitoids	0.15	0.14	14	4
Parasitoids of sap-suckers	0.19	0.18	14	4
Parasitoids of saprophages	0.21	0.15	20	0
Parasitoids of not ground living predators	0.24	0.13	4	0
Parasitoids of mycetophages	0.28	0.28	21	0
Parasitoids of ectophytophages	0.29	0.18	20	1
Parasitoids of gall-makers	0.34	0.18	26	2
Parasitoids of miners	0.39	0.15	13	0

Wasps which attack mining or gall-inducing insects (mainly Diptera and Lepidoptera) have (on average) sex ratios between 30 and 40% males. In this group I found only two (= 4%) thelytokous species (*Omphale aetius, Tetrastichus fageti*). Of the most dominant species (mean densities above 1 ind. m^{-2} a^{-1}, cf. U l r i c h 1998a)) *Acoelius erythronotus* produced 33% males, *Amblyaspis nodicornis* 35%, *Chrysocharis prodice* 28%, *Eulophus larvarum* 35%, *Gastrancistrus walkeri* 58%, *Tetrastichus brachycerus* 56%, and *T. luteus* 39%.

The second group contains the parasitoids of ectophytophagous hosts (Lepidoptera and Coleoptera), of soil-living mycetophagous or saprophagous Diptera, and of not-soil-living predators (Neuroptera and Hemiptera). The mean sex ratios were 20 to 30% males. Only 1

tophages two subgroups appeared (Fig. 1): one with mean sex ratios below 15% and one with ratios above 30%.

The third group is made up of the parasitoids of sap-suckers and egg-parasitoids. They (usually) had mean sex ratios below 20% and 8 out of 28 species (= 29%) were thelytokous. Of the four dominant egg-parasitoids (*Eustochus atripennis, Litus cynipseus, Polynema fumipenne* and *Trichogramma embryophagum*) no males were detected and only in the *Anagrus* and *Anaphes* spp. (Mymaridae) higher percentages of males occurred. Of *Eustochus atripennis* and *Polynema fumipenne* males are known (T r j a p i z y n 1978, Ulrich unpubl.). The males of *E. atripennis* are brachypterous and were sampled out of leaf litter (T r j a p i z y n 1978), but the males of *P. fumipenne* have wings and appeared to be
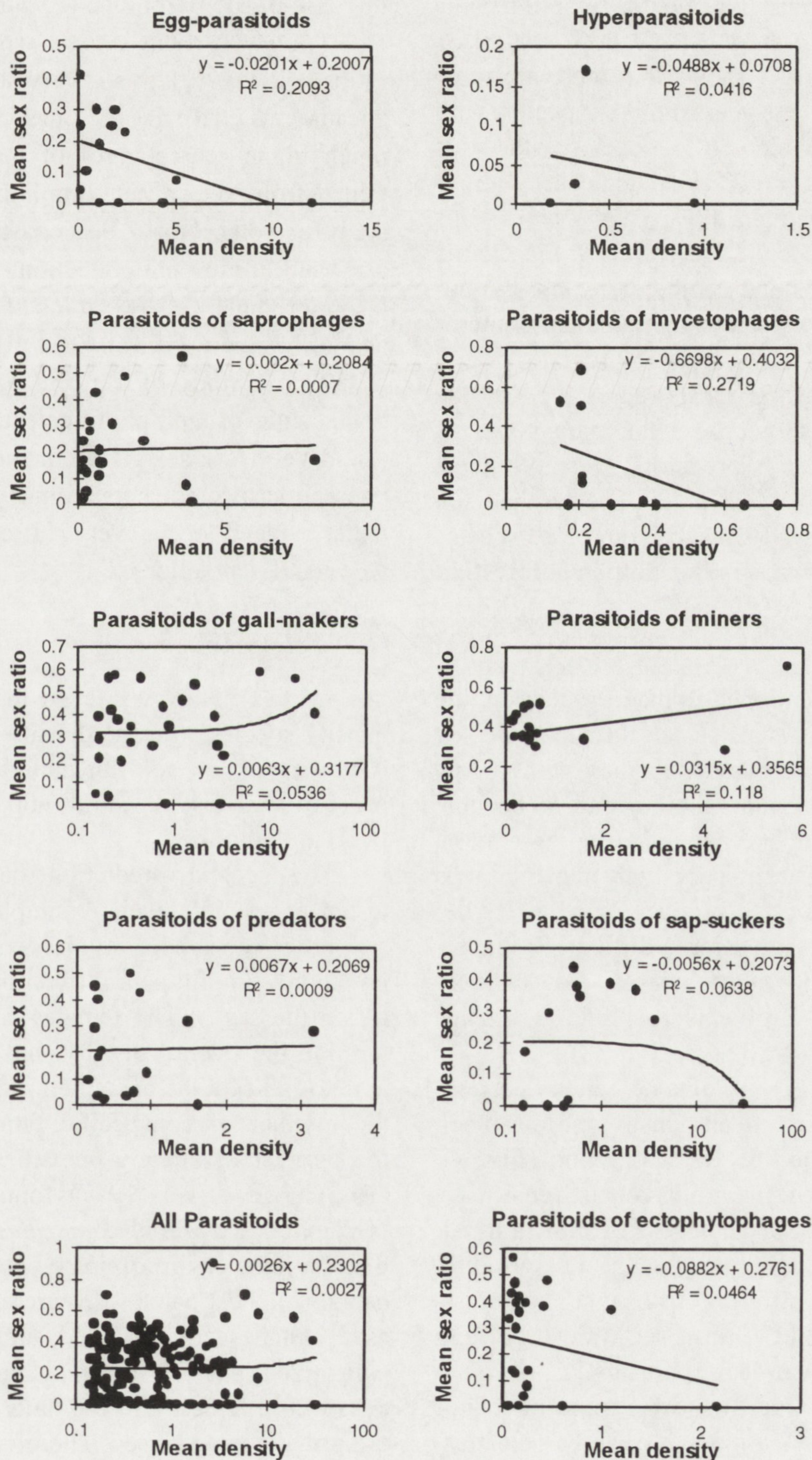
Fig. 1. Relationship between the mean sex ratio of the species of the main guilds of parasitic Hymenoptera in the Göttingen beech forest and their mean density. Each data point represents one species

rather common in eclector samplings on a nearby xerophytic meadow (Ulrich 1998c). Fig. 1 shows that there are three groups of egg-parasitoids: Species with sex ratios below 10%, species with ratios between 20 and 30% and species with ratios higher than 40%. Of the parasitoids of sap-suckers *Diaeretellus ephippium* is thelytokous and *Eretmocerus mundus* appeared to be nearly thelytokous (deutero-tokous, 12 males and 4359 females).

The last group is represented by the hyperparasitoids and the parasitoids of ground living predators (Staphylinidae, Carabidae). Most of the species had sex ratios below 10% and 3 out of 10 species are thelytokous in the Göttingen forest. In the case of the Serphidae (*Exallonyx* spp. and *Phaneroserphus calcar* which have ratios below 10%), this is very surprising, because Weidemann (1965) found much higher percentages of males (obtained from sweep net samplings) in his study of some North Sea coastal meadows, and in museum collections there are also more balanced sex ratios (Townes and Townes 1981). But Hilpert (1989) in a study of a mixed oak forest, done with ground-photo-eclectors, also found very low sex ratios in the Serphidae and suspected (pers. comm.) that the males indeed occur very infrequent in woodland populations.

