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## NICHE SEGREGATION AND COEXISTENCE OF PARASITIC HYMENOPTERA OF THE *ASPILOTA* GENUS GROUP (HYMENOPTERA, BRACONIDAE) IN A BEECH FOREST ON LIMESTONE

**ABSTRACT:** In a beech forest on limestone (Northern Germany) community structure and coexistence of a community of phorid (Diptera) parasitoids (*Aspilota* and *Orthostigma* spp., Hymenoptera, Braconidae) was studied. A classical niche analysis including character displacement, temporal and spatial segregation and density fluctuations could not clearly separate the species. In a case where such a separation by morphological factors was possible, hosts and spatial distribution of this species were the same as in morphologically different species. As predicted from aggregation theory of coexistence all species were highly aggregated but aggregation and density appeared not to be correlated. In line with the core-satellite hypothesis bimodal species rank order distributions (temporal and in relation to density) with a high number of rare species were found and patch density was correlated with number of patches occupied. Relative abundance distributions were fitted by Zipf-Mandelbrot but not by log-normal or log-series models.

**KEY WORDS:** Hymenoptera, Braconidae, *Aspilota*, coexistence, niche, core-satellite, aggregation, beech forest, Zipf-Mandelbrot

### 1. INTRODUCTION

The question what factors allow species of similar habitat and diet requirements to coexist has inspired ecologists from the beginning (Shelford 1913, Grinnell 1917). From

Hutchinson (1957, 1959) on there had been a rich literature on niche theory and niche overlap (reviewed in Colwell 1992 and Griesemer 1992). With the notion that species inhabiting a patchy or unpredictable environment may have undistinguishable niches the focus of interest changed to other models. Among these especially the aggregation model of coexistence (Gurney and Nisbet 1978, Shorrocks *et al.* 1979, Atkinson and Shorrocks 1981, 1984, Shorrocks *et al.* 1984, Shorrocks and Rosewell 1987, Comins and Hassel 1987) and the core-satellite hypothesis of Hanski (1982) have gathered much interest (Gotelli and Simberloff 1987, Maurer 1990, Nee *et al.* 1991, Sevenster 1996, Sevenster and Van Alphen 1996, Lee *et al.* 1998). Recently, the interest in niche theory renewed (Leibold 1995, 1998, Li Zizhen and Lin Hong 1997, Wisheu 1998, Austin 1999) mainly due to a redefinition of the classical niche concepts in terms of environmental impacts and requirements and due to the need of more general niche concepts in plant ecology.

All of the theories make explicit predictions on patterns of species abundance and morphology. In modern niche theory species

may coexist if there is a trade off in the requirements of the species and if there are different effects on the factor that most limits its growth (Leibold 1995). This means that species may coexist not only if they are sufficiently separated by classical niche dimensions (morphological, temporal, resources or habitats) but also in functional ones like dispersal ability, aggregation, growth rate or density fluctuations. Any analysis of niche segregation has therefore to embrace classical and functional niche dimensions.

The aggregation model and the core-satellite hypothesis especially refer to patchy and unpredictable environments. The first model predicts local coexistence of species with similar resource requirements if they are aggregated, if associations in distribution (spatial or temporal) are minimal, if superior competitors are more aggregated than inferior ones, and if inferior competitors have a higher reproduction rate. It also predicts local guild size to be rather independent of the regional species pool (Sevenster 1996). The core-satellite hypothesis predicts a bimodal relative abundance distribution with a high number of rare species. Local extinction probability and regional distribution correlate negatively and there should be a substantial species turnover through time. Additionally, Gotelli and Simberloff (1987) and Maurer (1990) inferred a positive relation between number of patches occupied and the mean density per patch (equivalent to the well known relation between local and regional abundance) and higher density variances of rare species.

Species of the closely related braconid genera *Aspilota* s. l. and *Orthostigma* (Wharton 1985, Fischer 1995, 1997) are very abundant in temperate European forests (Ulrich 1988, 1998). Although existing keys deal only with a limited number of species (Fischer 1971, 1972, 1976) there are probably several hundred species in Europe (Tobias 1986). *Aspilota* is in a process of rapid speciation and the intraspecific variability often makes the separation of species (even in

breeds) difficult and identification with published keys nearly impossible (Ulrich unpubl.). As far as known, all of the species are koinobiontic, internal larval parasitoids of phorid flies (Fischer 1976, Ulrich 1988) and existing breeding records indicate that most species are rather polyphagous and more confined to microhabitat than to certain hosts.

The present study deals with the *Aspilota*- and *Orthostigma*-community of a beech forest on limestone (Ulrich 1988, 1998). During an eight year study period 23 *Aspilota* and 2 *Orthostigma* species were found using ground-photo-electors (Ulrich 1998). 6 *Aspilota* spp. (*Aspilota* GW1, GW2, GW3, GW5, GW6, GW8) and *Orthostigma* GW1 were bred as polyphagous parasitoids of carrion exploiting Phoridae (*Megaselia ruficornis*, *M. angusta*, *M. ?pulicaria*, *Gymnophora arcuata*) out of dead snails (Ulrich 1999a).

The high number of species raises the question what allows these species to coexist. The group is a good candidate for a comparison between models of niche segregation and models which rely on patchiness and unpredictability. The present study tries to undertake such a comparison and will test some of the predictions from the above mentioned three models of coexistence.

## 2. MATERIALS AND METHODS

The studies were undertaken 1980 to 1987 on a chalk plateau in a mixed beech forest (Melico-Fagetum subassociation *Lathyrus vernus*, 420 m altitude, roughly 120 years old) on limestone near Göttingen (FRG). Sampling was done using ground-photo-electors. A detailed description of the study site and the sampling program is given in Ulrich (1988, 1998).

Additionally, data from breeding experiments were collected. 6 species of *Aspilota* and *Orthostigma* were bred as polyphagous primary parasitoids out of 4 phorid flies (*Megaselia* spp., *Gymnophora arcuata*) in 90

Table 1. Morphological characteristics, mean densities, and mean aggregation of 25 species of *Aspilota* and *Orthostigma*. Lengths are given in mm, areas in mm<sup>2</sup>, and volums in mm<sup>3</sup>, body-weight in g. Data of samplings from 1980 to 1987. Mean density in ind.m<sup>-2</sup> a<sup>-1</sup>. The numbering GWn refers to the numbering in Ulrich (1998). Aggregation measured by the Lloyd-index.

Species	Area of Mandibel	Thorax Volumen	Length of ovipositor	Length of hind leg	Wing area	Body weight	Mean density	Mean aggregation
<i>Aspilota</i> GW1	0.010	0.107	0.325	1.575	0.811	5.63E-05	0.01	
<i>Aspilota</i> GW2	0.007	0.087	0.500	1.700	1.398	4.55E-05	8.08	1.25
<i>Aspilota</i> GW3	0.012	0.216	0.575	2.100	1.384	1.13E-04	0.44	2.84
<i>Aspilota</i> GW5	0.010	0.131	0.325	1.750	1.332	6.87E-05	2.23	3.14
<i>Aspilota</i> GW6	0.021	0.454	0.400	2.275	1.753	2.38E-04	0.01	
<i>Aspilota</i> GW8	0.023	0.089	0.400	1.575	1.065	4.68E-05	0.03	
<i>Aspilota</i> GW11	0.011	0.125	0.375	1.875	1.447	6.57E-05	0.16	3.22
<i>Aspilota</i> GW12	0.014	0.208	0.600	2.200	1.748	1.09E-04	0.01	
<i>Aspilota</i> GW15	0.017	0.068	0.450	1.450	0.780	3.57E-05	0.02	
<i>Aspilota</i> GW16	0.009	0.098	0.500	1.625	1.153	5.12E-05	0.01	
<i>Aspilota</i> GW17	0.016	0.152	0.450	2.025	1.423	7.99E-05	0.01	
<i>Aspilota</i> GW19	0.013	0.203	0.550	2.075	1.665	1.06E-04	0.01	
<i>Aspilota</i> GW20	0.014	0.086	0.450	1.725	1.096	4.51E-05	0.77	5.74
<i>Aspilota</i> GW21	0.009	0.086	0.400	1.425	0.707	4.49E-05	0.32	4.92
<i>Aspilota</i> GW23	0.017	0.158	0.650	1.900	1.181	8.27E-05	3.91	1.32
<i>Aspilota</i> GW26	0.016	0.253	0.525	2.225	1.748	1.33E-04	0.01	
<i>Aspilota</i> GW27	0.047	1.059	0.900	3.275	3.542	5.56E-04	0.29	3.56
<i>Aspilota</i> GW28	0.038	0.310	0.700	2.700	2.270	1.63E-04	0.06	
<i>Aspilota</i> GW29	0.009	0.061	0.900	1.375	0.874	3.22E-05	0.01	
<i>Aspilota</i> GW30	0.019	0.197	0.500	2.100	2.270	1.03E-04	0.02	
<i>Aspilota</i> GW31	0.021	0.473	1.600	2.650	2.477	2.48E-04	0.05	
<i>Aspilota</i> GW32	0.004	0.035	–	1.250	0.679	1.84E-05	0.01	
<i>Aspilota</i> GW33	0.013	0.071	0.225	1.475	0.679	3.72E-05	0.01	
<i>Orthostigma</i> GW1	–	0.349	0.375	2.000	1.509	1.83E-04	0.04	
<i>Orthostigma</i> GW2	–	0.465	0.450	1.950	1.438	1.83E-04	0.11	2.56

dead snails (*Arion ater*) exposed 1986 in plastic tubes in a 100 × 100 m grid (every 10 m one snail). A detailed description of the experiments is given in Ulrich (1999a).

The present analysis is based on density data from eclector samplings and morphological data obtained by measuring 5 parameters: mandibel area, thorax volume, wing area, length of ovipositor and hind leg (Table 1). Body weight was inferred from thorax volume by a regression developed in Ulrich (1998), wing area was computed using the regression between wing length and width in Ulrich (1999b). Because of allometric relationships of mandibel and wing area as well as leg length on body weight, in K-means cluster analyses (STATISTICA version 6) the residuals of these allometric regressions were used. Raw data of the morphological variables were used in a canonical discriminant analysis which results in a set of linear combinations of the original variables (the canonical functions) (Juliano and Lawton 1990) and is especially appropriate to combine these variables with the above defined clusters.

As a measure of aggregation the index of Lloyd was used (Table 1) which assumes a negative binomial distribution and which is (except for very low densities) independent of density (Schenker and Streit 1980). Temporal and spatial associations of species were tested with the density based variance test of Schluter (1984) which compares row and column variances of species occurrence matrixes. The test was run with the emergence data from beginning of May to end of October.

The number of species in the regional species pool ( $S_{total}$ ) was estimated using an asymptotic linear model of species accumulation.

$$S_n = (an+b) / (1+(an+b) / S_{total}) \quad (1)$$

where  $S_n$  is the cumulative number of species after  $n$  samples,  $a$  and  $b$  are constants which determine the shape of the function and which are derived from the fitting process.

Ulrich (1999c) found this model to be the best parametric alternative of the second order jackknife estimator. If more than 80% of the species are already represented in the sample the function is slightly negatively biased and underestimates  $S_{total}$  at an order of around 10% (Ulrich 1999c).

### 3. RESULTS

#### 3.1. NUMBER OF SPECIES AND TEMPORAL STABILITY

After eight years of study 25 species of *Aspilota* and *Orthostigma* had been found. A collector's curve using all combinations of the yearly eclector data (according to the method of Ulrich 1998) and using a parametric asymptotic linear estimator (Ulrich 1999c) resulted in an estimate of  $27 \pm 3$  species (Fig. 1). Because the estimator is slightly negatively biased the most probable number ranges between 27 and 30 species. This is the species number after longer periods of sampling and (assuming a steady species turnover) may serve as an estimate of the regional species pool.

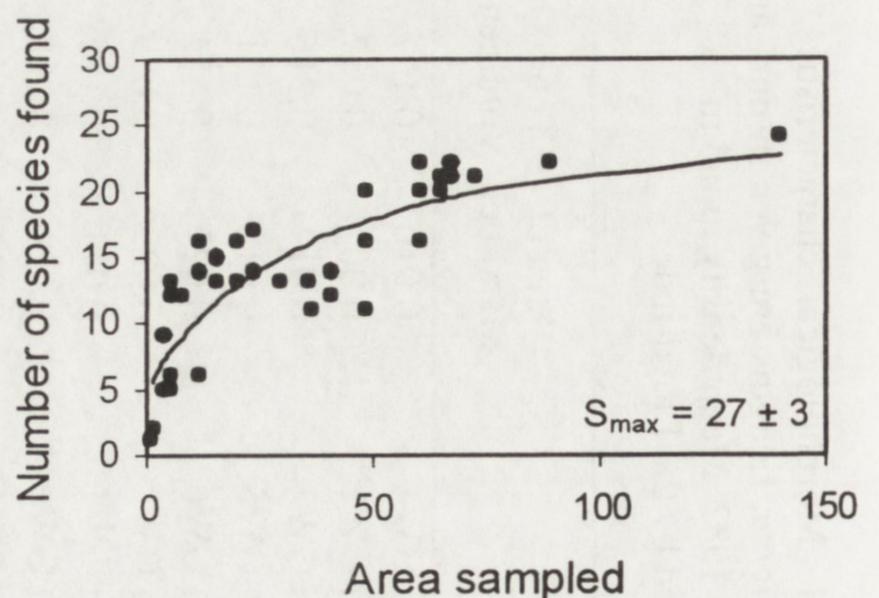


Fig. 1. Collector's curves of *Aspilota* and *Orthostigma* spp. of the Göttingen beech forest. Plotted are the numbers of species against the area sampled with ground-photo-eclectors (1981 to 1987). To eliminate trends in species numbers per year, all combinations of areas sampled were included in the graph. Included is the fit of the asymptotic linear model (formula 1) which results in a maximum of  $27 \pm 3$  species