3.2. SEX RATIO AND DENSITY

As mentioned in the introduction, the density of a species can influence the sex ratio in two ways: Species with a low mean abundance should tend to become thelytokous because mate finding may be difficult. But at very high densities it is advantageous to produce more males because it is increasingly difficult for the females to find hosts whereas males should have no problems in finding mates (King 1987, Strand 1988).

But from my data no general correlation between mean density and mean sex ratio of the species was found (Fig. 1). The plot of sex ratio versus density including all species does not show a trend. But if one compares the species sorted by host guild differences appear. The parasitoids with low mean sex ratio (egg- and hyper-parasitoids, parasitoids of sap-suckers, Table 2) show a trend of reducing their sex ratio with higher densities. The parasitoids of miners and gall-makers, which have the highest mean sex ratio show the opposite trend. My data do not allow conclusions to be drawn for the very low abundant species (below 0.01 ind. m^{-2} a^{-1}). However, even in the low-density-species (mean densities below 0.01 ind. m^{-2} a^{-1} and not included in the present analysis) I could not detect a trend to thelytoky.

The second prediction has to be tested at species level. A simple plot of sex ratio versus density is ecologically not as meaningful as a differentiation between the sexes. The females do not determine the overall density, but they are able to indicate the encounter with mates, the number of conspecific females and the number of already parasitized hosts. Gauthier *et al.* (1997) found in the pteromalid parasitoid *Dinarmus basalis* that the females discriminate between unparasitized host patches, where female biased clutches are produced, and already parasitized patches or encounters with conspecific females. In the latter case the offspring is male biased. Therefore higher densities tend to result in the production of more males. King (1996), however, also found a higher proportion of males in the progeny when the females encounter higher numbers of males or females. In-

terestingly, LMC-theory predicts a higher proportion of males only in the case of higher densities of conspecific females.

Table 3 shows correlations between sex ratio and both, density of males and density of females. Because the sex ratio mainly depends on the density of males, most sex ratios (16 out of 18 correlations) correlate positively with male density. 10 of these correlations are significant at the 5%-level. However, only in three cases did sex ratio significantly correlate with density of females. And in none of the species there was a significant correlation between sex ratio and total density. Therefore, at species level the data do not indicate a dependence of sex ratio on density.

For the six most abundant species it was possible to estimate the values of the sex ratio over all consecutive generations during the study period (7 years) (Fig. 2). Clearly detectable is the trend: high sex ratios were followed by lower ones in the next generation, low sex ratios by higher ones. However, this trend is not attributable to the density of the species. In none of the species were high densities followed by lowered sex ratios and only in three species there was a slight tendency of higher sex ratios after low densities.

Breeds out of dead snails gave more decisive results. In 1986 I undertook experiments with dead *Arion ater* as substrates for the development of necrophagous Diptera (mostly Phoridae and

Table 3. Density dependence of the sex ratios of the 18 most abundant species of parasitoids in the Göttingen beech forest. Given are the numbers of significant correlation coefficients between sex ratio and density of males or females (p < 0.05).
The computation was done only with species which had been found in at least 6 of the 7 study years and in each of these years with more than 20 specimens. Because most of these species are bivoltine the correlations were done with 6 to 14 data points

Correlation between sex ratio and density of		Number of correlations	No. of significant correlations		
Males	Females		Males	Females	Total density
positive	positive	7	5	0	0
positive	negative	9	5	2	0
negative	negative	2	0	1	0
negative	positive	0	0	0	0

Table 4. Correlations (Spearman's rank) between sex ratio and parasitism rate or density. Data of breeding experiments with dead snails. *K. psiloides* emerged out of *Limosina* spec. (Sphaeroceridae), *Aspilota* spp. and *Orthostigma* spec. out of 3 phorid species. For a detailed description of the experiments see U l r i c h (1998b)

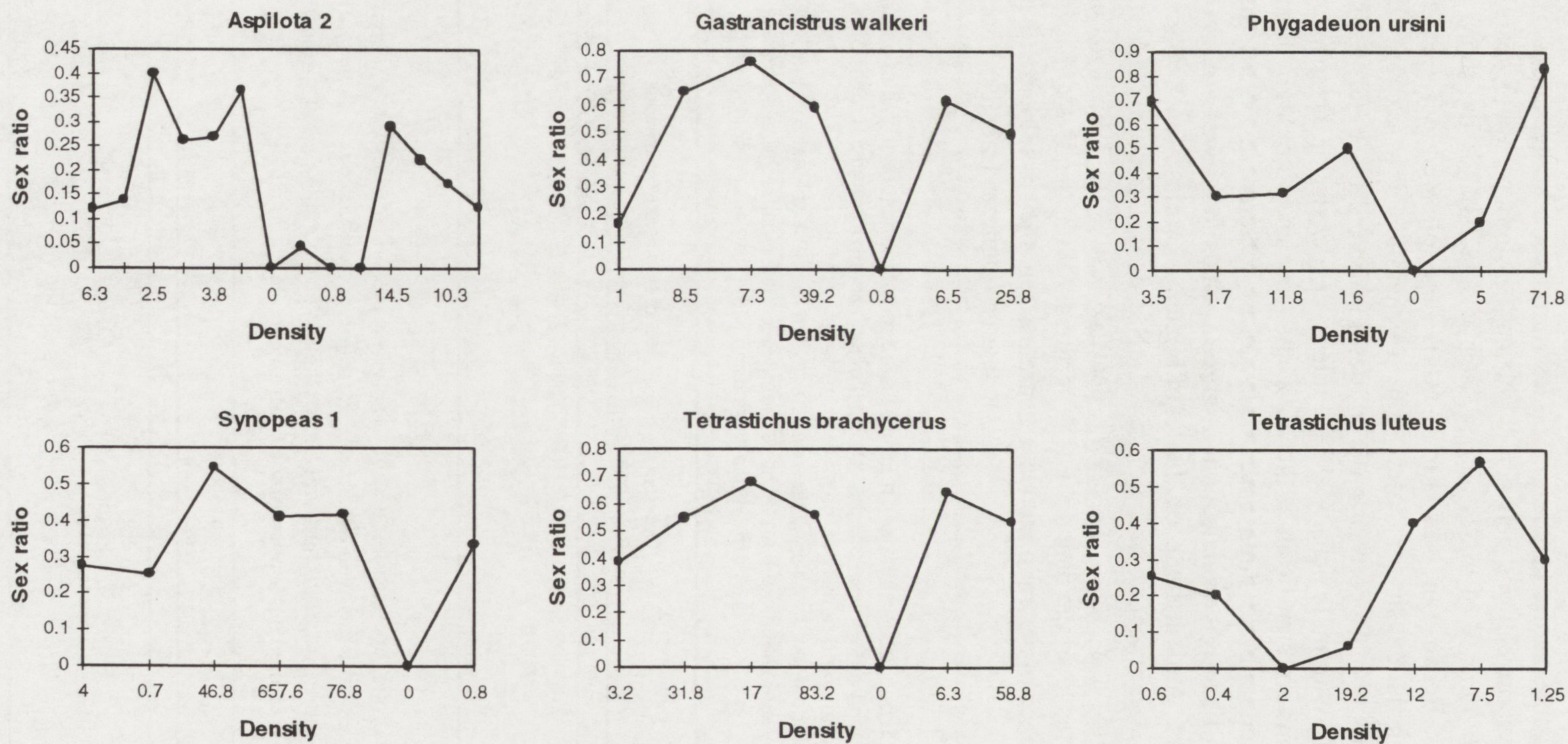| Species	No. of cases	Sex ratio versus No. of emerging wasps		Sex ratio versus No. of No. of hosts present		Sex ratio versus parasitism rate	
		r	p	r	p	r	p
Kleidotoma psiloides	45	0.37	0.01	0.29	0.05	0.02	n.s.
Orthostigma 1	37	-0.16	n.s.	-0.26	n.s.	0.03	n.s.
Aspilota 2	44	0.19	n.s.	0	n.s.	0.18	n.s.
Aspilota 3	37	0.4	0.01	0.27	n.s.	0.13	n.s.
Aspilota 5	17	0.66	0.001	0.09	n.s.	0.49	0.05

Fig. 2. Sex ratios of the six most abundant parasitoid species of the Göttingen forest during the study period 1981 to 1987. Instead of the years the annual densities in that year are given

Sphaeroceridae). The results concerning the sex ratio of the dominant parasitoids which emerged are shown in Table 4 (a detailed description of the experiments and the results are given in U l r i c h 1998b). It appears that the number of parasitoids bred has a significant effect on sex ratio. The ratios of three out of five species correlate significantly and positively with the number of wasps and only *Orthostigma* spec. shows a slight (and not significant) negative dependence. The parasitism rate, on the other hand, had only a minor impact. Surprisingly, no correlation occurred between host density and sex ratio. It seems that not the number of hosts present but only the number of eggs laid effected sex ratio.

3.3. SEX RATIO AND DENSITY FLUCTUATIONS

At first sight no dependence between the sex ratio of the parasitoid species and the degree of density fluctuation occurs (Fig. 3). But a closer look at the data reveals that the species of the different parasitoid guilds differ in their relationship between sex ratio and degree of density fluctuation (Table 5). In the parasitoids of mycetophagous Diptera and of ectophytophages there is a negative correlation between these two parameters, the higher the density fluctuation of the species the lower is the percentage of males ($r = -0.96$ and -0.50). The parasitoids of gall-makers show the opposite trend ($r = 0.59$). In total 6 out of 8 correlation are negative, an indication that the more stable K-selected species may tend to have higher mean sex ratios.
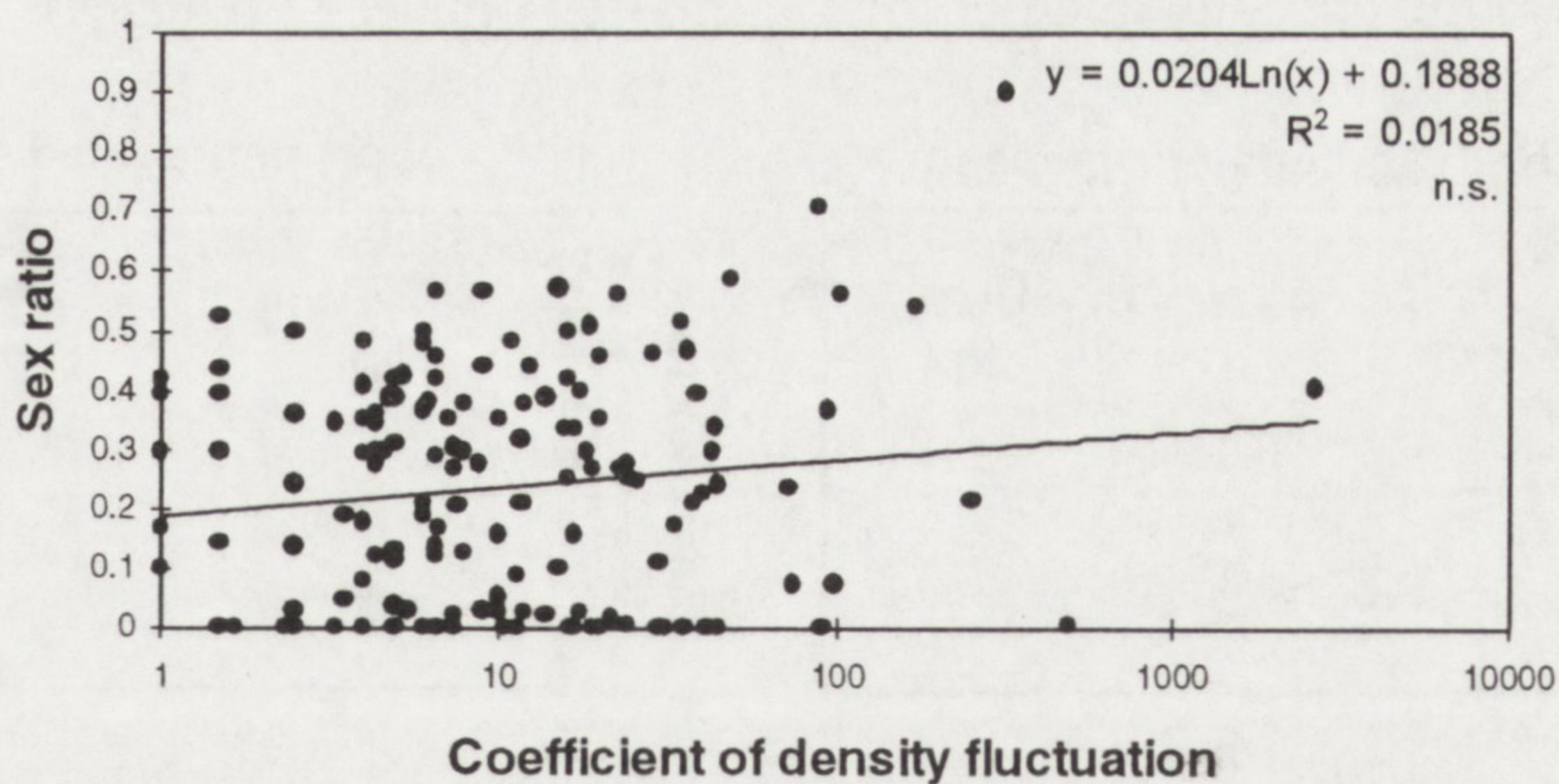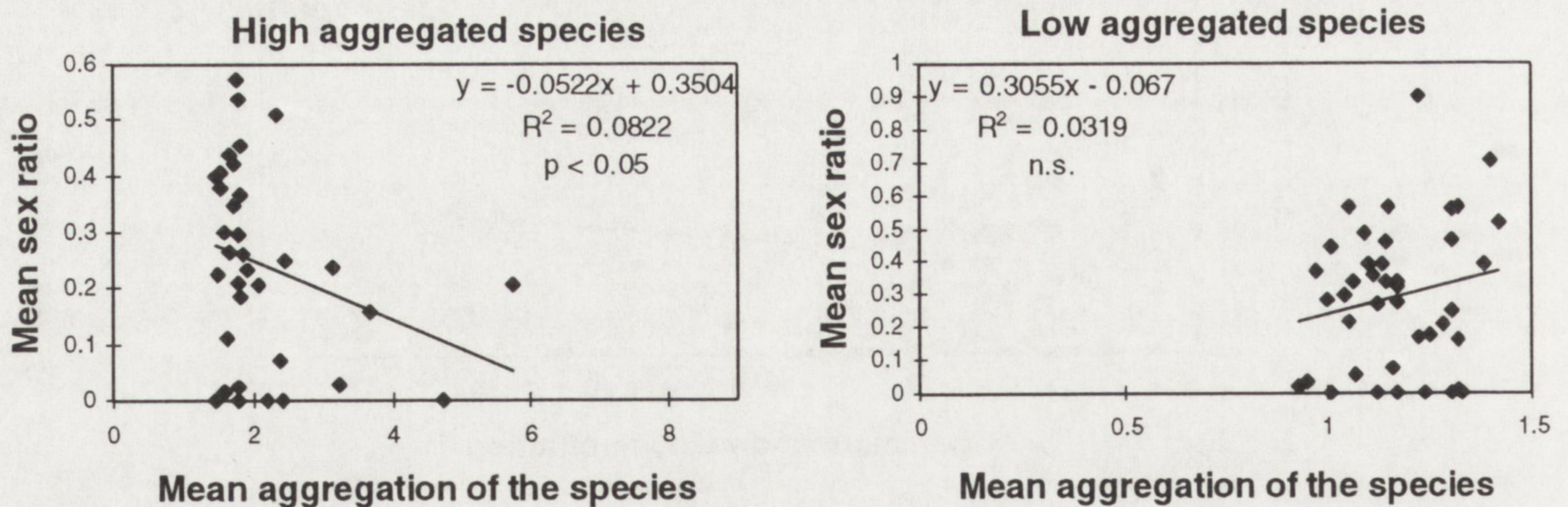