This number can be compared with estimations of the yearly number of species. Such estimations were possible for the years 1981 and 1987. In these years 61 and 20 m<sup>2</sup>, respectively, were sampled (see the detailed description in Ulrich 1998). Similar plots and computations as in Figure 1 resulted in estimates of  $17 \pm 2$  (1981) and  $11 \pm 1$  (1987) species (data not shown). That means that the annual number of species is around half of the species of the regional species pool and that the species turnover rate may be as high as 30%.

### 3.2. NICHE SEGREGATION

Morphological differences of the species were studied with a K-means cluster and a canonical discriminant analysis (Fig. 2, Table 2). The cluster analysis identified 5 clusters with 1 to 10 species (Table 2). The most abundant species are not evenly distributed throughout these clusters but concentrate in the first cluster. The species which were bred at the same time out of the same host species do not cluster together but are found in clusters 1 (*Aspilota* GW1, GW3), 2 (*Aspilota* GW5, GW8), 3 (*Aspilota* GW6, *Orthostigma* GW1), and 4 (*Aspilota* GW2).

A canonical discriminant analysis is able to visualize graphically the resolution of the cluster analysis (Fig. 2). The analysis resulted in 3 roots of which 2 were significant at the 5%-level and 24 of 25 assignments to clusters using these roots were correct. The exception

is *Aspilota* GW6 of the third cluster which may better be assigned to the first cluster. The analysis separates therefore *Aspilota* and *Orthostigma* spp. Figure 1 shows a rather weak separation of clusters 2 and 4 that contain most of the species. Root 1 correlates highly with wing area and root 2 with biomass.

A ranking of the species according to their body-weight and the wing area, however, gave low mean quotients between the weights of subsequent species of  $1.14 \pm 0.17$  and between the wing areas of  $1.08 \pm 0.11$ . Taking only the 8 dominant species (Table 1) these values are  $1.18 \pm 0.19$  and  $1.14 \pm 0.10$ . Both values are much lower than predicted by models of coexistence (Mac Nally 1988). To test whether the observed quotients are more regularly spaced than expected by chance I compared the above given standard deviations with the one obtained after 50 randomizations of values inside the observed range of quotients (Strong *et al.* 1979). Such a randomization process resulted in a standard deviation of  $0.13 \pm 0.03$  for the biomass and  $0.06 \pm 0.02$  for the wing area. Therefore, the observed values are even larger than the ones expected just by chance. The result does not point to a regular spacing of quotients and to a community wide character displacement.

The more abundant *Aspilota* and *Orthostigma* species are bi- or trivoltine with activity periods in May/June and August (Fig. 3). Probably, this is also true for the rare species which were found in only one season. All

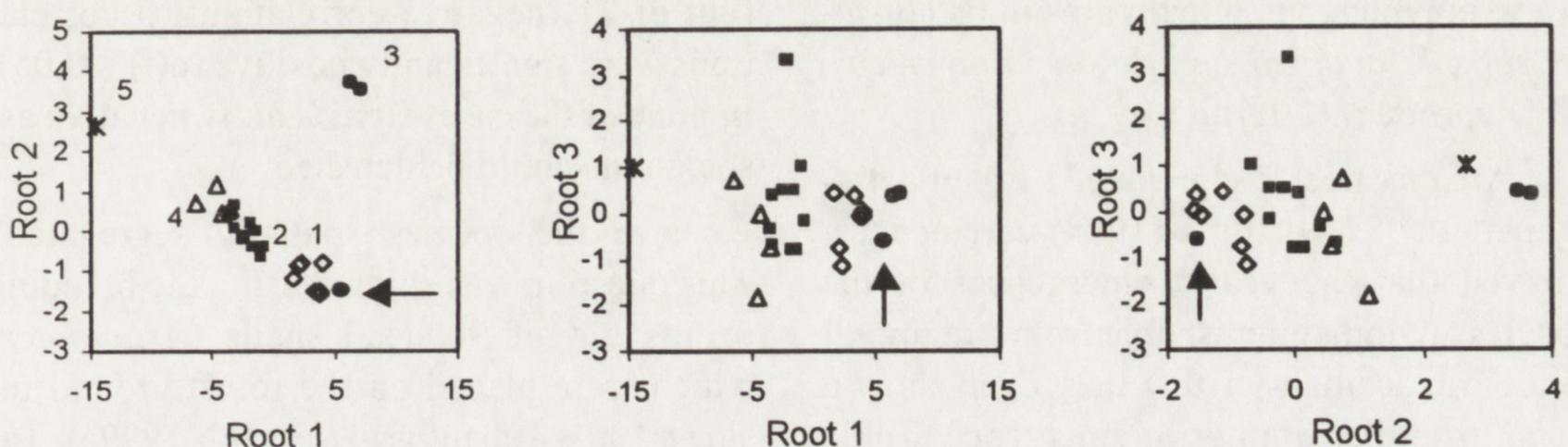


Fig. 2. Canonical discriminant analysis of 5 morphological factors (given in Table 2) of *Aspilota* and *Orthostigma* spp. Root 1: Eigenvalue: 15.92,  $\text{CHI}^2$ : 67.97,  $p < 0.001$ ; root 2: Eigenvalue 1.12,  $\text{CHI}^2$ : 15.64,  $p < 0.05$ ; root 3: Eigenvalue 0.01,  $\text{CHI}^2$ : 1.74,  $p = 0.63$ .  $\diamond$ : species of cluster 1,  $\blacksquare$ : cluster 2,  $\bullet$ : cluster 3,  $\Delta$ : cluster 4,  $*$ : cluster 5. The arrow marks *Aspilota* GW6 of the third cluster.

Table 2. Cluster analysis (K-means clustering module of STATISTICA; 5 clusters, Euclidian distance) of *Aspilota* and *Orthostigma* spp. Morphological variables: body-weight, residuals of allometric regressions between body-weight and ovipositor length, wing area, length of hind leg, and mandibel area. The most abundant species (mean densities above 0.15 ind. m<sup>-2</sup> a<sup>-1</sup>) are marked in bold type

Cluster	Species	Distance from cluster centre	Peak of emergence
1	<i>Aspilota</i> GW1	0.068	bred in 1 October
1	<b><i>Aspilota</i> GW3</b>	0.041	2 June, 2 July, 2 August
1	<i>Aspilota</i> GW15	0.061	1 August
1	<b><i>Aspilota</i> GW21</b>	0.075	1 June, 2 July, 1 September
1	<b><i>Aspilota</i> GW23</b>	0.035	1 June, 2 July, 2 August
1	<b><i>Aspilota</i> GW27</b>	0.057	1 July, 1 August
1	<i>Aspilota</i> GW33	0.023	found in 2 July
2	<b><i>Aspilota</i> GW5</b>	0.044	2 June, 1 August, 1 September
2	<i>Aspilota</i> GW8	0.032	2 May
2	<i>Aspilota</i> GW16	0.029	—
2	<i>Aspilota</i> GW17	0.07	—
2	<i>Aspilota</i> GW19	0.024	found in 1 September
2	<b><i>Aspilota</i> GW20</b>	0.069	2 May, 1 August, 1 September
2	<i>Aspilota</i> GW26	0.037	2 June
2	<i>Aspilota</i> GW29	0.051	found in 2 August
2	<i>Aspilota</i> GW31	0.008	2 August
2	<i>Aspilota</i> GW32	0.013	found in 1 September
3	<i>Aspilota</i> GW6	0.138	1 May
3	<i>Orthostigma</i> GW1	0.096	2 May, 1 July, 1 September
3	<i>Orthostigma</i> GW2	0.232	2 July, 1 September
4	<b><i>Aspilota</i> GW2</b>	0.076	1 June, 2 July, 2 September
4	<b><i>Aspilota</i> GW11</b>	0.054	2 June, 1 August, 1 September
4	<i>Aspilota</i> GW12	0.07	—
4	<i>Aspilota</i> GW28	0.115	1 August
5	<i>Aspilota</i> GW30	0	1 June

species hibernate as larvae or pupae inside the host puparium. There they are attacked by a few polyphagous pupal parasitoids (*Basalyis* spp., *Trichopria* spp., *Idiotype nigriceps*, all Diapriidae) (Ulrich 1999a).

Are the species segregated by their activity pattern? Schluter's (1984) variance test showed that the yearly emergences of the species are indistinguishable from a temporal random placement or that they even show a trend to similar timings of emergence (Table 3). The latter trend is indicated by the fact that 7 out of 8 pairwise comparisons have W-values above the mean of 12. The same trend came up after pairwise correlations of the 7

most abundant species (densities above 0.3 ind. m<sup>-2</sup> a<sup>-1</sup>) (Table 1). This resulted in only 6 (out of 21) negative correlations. 5 correlations were significantly positive ( $p(t) < 0.05$ ). In none of the cases significantly negative associations could be detected.

Are the species spatially segregated? This question was studied using the breeding results out of 90 dead snails (*Arion ater*) which were placed on the forest ground inside a 100 × 100 m<sup>2</sup> grid (Ulrich 1999a). Table 4 shows the test statistic of Schluter's variance test for the 90 snails separated into 10 weight classes. 40 out of 50 comparisons are indistinguishable from random distribu-