Fig. 3. Dependence of the mean sex ratio of the parasitoid species of the Göttingen forest on their degree of density fluctuation (maximal density / minimal density)

Table 5. Relationship between the sexual index and the density fluctuations of the species of the most important parasitoid guilds in the Göttingen forest

Guild	No. of species	Coefficient of correlation	p (t)
Parasitoids of gall-makers	26	0.09	n.s.
Parasitoids of miners	16	0.59	0.01
Parasitoids of sap-suckers	14	-0.25	n.s.
Parasitoids of ectophytophages	17	-0.50	0.05
Parasitoids of mycetophages	9	-0.96	0.001
Parasitoids of saprophages	20	-0.36	n.s.
Egg-parasitoids	13	-0.19	n.s.
Parasitoids of predators	16	0.24	n.s.

3.3. SEX RATIO AND AGGREGATION

According to the theory of "local mate competition" (H a m i l t o n 1967) parasitoid species should reduce the number of males if they are highly aggregated. Fig. 4 shows that there is in fact a lowered sex ratio in species which are very patchily distributed. But this trend is apparent only at very high degrees of aggregation. At Lloyd-index values below 2.5 all possible sex ratios occur. There is no negative correlation between the percentage of males and the aggregation. But higher aggregated species (11 species with index values above 2.0) reduce the number of males below 25% and two of the three species with values of the Lloyd-index above 4 (*Copidosoma* spec. and *Cleruchus* spec.) produce 7% males at most.

In the case of the lower aggregated species (Fig. 4) the opposite trend occurs.

Regularly or randomly dispersed species in general have lower sex ratios than slightly aggregated species. The highest sex ratios occur in species with values of the Lloyd index between 1.2 and 2.

Crown living species mostly reach the ground with the autumn leaf fall, hibernate in the soil or the leaf litter and emerge the next year. The result is a spreading out of the distribution which can be seen in the low values (mostly below 1.5) of the Lloyd-index of that species (Appendix). Therefore, in the parasitoid species which attack hosts in the crown layer sex ratio does not depend on the degree of aggregation. However, in the only species with an index value above 2 (*Dendrocerus carpenteri*, a hyperparasitoid of aphids) I found only 2% males (1 male, 42 females).

Fig. 4. Dependence of the mean sex ratio of the parasitoid species of the Göttingen forest on their mean degree of aggregation (Lloyd-index). Mean values 1981 to 1987

3.4. DEPENDENCE OF THE SEX RATIO ON STRATUM, MODE OF HIBERNATION AND PARASITOID TYPE

The stratum of the host, the mode of hibernation of the wasps, or the parasitoid type (koino- or idiobiontic) may also influence sex ratio. Koinobiontic species are parasitoids which do not kill their host immediately but allow them a further development. Idiobionts, on the other hand,

do not let their host reach the next developmental stage (H a e s e l b a r t h 1979). Most, but not all larval parasitoids are koinobiontic, nearly all pupal and eggparasitoids are idiobiontic. This differentiation is more adequate for parasitoids than the older differentiation between

ento- and ectoparasitoids (A s k e w and S h a w 1986).

Koinobiontic and idiobiontic species had (on average) the same sex ratios (27.4% and 24%). Koinobiontic species (mostly larval parasitoids of saprophagous Diptera, gall-makers and miners) had significantly higher sex ratios if their host lives in the herb or crown layer than in the soil or leaf litter (31% versus 21%) (Table 6). They also produced more males if they are univoltine (32% versus 22%) and hibernate as larvae or pupae (30% versus 17%).

In the first two cases the idiobiontic species did not show such trends. The sex ratios were very similar in these categories (mean values between 20% and 28% males). But, like the koinobiontic species, there were more males if the species hiber-

Table 6. Sex ratios and their dependence on stratum, mode of hibernation and parasitoid type (idio- or koinobiont). Comparison of mean sex ratios using the U-test of Wilcoxon, Whitney and Mann. Included in the computation are all species of which more than 10 specimens were found

	Factor	No. of species	Mean sex ratio	Variable	z (U)	p
Koinobionts	leaf litter / soil	25	0.21			
	canopy / herb layer	52	0.31	Stratum	-2.46	0.01
	univoltine	44	0.32			
	polyvoltine	37	0.22	Voltinism	-2.89	0.004
	larvae / pupae	55	0.30			
	imago	10	0.17	Mode of Hibernation	-2.15	0.03
Idiobionts	leaf litter / soil	16	0.20			
	canopy / herb layer	28	0.28	Stratum	-1.31	0.19
	univoltine	17	0.28			
	polyvoltine	36	0.22	Voltinism	-0.93	0.35
	larvae / pupae	22	0.33			
	imago	12	0.16	Mode of Hibernation	2.2	0.03

Table 7. Multiple analysis of variance to dectect the dependence of voltinism, stratum of the hosts, and mode of hibernation on the sex ratio of the parasitic wasps in the Göttingen forest

Idiobiontic species	Factors	SS	F (1;25)	p
	Stratum	0.001	0.21	0.89
	Voltinism	0.187	5.78	0.02
	Mode of hibernation	0.115	3.55	0.07
	Stratum + Voltinism	0.147	4.52	0.04
	Stratum + Hibernation	0.002	0.05	0.83
	Voltinism + Hibernation	0.001	0.16	0.90
Koinobiontic species	Factors	SS	F (1;58)	p
	Stratum	0.006	0.28	0.56
	Voltinism	0.031	15.26	0.0002
	Mode of hibernation	0.001	0.27	0.60
	Stratum + Voltinism	0.200	9.90	0.003
	Stratum + Hibernation	0.000	-	-
	Voltinism + Hibernation	0.360	1.76	0.19

nates as larvae or pupae (33% versus 16%).

The three factors, the mode of hibernation, stratum and voltinism, are not independent of one another. To detect a possible interaction, an analysis of variance was performed (Table 7). Again voltinism turned out to be the dominant factor: Univoltine species had higher sex ratios on average than polyvoltine species. This trend holds for both types of parasitoids. Stratum of the host and mode of hibernation were of minor significance. In the idiobiontic species there was a minor combined effect of stratum and voltinism detectable. Polyvoltine species with hosts in the soil had markedly lower sex ratios than univoltine species of the herb or crown layer.