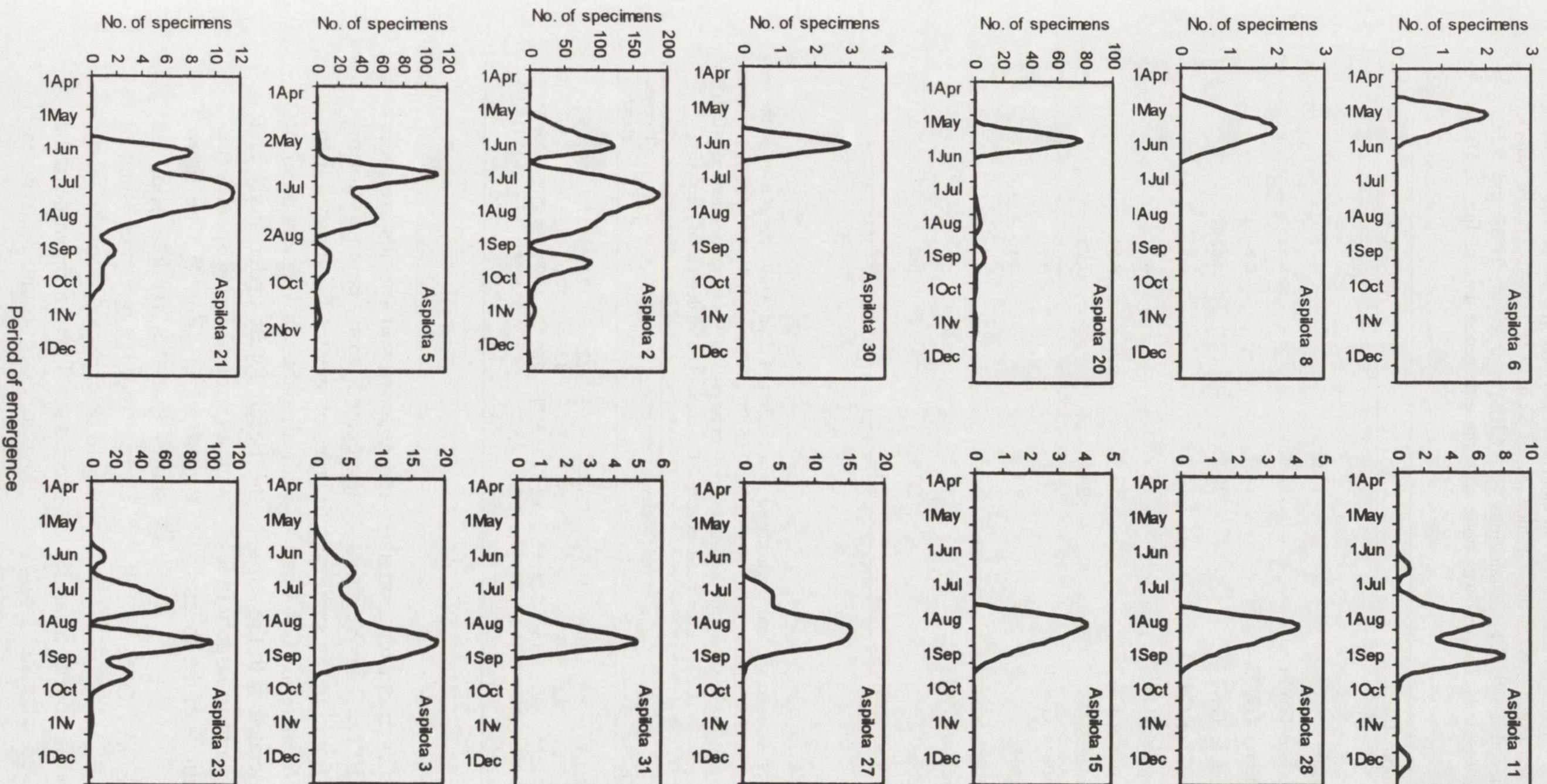


Fig. 3. Phenologies of the most abundant *Aspilota* spp. of the Göttingen beech forest. Combined data from elector samplings of 1981 to 1987. Sampling dates each of the first or the second half of a month were combined and 1 June or 1 September denote sampling in the first two weeks of each month.

Table 3. Variance test to detect temporal associations in emergence between species of *Aspilota* and *Orthostigma*. Given is the test statistic *W* of the variance test of Schluter (1984). The *W* values for positive (*W* pos) or negative (*W* neg) associations at  $p(\text{CHI}^2) = 0.05$  are 21.03 and 5.23, respectively. 12 degrees of freedom. The test was done with the emergence data of Fig. 3. Data from 1 May to 2 October.

Species combination	<i>W</i>	$p(\text{CHI}^2)$
All species	22.0	0.05
All species of 1. Cluster	13.0	n.s.
<i>Aspilota</i> GW3 – <i>Aspilota</i> GW21	12.9	n.s.
<i>Aspilota</i> GW3 – <i>Aspilota</i> GW23	14.0	n.s.
<i>Aspilota</i> GW3 – <i>Aspilota</i> GW27	20.5	n.s.
<i>Aspilota</i> GW21 – <i>Aspilota</i> GW23	12.2	n.s.
<i>Aspilota</i> GW21 – <i>Aspilota</i> GW27	13.9	n.s.
<i>Aspilota</i> GW23 – <i>Aspilota</i> GW27	13.4	n.s.
All species of 2. Cluster	23.0	0.05
<i>Aspilota</i> GW5 – <i>Aspilota</i> GW20	9.2	n.s.
All species of 3. Cluster	13.4	n.s.
All species of 4. Cluster	12.3	n.s.
<i>Aspilota</i> GW2 – <i>Aspilota</i> GW11	12.3	n.s.
8 most abundant species	20.9	n.s.
Species bred out of dead snails	20.5	n.s.

Table 4. Spatial segregation of *Aspilota* spp and *Orthostigma* 1 in patches of dead *Arion ater*. Given is the test statistic *W* of the variance test of Schluter (1984). \*  $p(\text{CHI}^2) < 0.05$ , \*\*  $p(\text{CHI}^2) < 0.01$ , \*\*\*  $p(\text{CHI}^2) < 0.001$ . Positive associations in bold type. The *W* values for positive (*W* pos) or negative (*W* neg) associations at  $p(\text{CHI}^2) = 0.01$  are 25.19 and 2.16, respectively. 10 degrees of freedom each (all weight-class 90 degrees of freedom).

Species combination	Weight-class of the snails									All weight-classes
	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–12	
All species	11.3	8.9	10.0	11.5	12.0	9.1	12.7	12.2	11.5	97
<i>Aspilota</i> 2 – <i>Aspilota</i> 3	7.1	8.8	9.4	10.8	11.4	8.8	12.6	12.6	13.0	101.7
<i>Aspilota</i> 2 – <i>Orthostigma</i> 1	0.8***	9.1	16.0	<b>38.6***</b>	5.2	<b>33.5***</b>	<b>27.9**</b>	11.2	<b>58.9***</b>	<b>206.1***</b>
<i>Aspilota</i> 3 – <i>Orthostigma</i> 1	0.9***	<b>37.7***</b>	11.8	9.3	8.3	8.2	9.3	<b>35.6***</b>	15.2	116.1
<i>Aspilota</i> 2, 3, <i>Orthostigma</i> 1	0.8***	8.0	8.3	9.8	5.2	7.4	7.4	10.7	12.6	86

tions and the *W*-values even cluster around the mean value of 10 ( $10.1 \pm 2.3$ ). Negative associations were only found in the smallest weight class of *Arion*. *Orthostigma* GW1 had the tendency to be associated with the *Aspilota* spp. These results point to largely independent spatial distributions of the species.

### 3.3. AGGREGATION

Most arthropod species occur in an aggregated manner. To see whether *Aspilota*

and *Orthostigma* species are more aggregated than random assemblages of species I compared them with all parasitic Hymenoptera of the beech forest under study and with all ground living species (except *Aspilota*) (Fig. 4). The figure shows that the *Aspilota* spp. are clearly more aggregated than it would be expected from the whole species set. Their mean value of the Lloyd index is around 3.5 whereas

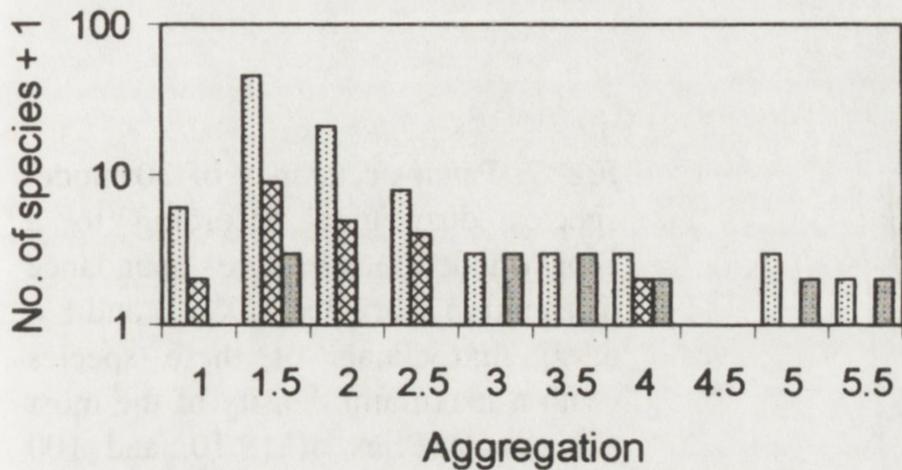


Fig. 4. Number of species of parasitic Hymenoptera of the Göttingen beech forest in each class of aggregation (Lloyd index). Data from all species of which more than 20 specimen were found in one year. Stippled bars: all Hymenoptera, checked bars: all ground living species (except *Aspilota* and *Orthostigma*), shaded bars: *Aspilota* and *Orthostigma* spp

all species and the ground living ones have mean values around 1.5. In all 3 species sets the degree of aggregation appeared to be independent of mean density (data not shown). The *Aspilota* and *Orthostigma* species did not show a trend to higher aggregations in the more abundant species but even the opposite (correlation between Lloyd index and mean density:  $r = -0.65$ ,  $p(t) = 0.06$ ).

### 3.4. CORE-SATELLITE SPECIES

The core-satellite hypothesis states a bimodality in species number–density plots (Hanski 1982). This had been criticized by Nee *et al.* (1991) because it is often possible to receive in a bimodality by an adequate choice of scale. Indeed, figure 5 shows no bimodality when plotting species numbers against logarithmic density classes. Bimodality appeared however when lumping classes of the most abundant species.

One can overcome this problem by a different reasoning. Communities are characterized by a certain relative abundance distribution and Maurer (1990) and Nee *et al.* (1991) have shown that for a log-series and log-normal distributions only certain parameter settings and density ranges are able to produce bimodal abundance class distributions. One can generalize these findings and

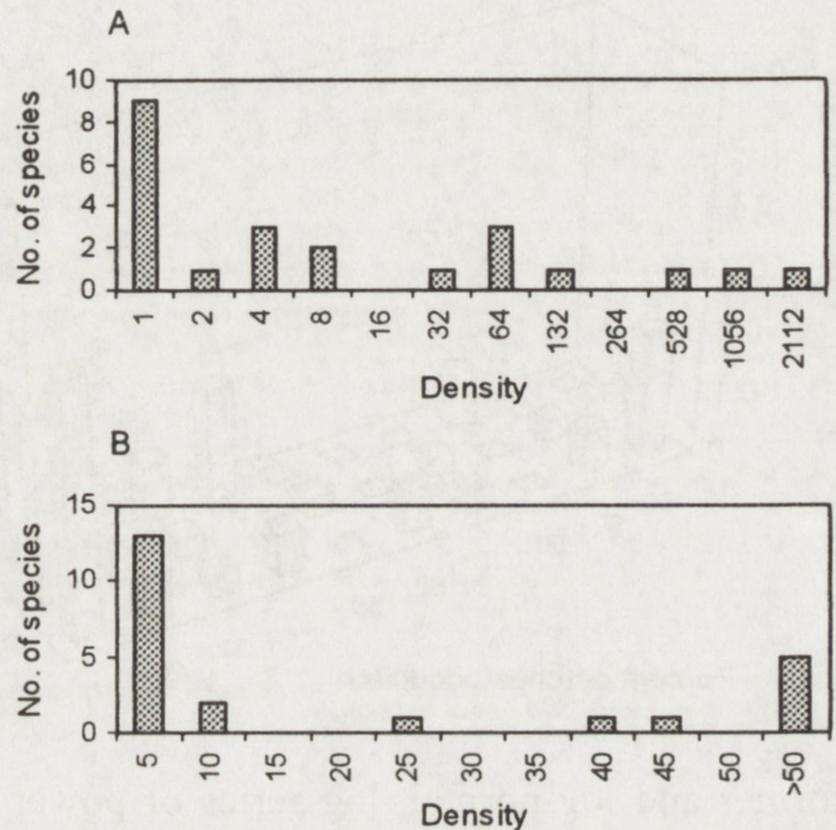


Fig. 5. Number of species of *Aspilota* and *Orthostigma* spp.: in logarithmic (A) and linear density classes (B)

show that this is the case for all types of relative abundance distributions (Ulrich unpubl.).

Figure 6 shows that the *Aspilota* and *Orthostigma* species of the beech forest under study are best fitted by a Zipf-Mandelbrot distribution (Frontier 1985) of the form:

$$p_r = (r + X)^{-z} \quad (2)$$

with  $p_r$  being the relative abundance of species  $r$  with parameters  $X = 3.0$  and  $z = 3.99$ . Of other theoretical distributions a random fraction model fitted well but not as good as the

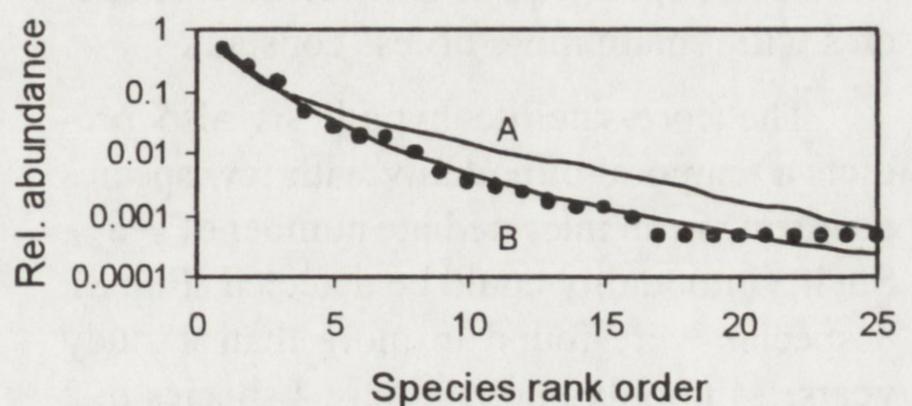


Fig. 6. Relative abundance distribution of *Aspilota* and *Orthostigma* spp. in the Göttingen beech forest. Given are also fits of a random fraction (A) and a Zipf-Mandelbrot model (B). The fits were done with the computer program Frequency Distribution (Ulrich 2000) assuming a total number of 30 species. Parameters of the Zipf-Mandelbrot model:  $x = 3.0$ ,  $z = 3.99$