3.5. SEX RATIO AND GENERATION

Some parasitoid species of the Göttingen forest showed marked differences in the sex ratio between the generations (Table 8). In 14 out of 22 cases the first generation had a lower ratio than the second one, the reverse occurred in 7 species. 5 out of 7 parasitoids of saprophages had a lower sex ratio in the first generation.

These results coincide with those of D e l u c c h i (1958), A s k e w and R u s e (1974) and G o d f r a y and S h a w (1987). The latter authors discussed two hypotheses to explain the phenomenon:

1. a pronounced egg deposition of the females before mating

2. a high degree of intersexual food competition.

An egg deposition of females before mating is reported for many species (cf. K i n g 1987) and the better climatic conditions in the summer months may favor this behavior. But convincing data in support of this hypothesis are lacking. A high degree of intersexual competition should favor the production of males because they normally live shorter and need no food to produce eggs. But it is unclear why there should be differences between the generations and data on the degree of competition are lacking. Therefore, this hypothesis is not more than an ad hoc assumption.

A better explanation may be that there are differences in the abundance or in the degree of clumping between the generations. As shown above high densities or low aggregations may lead to a higher production of males. Because the data of Table 8 rely on all samplings of 7 study years, it is not possible to compare aggregation and density of the generations. But in some years some of the species had densities high enough for such a comparison. The results are shown in Table 9. In *Charitopes gastricus*, *Aspilota* spec. and *Cleruchus* spec. the sex ratio changes corresponded with the changes in abundance. The higher abundance the higher the percentage of males. *Chrysocharis prodice* and *Anagrus atomus* do not show a definite trend, but it should be mentioned that the density differences between the generations of both species are quite small. But no influence of the degree of clumping is detectable. If density differences between the generations are responsible for sex ratio differences, then the usually higher abundances of the species in the summer generation may account for the trend indicated in Table 8.

Table 8. Sex ratios of the 1. and the 2. generation of important parasitoid species
in the Göttingen forest. Mean values of all individuals sampled 1981 to 1987

Species	Parasitoids of	1. Generation		2. Generation		1. Generation / 2. Generation
		N	sex ratio	N	sex ratio	
Aclastus micator	eggs	31	0.32	96	0.14	>
Alaptus 1	eggs	199	0.27	27	0.11	>
Anagrus atomus	eggs	64	0.28	195	0.3	<
Anaphes dorcas	eggs	130	0.22	129	0.24	<
Anaphes longicornis	eggs	69	0.28	64	0.34	<
Cleruchus 1	eggs	542	0.09	174	0.01	>
Tetrastichus ?charoba	gall-makers	108	0.52	119	0.56	<
Acoelius erythronotus	miners	114	0.32	70	0.44	<
Chrysocharis prodice	miners	246	0.22	226	0.33	<
Derostenus gemmeus	miners	37	0.43	47	0.32	>
Aspilota 2, breeding	saprophages	276	0.25	45	0.34	<
Aspilota 3, breeding	saprophages	284	0.35	77	0.41	<
Aspilota 5	saprophages	157	0.22	132	0.28	<
Basalys abrupta	saprophages	88	0.28	14	0.36	<
Basalys pedisequa	saprophages	25	0.04	478	0.07	<
Entomacis perplexa	saprophages	51	0.16	45	0.16	=
Kleidotoma psiloides	saprophages	41	0.12	44	0.2	>
Anacharis eucharioides	predators	70	0.27	106	0.34	<
Charitopes gastricus	predators	172	0.25	218	0.28	<
Aphelopus melaleucus	sap-suckers	364	0.27	49	0.33	<
Ephedrus lacertosus	sap-suckers	23	0.43	306	0.36	>
Rhyssalus clavator	?	40	0.5	23	0.3	>

Table 9. Comparison between sex ratio, density and aggregation of important parasitoid species in the Göttingen forest. Only that species are included of which in both generations more than 10 individuals were colleced. Data from the same sampling year

Species	Parasitoids of		1. Generation				2. Generation			
		Year	N	Sex ratio	Density (ind./m^2)	Lloyd-index	N	Sex ratio	Density (ind./m^2)	Lloyd-index
Charitopes gastricus	Predators	1986	13	0.23	3	0.93	64	0.27	16	0.99
Aspilota 2	Saprophages	1986	58	0.29	15	1.4	49	0.22	12	1.01
		1987	41	0.17	10	1.09	32	0.13	8	1.83
Chrysocharis prodice	Miners	1981	90	0.14	4	0.89	46	0.35	2	0.63
		1982	23	0.22	2	0.95	37	0.35	3	1.11
		1986	35	0.29	3	1.1	58	0.29	5	0.99
Anagrus atomus	Egg-parasitoids	1982	22	0.45	4	0.77	42	0.19	7	1.6
Cleruchus 1	Egg-parasitoids	1982	101	0.12	17	1.43	43	0.02	7	2.99
		1986	113	0.17	28	1.68	85	0	21	1.46

4. SUMMARY

The sex ratio of the parasitic Hymenoptera of a beech forest on limestone near Göttingen (FRG) was studied using ground--photo-eclectors.

Judged from the mean sex ratios the parasitoids could be separated into 4 groups (Table 2). Parasitoids of miners and gall-makers had the highest sex ratios (30 to 40% males) and less than 5% of the species were thelytokous. The species which attack soil-living sapro- or mycetophagous Diptera as well as the parasitoids of ectophytophages had (on average) 20 to 30% males and only 1.5 % of them were thelytokous. Parasitoids of sap-suckers and egg-parasitoids had mostly sex ratios below 20% males and 29% of them were thelytokous. The lowest sex ratios (below 10% males) and the highest number of thelytokous species (30%) were found among hyperparasitoids and parasitoids of soil-living Staphylinidae.

No clear trend was detectable between sex ratio and density of the species (females and males tested) (Table 3, 4; Fig. 1, 2). In some species a male biased sex ratio was produced at higher densities (as predicted by LMC-theory); some species showed the opposite trend, but in most species the null-hypothesis of density independence could not be rejected. The density fluctuations of the species also influenced the sex ratio (Table 5, Fig. 5). This impact appeared to be guild specific: Soil-living species tended to lower sex ratio with higher density fluctuations, parasitoids of miners and gall-makers tended to increase their sex ratio. The data are consistent with the hypothesis that K-selected parasitoid species have higher sex ratios on average.

Koinobiontic species (mostly parasitoids of gall-makers and miners) had (on average) significantly higher sex ratios if their host lives in the herb or crown layer (32% versus 21%) (Table 6). They also produced more males if they are univoltine (32% versus 22%) and hibernate as larvae or pupae (30% versus 17%). After a MANOVA-analysis (Table 7) the voltinism turned out to be the main influencing factor.

As predicted by the theory of "local mate competition", species with a high degree of clumping tended to decrease their sex ratio (Table 9; Fig. 4). All species with mean values of the Lloyd index above 2.0 produced at most 25% males.

Many bivoltine species showed differences in sex ratio between the spring and the summer generations (Table 8). There was a trend towards higher percentages of males in the summer generation.

5. REFERENCES

Askew R.R., Ruse J.M. 1974 – Biology and taxonomy of species of the genus *Enaysma* DELUCCHI (Hymenoptera, Eulophidae, Entedontinae), with special reference to the British fauna – Trans. R. Ent. Soc. Lond. 125: 257–294.

Askew R.R., Shaw M.R. 1986 – Parasitoid communities: their size, structure and development – In J.K. Waage, Greathead D.J. (Ed.): Insect Parasitoids – 13th Symp. R. Entomol. Soc. London. London (Academic Press): 225–264.

Charnov E.L. 1982 – The Theory Of Sex Allocation. Princeton (Univ. Press).

Delucchi V.D. 1958 – *Lithocolletis messaniella* Zeller (Lepidoptera, Gracillariidae). Analysis of some mortality factors with particular reference to its parasit complex – Entomophaga 3: 203–270.

Dierschke H., Song Y. 1982 – Vegetationsgliederung und kleinräumige Horizontalstruktur eines submontanen Kalkbuchenwaldes – In: H. Dierschke (Ed.): Struktur und Dynamik von Wäldern. Berichte der internationalen Symposien der internationalen Vereinigung für Vegetationskunde – Rinteln 1981, 513–539.

Gauthier N., Monge J.P., Huignard J. 1997 – Sex-allocation behavior of a solitary ectoparasitoid: Effects of host-patch characteristics and female density – Entomol. Exper. Appl. 82: 167-174.

Godfray H.C.J., Shaw M.R. 1987 – Seasonal variation in the reproductive strategy of the parasitic wasp *Eulophus larvarum* (Hymenoptera: Chalcidoidea: Eulophidae) – Ecol. Entomol. 12: 251–256.

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.

Hamilton W.D. 1967 – Extraordinary sex ratios – Science 156: 477–488.

Hilpert H. 1989 – Zur Hautflüglerfauna eines südbadischen Eichen-Hainbuchenmischwaldes – Spixiana 12: 57-90.

Jackson D.J. 1958 – Obersations on the biology of *Caraphractus cinctus* Walker (Hymenoptera: Mymaridae), a parasitoid of the eggs of Dytiscidae – Trans. R. Entomol. Soc. Lond. 110: 533–554.

King B.H. (1987) – Offspring sex ratios in parasitoid wasps – Quart. Rev. Biol. 62: 367–396.

King B.H. (1996) – Sex ratio responses to other parasitoid wasps: Multiple adaptive explanations – Behavioral Ecology and Sociobiology 39: 367–374

Mayhew P.J., Godfray H.C.J. 1997 – Mixed sex allocation strategies in a parasitoid wasp – Oecologia 110: 218–221

Sandlan K. (1979) – Sex ratio regulation in *Coccygomimus turionella* LINNAEUS (Hymenoptera: Ichneumonidae) and its ecological implications – Ecol. Entomol. 4: 365–378.

Ode P.J., Antolin M.F., Strand M.R. 1997 – Constrained oviposition and female-biased sex allocation in a parasitic wasp – Oecologia 109: 547-555.

Schaefer M. 1990 – The soil fauna of a beech forest on limestone: trophic structure and energy budget – Oecologia 82: 128–136.

Schaefer M., SchauerMann J. 1990 – The soil fauna of beech forests: comparison between a mull and a moder soil – Pedobiologia 34: 299–314.

Strand M.R. 1988 – Variable sex ratio strategy of *Telenomus heliothidis* (Hymenoptera, Scelionidae) – adaptation to host and conspecific density – Oecologia 77: 219–224.

Strohm E., Linsenmair K.E. 1997 – Low resource availability causes extremely male-biased investment ratios in the European beewolf, *Philanthus triangulum* F. (Hymenoptera, Sphecidae) – Proceedings of the Royal Society of London Series B Biological Sciences 264(1380): 423–429:

Thiede U. 1975 – Untersuchungen über die Arthropodenfauna in Fichtenforsten (Populationsökologie, Energieumsatz)– Thesis Göttingen.

Townes H., Townes M. 1981 – A Revision Of The Serphidae – Mem. Am. Entomol. Inst. 32. Ann Arbor.

Trjapizyn W.A. 1978 – Proctotrupoidea. In Trjapizyn W.A., Alekseev W.N., Dzhanokmen K.A., Zerova M.D., Koslow M.A., Kostjukow W.W., Nikol'skaja M.N., Ponomarenko N.G., Sorokina A.P., Sugonjaev E.S., Jasnosh W.A. 1978: Bethyloidea, Chalcidoidea, Proctotrupoidea, Ceraphronoidea - Opred. Fauna SSSR 120. Leningrad: 516–538.

Ulrich W. 1987 – Wirtsbeziehungen der parasitoiden Hautflügler in einem Kalkbuchenwald – Zool. Jahrb. Syst. 114: 303–342.

Ulrich W. 1988 – Welche Faktoren beeinflussen die Populationen und die Strukturen der Gemeinschaften von bodenlebenden parasitoiden Hymenopteren in einem Buchenwlad – Thesis Göttingen.

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 car-

rion exploiting community composed of necrophagous Diptera and their parasitoids – Pol. J. Ecol. in press

Ulrich W. 1998c – The Hymenoptera of a dry meadow on limestone I: Species composition, abundance and biomass – Pol. J. Ecol. in press

Van Alphen J.J.M., Thunnissen I. 1983 – Host selection and sex allocation by *Pachycrepoideus vindemiae* RONDANI (Pteromalidae) as a facultative hyperparasitoid of *Asobara tabida* NEES (Braconidae: Alysiinae) and *Leptopilina heterotoma* (Cynipoidea: Eucoilidae) – Neth. J. Zool. 33: 497-514.

Waage J.K. 1986 – Family planning in parasitoids: adaptive patterns of progeny and sex allocation – In: Waage J.K, Greathead D.J. (Ed.): Insect Parasitoids – 13th Symp. R. Entomol. Soc. London. London (Academic Press): 63–95.

Waage J.K., NG S.M. 1984 – The reproductive strategy of a parasitic wasp. I. Optimal progeny and sex allocation in *Trichogramma evanescens* – J. Animal Ecol. 53: 401–416.

Weidemann G. (1965) – Ökologische und biometrische Untersuchungen an Proctotrupiden (Hymenoptera: Proctotrupidae s. str.) der Nordseeküste und des Binnenlandes – Z. Morph. Ökol. Tiere 55: 425–514.

Appendix. List of all parasitoid species of the Göttingen forest with more than 20 indviduals caught.
Mean density 1981-1987 (all areas sampled): ind. $m^{-2} a^{-1}$; mean aggregation: Value of Llyod-index
Tree crowns: Tree; herb layer: Herb; tree crowns or herb layer: tree/herb; soil, dead wood: Soil