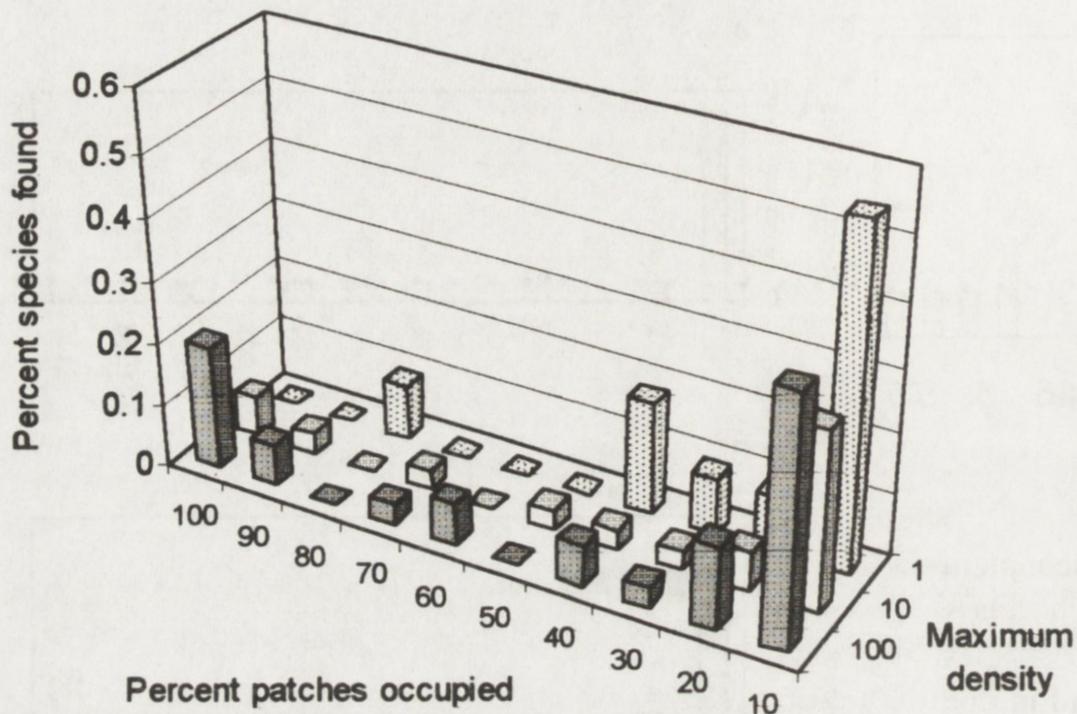


Fig. 7. Patch occupancy of 30 model species distributed according to a Zipf-Mandelbrot relative abundance distribution (parameters  $X = 3$  and  $z = 3.99$ ). Individuals of these species (with a maximum density of the most abundant species of 1, 10, and 100 ind. per patch) were placed at random inside a grid of  $300 \times 300$  cells, afterwards 100 cells were chosen at random and the number of species counted

former and log-normal, log-series or power fraction models failed to fit. This Zipf-Mandelbrot distribution will indeed result in a bimodality of patch occupancy (Fig. 7), however, only if the most abundant species have densities of 10 to 100 ind. per patch. Lower densities lack typical core species. These densities required for a typical core-satellite pattern are slightly higher than the one observed (mean density of the dominant *Aspilota* GW2:  $8 \text{ ind. m}^{-2} \text{ yr}^{-1}$ ; maximum annual density of this species:  $27 \text{ ind. m}^{-2}$ ; the species had densities above  $10 \text{ ind. m}^{-2}$  only in 1986 and 1987 (Ulrich 1998). The model pattern for 10 ind. per patch resembles very much the real pattern in figure 5. Of course, the pattern of figure 7 is scale dependent. However, enhancing or reducing the number of patches will mainly influence the number of satellite species. The fraction of core species will remain more or less constant.

The core-satellite hypothesis also predicts a temporal bimodality with few species occurring in an intermediate number of years. Such a bimodality could be detected (Fig. 8). 8 species were found in more than 4 study years, 14 in only one, but only 4 species in 2 to 4 years.

Gotelli and Simberloff (1987) and Maurer (1990) predicted on the basis of the core-satellite hypothesis higher mean patch densities and lower density variances of the more abundant species. Figure 9 shows a tendency of the parasitoid species bred out of

dead snails to obey the first prediction ( $r = 0.76$ ,  $p(t) < 0.05$ ). However, more abundant species had clearly higher variances in patch

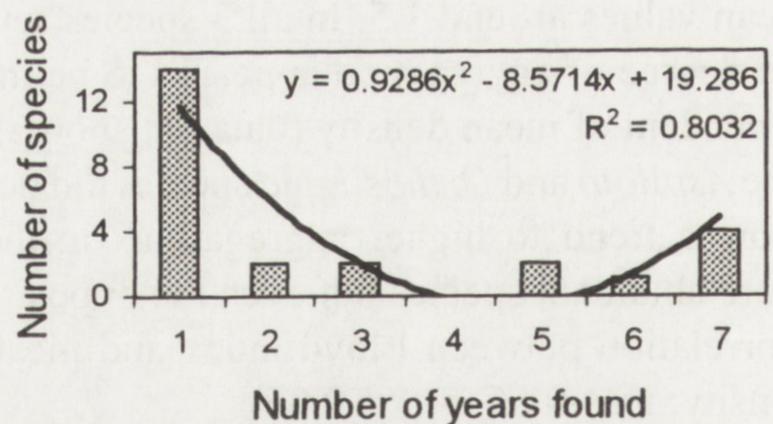


Fig. 8. Number of *Aspilota* and *Orthostigma* spp. found in exactly 1, 2...7 of the study years. The distribution is bimodal ( $R^2 = 0.80$ ) and can be fitted by a second order polynomial

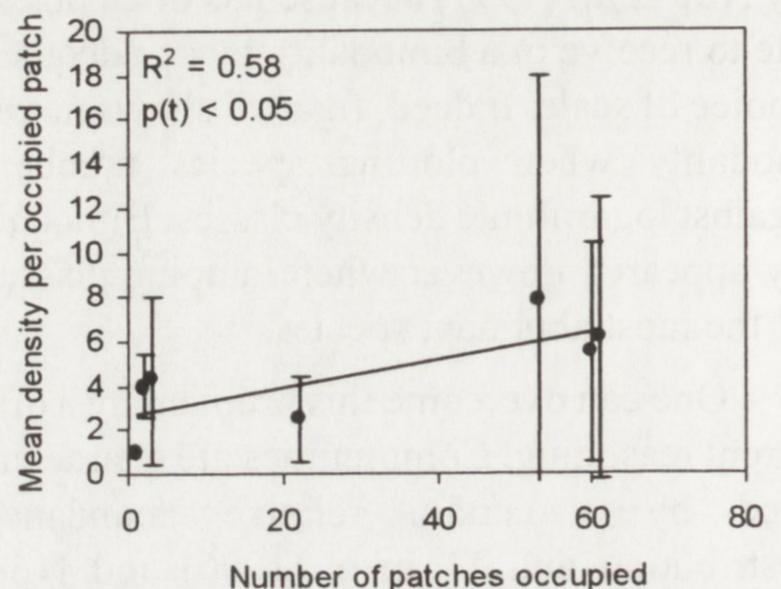


Fig. 9. Mean patch density in dependence of the number of patches occupied of 6 parasitoids of necrophagous Phoridae bred out of 90 dead *Arion ater* snails. Given are also the standard deviations of density and a linear regression fit

density than less abundant species. This is the reverse of the prediction of Maurer (1990).