Species	Stratum	Number of generations per year	Mode of Hibernation	Parasitoid typ	Number of individuals caught	Mean density	Sex ratio	Factor of density-fluctuation	Mean aggregation of the species
Achrysocharoides cilla	Tree	2	Larve	Koinobiont	69	0.49	0.33	44.00	1.17
Aclastus micator	Soil	3	Imago	Idiobiont	166	1.19	0.17	6.00	1.81
Aclastus solutus	Soil	2	?	Idiobiont	24	0.17	0.25	16.00	2.44
Acoelius erythronotus	Tree	2	Larve	Koinobiont	222	1.59	0.33	16.67	1.06
Acropiesta flavipes	Soil	1	Larve	Koinobiont	21	0.15	0.52	1.50	
Acropiesta rufiventris	Soil	1	Larve	Koinobiont	29	0.21	0.48	2.50	
Alaptus GW1	Tree	3	?	Idiobiont	244	1.74	0.24	26.00	1.30
Alloxysta victrix	Tree/Herb	2	?	Koinobiont	53	0.38	0.17	6.67	1.22
Amblyaspis nodicornis	Tree/Herb	2	Larve	Koinobiont	52	0.37	0.35	4.33	
Amitus minervae	Tree/Herb	1	Larve	Koinobiont	22	0.16	0.00	1.67	
Anacharis eucharioides	Tree	2	Larve	Koinobiont	208	1.49	0.32	11.67	1.17
Anacharis immunis	Tree	2	Larve	Koinobiont	49	0.35	0.20	7.67	2.05
Anagrus atomus	Tree	3	?	Idiobiont	269	1.92	0.29	42.80	1.78
Anagrus GW1	Tree/Herb	2	?	Idiobiont	59	0.42	0.10	1.00	
Anagrus GW2	Tree/Herb	3	Larve	Idiobiont	21	0.15	0.43	4.00	
Anaphes dorcas	Herb	2	Imago	Idiobiont	346	2.47	0.21	40.00	1.48
Anaphes longicornis	?	2	?	Idiobiont	141	1.01	0.30	4.60	1.57
Aoplus ochropis	Soil	3	Imago	Idiobiont	39	0.28	0.10	5.00	
Aphanogmus GW3	?	2	?	?	246	1.76	0.21	37.50	1.28
Aphelinus GW1	Tree	2	?	?	39	0.28	0.00	2.33	
Aphelopus holomelas	Tree	2	Larve	Koinobiont	75	0.54	0.44	12.50	1.01
Aphelopus melaleucus	Tree	2	Larve	Koinobiont	521	3.72	0.26	19.00	1.12
Aphelopus serratus	Tree	1	Larve	Koinobiont	179	1.28	0.38	4.80	1.38
Aspilota GW"2"	Soil	3	Larve	Koinobiont	1131	8.08	0.18	33.50	1.25
Aspilota GW11	Soil	2	Larve	Koinobiont	23	0.16	0.04	12.00	3.22
Aspilota GW20	Soil	2	Larve	Koinobiont	108	0.77	0.21	11.67	5.74
Aspilota GW21	Soil	2	Larve	Koinobiont	45	0.32	0.16	6.50	
Aspilota GW23	Soil	2	Larve	Koinobiont	547	3.91	0.01	24.33	1.32
Aspilota GW27	Soil	2	Larve	Koinobiont	40	0.29	0.05		
Aspilota GW3	Soil	2	Larve	Koinobiont	61	0.44	0.30	4.33	
Aspilota GW5	Soil	2	Larve	Koinobiont	312	2.23	0.25	45.00	3.14
Atractodes GW1	Soil	1	Larve	Koinobiont	58	0.41	0.31	5.00	
Basalys abrupta	Soil	2	Imago	Idiobiont	169	1.21	0.22	7.50	
Basalys parva	Soil	3	Larve	Idiobiont	22	0.16	0.14	2.50	
Basalys pedisequa	Soil	3	Larve	Idiobiont	523	3.74	0.07	75.20	1.16
Bathytrix pellucidator	Tree	1	Larve	Idiobiont	33	0.24	0.45	6.50	
Blacus GW1	?	2	?	Koinobiont	28	0.20	0.07		
Blacus GW2	?	2	?	Koinobiont	30	0.21	0.00	4.00	
Bothriothorax intermedia	Tree/Herb	1	Larve	Koinobiont	22	0.16	0.09	11.50	
Ceranisus pacuvius	Herb	1	?	Koinobiont	86	0.61	0.35	20.00	1.72
Charitopes clausus	Tree/Herb	1	Larve	Idiobiont	43	0.31	0.12	4.00	
Charitopes gastricus	Tree/Herb	2	Larve	Idiobiont	444	3.17	0.27	24.38	1.00
Charmon extensor	Tree	2	?	Koinobiont	25	0.18	0.36	2.50	
Chorebus phaedra	Herb	1	Larve	Koinobiont	29	0.21	0.34	3.33	
Chrysocharis ?laomedon	Tree	2	Larve	Idiobiont	69	0.49	0.51	18.67	2.30
Chrysocharis prodice	Tree	2	Larve	Koinobiont	622	4.44	0.28	8.80	1.17
Cirrospilus diallus	Tree	2	Larve	Idiobiont	55	0.39	0.49	6.00	
Cirrospilus vittatus	Tree	2	Larve	Idiobiont	100	0.71	0.51	34.67	1.42

Cleruchus GW1	?	2	Imago	Idiobiont	721	5.15	0.07	99.00	2.38
Colastes braconius	Tree	2	Larve	Idiobiont	24	0.17	0.42	1.50	
Conostigmus GW4	?	2	?	?	155	1.11	0.23	72.00	1.89
Copidosoma GW2	Tree/Herb	1	Larve	Koinobiont	303	2.16	0.00	90.00	4.73
Cratichneumon culex	Soil	2	?	Idiobiont	25	0.18	0.00	2.50	
Cratichneumon fabricator	Soil	2	Imago	Idiobiont	31	0.22	0.03	5.00	
Cratichneumon rufifrons	Soil	1	?	Idiobiont	85	0.61	0.00	6.67	0.99
Dendrocerus carpenteri	Tree	1	Larve	Idiobiont	44	0.31	0.02	10.00	1.77
Derostenus gemmeus	Tree	2	Larve	Koinobiont	91	0.65	0.36	4.33	
Diaeretellus ephippium	Tree/Herb	2	?	Idiobiont	59	0.42	0.00	20.00	1.44
Diaeretiella rapae	Tree/Herb	1	?	Idiobiont	65	0.46	0.02	21.50	1.59
Dibrachys cavus	?	2	?	Idiobiont	26	0.19	0.00	6.50	
Diplazontinae GW3	Tree/Herb	1	?	Koinobiont	40	0.29	0.40	17.50	1.45
Disogmus areolator	?	1	?	Koinobiont	37	0.26	0.30	1.00	
Encarsia GW1	Tree	1	Larve	?	39	0.28	0.00	6.50	
Entedon GW1	?	1	Larve	?	123	0.88	0.33	15.67	1.14
Entomacis perplexa	Soil	3	Imago	Idiobiont	107	0.76	0.15	16.67	1.32
Ephedrus lacertosus	Tree/Herb	2	?	Idiobiont	329	2.35	0.37	94.00	1.80
Eretmocerus mundus	Tree	1	Larve	?	4359	31.14	0.003	492.50	1.24
Ethelurgus sodalis	?	2	?	Idiobiont	51	0.36	0.02	14.00	0.93
Eulophus larvarum	Tree	2	Larve	Idiobiont	154	1.10	0.35	6.00	0.97
Eumacepolus grahami	Tree	1	Larve	Koinobiont	178	1.27	0.47	36.50	1.30
Eustochus atripennis	Soil	2	?	Idiobiont	613	4.38	0.00	45.00	2.19
Exallonyx ater	Soil	2	Imago	Koinobiont	93	0.66	0.03	5.40	0.95
Exallonyx microcerus	Soil	2	Imago	Koinobiont	40	0.29	0.03	9.00	
Exallonyx quadriceps	Soil	2	Imago	Koinobiont	230	1.64	0.00	16.67	1.01
Exallonyx subserratus	Soil	2	Imago	Koinobiont	133	0.95	0.09	4.33	
Exallonyx trichomus	Soil	2	Imago	Koinobiont	109	0.78	0.04	10.00	1.07
Gastrancistrus autumnalis	Tree/Herb	1	Larve	Koinobiont	114	0.81	0.44	9.00	1.64
Gastrancistrus GW1	Tree/Herb	1	Larve	Koinobiont	30	0.21	0.57	9.00	1.05
Gastrancistrus GW6	Tree/Herb	1	Larve	Koinobiont	65	0.46	0.49	22.50	1.32
Gastrancistrus walkeri	Tree	1	Larve	Koinobiont	1129	8.06	0.58	49.00	1.42
Glauraspidia microptera	Soil	1	Imago	Koinobiont	498	3.56	0.56	6.63	1.15
Glypta GW1	Tree	1	?	Koinobiont	20	0.14	0.05	8.00	
Gnaptodon pumilio	Tree	2	Larve	Koinobiont	69	0.49	0.38	14.00	1.10
Ismarus dorsiger	Tree	1	Larve	?	134	0.96	0.00	30.00	1.30
Kleidotoma psiloides	Soil	2	Imago	Koinobiont	115	0.82	0.15	10.00	3.67
Lagynodes pallidus	Soil	3	Imago	?	229	1.64	0.41	28.80	1.14
Leiophron basalis	Tree	1	Larve	Koinobiont	21	0.15	0.29	8.00	
Leiophron fascipennis	Tree/Herb	1	?	Koinobiont	28	0.20	0.14	1.50	
Litus cynipseus	Soil	2	Imago	Idiobiont	1679	11.99	0.00	31.20	2.40
Megastylus cruentator	Soil	3	Imago	Koinobiont	53	0.38	0.02	7.50	
Melanips opacus	?	1	?	Koinobiont	37	0.26	0.35	7.20	
Mesopolobus GW1	?	2	?	Idiobiont	388	2.77	0.90	320.00	1.22
Microctonus GW1	?	2	?	Koinobiont	58	0.41	0.38	8.00	1.50
Microterys GW1	Tree	1	?	Idiobiont	23	0.16	0.04		
Olesicampe GW1	Tree/Herb	1	Larve	Koinobiont	20	0.14	0.30	1.50	
Omphale aetius	Tree/Herb	1	Larve	Koinobiont	115	0.82	0.00	42.00	1.17
Omphale GW1	Tree	1	Larve	Koinobiont	85	0.61	0.26	24.00	1.82
Omphale GW2	Tree	1	Larve	Koinobiont	463	3.31	0.22	252.00	1.05
Omphale versicolor	Tree	1	Larve	Koinobiont	52	0.37	0.27	7.50	
Pantoclis similis	Soil	2	?	Koinobiont	30	0.21	0.13	6.50	
Pantolyta GW5	Soil	2	?	Koinobiont	29	0.21	0.69		
Pediobius alcaeus	Tree	2	Larve	Koinobiont	84	0.60	0.30	18.33	1.04
Pentapleura GW1	Soil	2	Larve	Koinobiont	25	0.18	0.24	2.50	
Peristenus GW1	Tree	1	Larve	Koinobiont	104	0.74	0.49	16.00	
Peristenus GW2	Tree	1	Larve	Koinobiont	121	0.86	0.40	16.00	1.71

Phaedroctonus transfuga	Tree/Herb	2	Larve	Koinobiont	64	0.46	0.34	6.00	
Phaneroserphus calcar	Soil	2	Imago	Koinobiont	34	0.24	0.24	4.33	
Phobocampe GW1	Tree/Herb	1	Larve	Koinobiont	34	0.24	0.38	1.00	
Phygadeuon GW3	?	2	?	Idiobiont	40	0.29	0.03	17.50	
Phygadeuon GW4	?	2	?	Idiobiont	30	0.21	0.10	15.00	
Phygadeuon ursini	Soil	1	Larve	Idiobiont	797	5.69	0.71	89.75	1.40
Picrostigeus GW1	Soil	2	?	Koinobiont	105	0.75	0.00		
Piestopleura flavimanus	Tree/Herb	1	Larve	Koinobiont	36	0.26	0.56	15.00	1.73
Pimpla GW1	Soil	2	?	Idiobiont	35	0.25	0.06	4.00	
Platygaster GW1	Tree/Herb	1	Larve	Koinobiont	126	0.90	0.34	4.00	
Platygaster GW2	Tree	1	Larve	Koinobiont	404	2.89	0.26	23.13	1.64
Platygaster GW8	Tree/Herb	1	Larve	Koinobiont	24	0.17	0.21	12.00	1.76
Polynema fumipenne	Tree/Herb	1	Larve	Idiobiont	26	0.19	0.04		
Praon GW"1"	Herb	?	?	Koinobiont	41	0.29	0.27	6.50	
Pteromalus GW1	?	2	Imago	Idiobiont	22	0.16	0.18	6.00	
Pygostolus sticticus	Tree	1	Larve	Koinobiont	24	0.17	0.42	1.00	
Rhyssalus clavator	Tree	2	?	Idiobiont	85	0.61	0.48	4.00	
Seladerma GW1	Tree	1	?	Koinobiont	20	0.14	0.40	5.00	
Spaniopus amoenus	Tree/Herb	2	?	?	24	0.17	0.21	4.00	
Stilpnus GW1	Soil	1	Larve	Koinobiont	85	0.61	0.42	5.33	
Sympiesis sericeicornis	Tree	1	Larve	Idiobiont	33	0.24	0.45	20.00	1.80
Synopeas GW1	Tree	1	Larve	Koinobiont	4174	29.81	0.40	2630.40	1.52
Synopeas GW2	Tree/Herb	1	Larve	Koinobiont	42	0.30	0.19	3.50	
Synopeas GW3	Tree/Herb	1	Larve	Koinobiont	22	0.16	0.05	3.50	
Synopeas GW5	Tree/Herb	1	Larve	Koinobiont	30	0.21	0.03	2.50	
Tates heterocera	Herb	1	Larve	Koinobiont	51	0.36	0.35	10.00	1.11
Telenomus GW1	Tree	2	Imago	Idiobiont	304	2.17	0.00	1.50	
Tetrastichus ?charoba	Tree/Herb	2	Larve	Idiobiont	233	1.66	0.54	171.00	1.76
Tetrastichus brachycerus	Tree	1	Larve	Idiobiont	2648	18.91	0.56	104.00	1.30
Tetrastichus fageti	Tree	1	Larve	Idiobiont	440	3.14	0.00	10.40	1.33
Tetrastichus GW1	?	1	?	Idiobiont	213	1.52	0.00	41.50	1.12
Tetrastichus luteus	Tree	1	Larve	Idiobiont	392	2.80	0.39	38.40	1.13
Torymus fulgens	Soil	1	Larve	Idiobiont	31	0.22	0.42	6.50	
Torymus persicariae	Tree	1	Larve	Idiobiont	37	0.26	0.38	12.00	
Trichacis pisis	Tree/Herb	1	Larve	Koinobiont	23	0.16	0.39	1.50	
Trichionotus flexorium	Tree	1	Imago	Koinobiont	20	0.14	0.35	5.00	
Trichogramma embryophagu	Tree	2	Larve	Idiobiont	162	1.16	0.00	35.67	1.76
Trichopria aequata	Soil	1	Imago	Idiobiont	232	1.66	0.31	11.00	1.09
Trichopria evanescens	Soil	1	Imago	Idiobiont	103	0.74	0.11	30.00	1.62
Trichopria GW2	Soil	2	?	Idiobiont	30	0.21	0.17	1.00	
Trioxys bicuspis	Herb	1	Larve	Idiobiont	79	0.56	0.38	6.33	
Trybliographa melanoptera	Herb	1	?	Koinobiont	23	0.16	0.00	2.50	
Zygota ruficornis	Soil	2	?	Koinobiont	30	0.21	0.10	5.00	