The model also predicts high species turnover rates both in the core and in the satellite species. However, despite high density fluctuations (factor 10 to factor 100) the species composition of the core group remained rather constant. 6 of the 8 dominant species were found in 5 of the 7 study years. The rank abundance order however changed considerably (Fig. 10). Mean value of Kendall's Tau was  $0.33 \pm 0.26$  but no trend to lower concordance values in more distant years was observed.

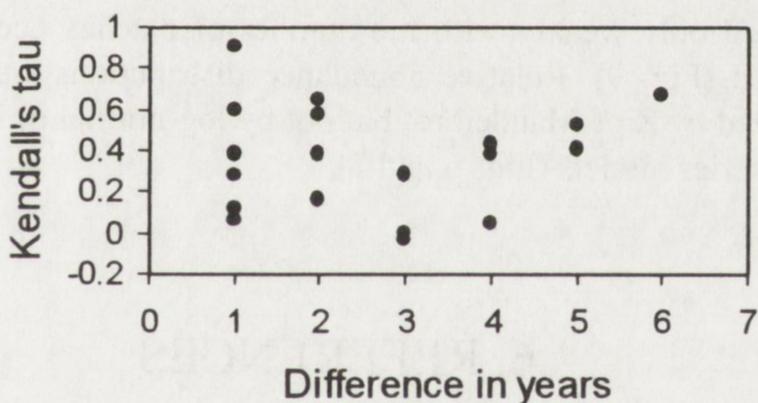


Fig. 10. Concordance (Kendall's Tau) as a measure of constancy in species rank order between different study years. Given are all combinations of years (1981 to 1987: 21 correlations)

#### 4. DISCUSSION

The aim of the present study was to compare three models about species coexistence. A classical niche analysis largely failed to separate the species. Morphological differences appeared to be rather small and only the species of the genus *Orthostigma* and the large species *Aspilota* GW30 could clearly be distinguished by their morphology. A community wide character displacement could not be detected. The data also show that morphological separation has its fallacies. Although *Orthostigma* GW1 could be separated by the cluster analysis it has the same hosts than the abundant *Aspilota* species of the first, second, and third cluster and even shows a trend to be spatially associated with

these species. From a host point of view the niches are indistinguishable.

Douglas and Matthews (1992) compared fish species and found morphological differences mainly to be related with phylogeny but not with diet requirements. Similar conclusions were drawn by Wiens and Rotenberry (1980) after a comparison of morphology and ecology of shrub-steppe bird populations. In arthropods morphological studies (mostly in the form of cluster and discriminant analysis) are often used to infer niche segregation (Pearson 1980, Greene 1987, Warren and Lawton 1987, Juliano and Lawton 1990). The present study indicates that such reasoning has to be accompanied with an analysis of ecological requirements.

Of the annual numbers of species a constant fraction of only 3 to 5 species (out of a pool of 8 dominant species, Table 1) reached densities of  $1 \text{ ind. m}^{-2} \text{ a}^{-1}$  or more (Table 1, Fig. 8). 3 of these 8 species were bred out of the same phorid species (*Aspilota* GW2, 3, 5). The species could not be separated unambiguously by morphology and activity period but host preferences and differences in microhabitat requirements could not be studied in detail.

As predicted by the aggregation theory of local coexistence all species studied were highly aggregated and the degree of aggregation was higher than that of two random sets of parasitoid species that served as null models (Fig. 4). If one takes the yearly density fluctuations of the species as a rough estimate of the reproductive potential the second prediction of the aggregation theory also holds: less abundant species had higher density fluctuations. However, contrary to prediction (Atkinson and Shorrocks 1984) they were not less aggregated but even showed a trend to higher degrees of clumping.

Spatial bimodality of species rank order distributions are often a matter of scale (Nee *et al.* 1991), but figures 5 and 8 show that the *Aspilota* and *Orthostigma* species of the

beech forest under study had indeed spatial and temporal bimodal distributions with a high number of rare species. There had also been a tendency for higher local patch densities in the more abundant species. That this trend was rather weak may be due to the fact that the predicted pattern should be produced especially by species which colonize more than two thirds of all patches (Gotelli and Simberloff 1987, Maurer 1990) which was not the case in the breeding experiments used for analysis. However, the predicted lesser variance in density of the more abundant species could not be detected (Fig. 9). The species composition of the core species set was also rather constant (Table 1, Fig. 8) and did not change through time (Fig. 9).

Interestingly, the densities of the species ranged at the lower end of the density spectrum required for a typical core-satellite mode (Fig. 7). Only in 1986 and 1987 densities well above  $10 \text{ ind. m}^{-2} \text{ yr}^{-1}$  occurred (Ulrich 1998) in the other years the densities remained below  $5 \text{ ind. m}^{-2} \text{ yr}^{-1}$ . The modeling of figure 7 indicates that such densities will not result in a typical core-satellite pattern but will lack the core species end. A core-satellite pattern is therefore density dependent and may not occur in every year. The pattern seems not necessarily to be an intrinsic feature of communities of patchily distributed species.

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## 5. SUMMARY

In a beech forest on limestone (Northern Germany) community structure and coexistence of a community of phorid (Diptera) parasitoids (*Aspilota* and *Orthostigma* spp., Hymenoptera, Braconidae) was stu-

died using samplings from ground-photo-electors and breeding experiments (Fig. 1, Table 1).

A classical niche analysis including morphological character displacement, temporal and spatial segregation and density fluctuations could not clearly separate the species (Tables 1, 2, 3 and 4, Figs 2 and 3). In a case where such a separation by morphological factors was possible, hosts and spatial distribution of this species were the same as in morphological different species.

As predicted from aggregation theory of coexistence all species were highly aggregated (Fig. 4) but aggregation and density appeared not to be correlated. Temporal sequences of the species rank orders of the abundant species (Fig. 10) were more or less stable.

In line with the core-satellite hypothesis bimodal species rank order distributions (temporal and in relation to density) with a high number of rare species were found (Figs 5 and 8). Mean patch density correlated only weakly with the number of patches occupied (Fig. 9). Relative abundance distributions were fitted by Zipf-Mandelbrot but not by log-normal or log-series models (Figs 6 and 7).

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