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THE HYMENOPTERA OF A DRY MEADOW ON LIMESTONE: SPECIES COMPOSITION, ABUNDANCE AND BIOMASS

ABSTRACT: In 1986 and 1988 the hymenopterous fauna of a semixerophytic meadow on limestone near Göttingen (FRG) was studied using ground-photo-eclectors. A total of 4982 specimens belonging to 475 different species were collected. Extrapolations from double-log functions revealed that there may be as many as 1330 parasitoid species present per year. 455 of the 475 species were parasitoids. 155 of them attack dipterans, 48 lepidopterans, 36 beetles, 23 wasps, 22 plant hoppers and 13 aphids. 47 of the species are egg-parasitoids and parasitoids of miners, ectophytophages count for 44 of the wasp species. The abundance of the wasp fauna was rather high (1120 ± 53 ind. m^{-2} a^{-1} (1986) and 335 ± 42 ind. m^{-2} a^{-1} (1988). Most abundant were the parasitoids of miners, gall-makers and the egg-parasitoids. Compared with the high abundance the biomass was low. In 1986 the wasps weighed a total of 194 ± 24 mgDW m^{-2} a^{-1} and in 1988 only 69 ± 20 mgDW m^{-2} a^{-1}. The parasitoids of ectophytophagous lepidopterans and coleopterans counted for more than half of the whole biomass.

KEY WORDS: Hymenoptera, parasitoids, faunal composition, density, biomass, species numbers, local extinction.

1. INTRODUCTION

The insect order Hymenoptera is the order with the largest number of species in the temperate regions (Gaston et al. 1996). In Europe many more than 10,000 species occur (Townes 1969, Kasparjan et al. 1981, Trjapitzin et al. 1978, Krombein et al. 1979, Tobias 1986) of which over 85% are parasitoids.

However, our knowledge about the biology, hosts and habitats of most the species is very limited. Most studies on the community structure and faunal composition only dealt with parts (normally families) of the Hymenoptera and used sweeping samples, and color or light traps, that have a great bias towards active and relatively large species (Weidemann 1965, König 1969, Abraham 1969, Horstmann 1970, Owen and Svensson 1974, Janzen and Pond 1975, Copland and Askew 1977, Garbarczyk 1981, Sawoniewicz 1981, Sterzyński 1981). Quantitative samples with ground-photo-eclectors, which should minimize the bias, have only seldom been undertaken: Thiede (1975) studied the fauna of a spruce forest in the Solling (FRG), Ulrich (1987, 1998) described the results about the fauna of a beech forest on limestone near Göttingen and Hilpert (1989) presented data on the hymenopterous fauna of a mixed forest near Freiburg (southern FRG). These studies showed that in temperate habitats the parasitoids not only have the highest species diversity of all insect groups but also account for a large part of the insect abundance and biomass.

The aim of this study together with some forthcoming ones is to analyze the community structure of the parasitic Hymenoptera of a dry grassland on species level and to present data on the species number, abundance, and biomass.

2. STUDY AREA AND METHODS

The studies were undertaken at the Drakenberg in the vicinity of Göttingen (FRG). The plateau of the hill (= 350 m altitude) is formed by huge layers of chalk, which is covered by Löß-layers (Thöle & Meyer 1979). The soil is characterized by a thin rendzina (Thöle & Meyer 1979), with pH ranging from 6.2 to 7.6. The summers are (normally) relatively cool (around 16 °C) with low precipitation (Bornkamm 1960). The mean annual temperature is 8.5 °C, the mean annual precipitation is 685 mm.

The samplings were done on a dry meadow on the plateau of the hill. This meadow is roughly 1 ha large and is surrounded by mixed beech / hazel hedges. Normally, the meadow is cut in June. A detailed account on the flora of the Drakenberg is provided by Nauenburg (1980). He describes the dry meadows of the plateau as forms of the Gentiano-Koelerietum association. Dominating plant species are *Cirsium acaule, Poa pratensis, Brachypodium pinnatum, Plantago media, P. lanceolatum, Pimpinella saxifraga, Galium album, Lotus corniculatus, Viola hirta, Medicago falcata, Linum carthaticum, Campanula rotundifolia, Achillea millefolium, Agrimonia eupatoria*, and *Rhinanthus minor*. Frequent are also *Bromus erectus* and *Carex flacca*.

During 1986 and 1988 samples were taken using ground-photo-eclectors. Detailed descriptions of the sampling method provided Ulrich (1987, 1988, 1998). In 1986 12 eclectors, which covered 0.25 m^2 each, were placed. From April to July groups of 4 were transposed every 2 weeks; from July to December half of them were transposed every 4 weeks. In 1988 8 eclectors were placed. From April to mid July they were transposed every 4 weeks in groups of 4. From July to the end of November the traps remained in place. Picric-acid was used as killing liquid.

The sampling boxes were checked weekly but only the boxes of those eclectors were analyzed that stood for more than 2 weeks in place. Due to this procedure only those insects were counted that had probably emerged under the trap. Insects that were trapped during the installation of the eclector should mostly have been captured the week after installation (Ulrich 1985).

All the specimens were sorted into species and at least identified to genus level. The literature used is given in Ulrich (1987, 1988). The ichneumonids were kindly determined by K. Horstmann, R. Hinz, E. Diller and W. Schwenke. The determination of the diapriids were checked by H. Hilpert. A list of all species is provided in the appendix.

The biomass was assessed by the formula developed by Ulrich (1998): dry-weight (mg) = thorax volume (mm^3) 0.52493 (mg mm^{-3}); $r = 0.97$; $p < 0.001$. Both, data on biomass and on density refer to individuals or dry-weight per square meters and year (m^{-2} a^{-1}).

3. RESULTS

3.1. NUMBER OF SPECIES

Tables 1 and 2 (see also the appendix) give an overview over the species found at the Drakenberg up to now. The whole material comprises 4982 specimens. In the two study years I was able to identify 475 different species of Hymenoptera.

Only 20 species are nonparasitic. Out of the 5 ant species detected, *Myrmica rubra* (387 specimens), *Lasius niger* (137) and *Lasius flavus* (82) were the most abundant. *Formica rufa* and *Lasius ruginodis* reached only minor densities. Only 8 solitary nest building Aculeata were caught (*Anoplius viaticus*, *Priocnemis perturbator* and *P. femoralis*, *Spilomena troglodytes*, *Oxybelus uniglumis*, *Osmia* sp., *Andrena* spp.); however, this number is much to low due to the sampling method. The two species of *Priocnemis* (Pompilidae)) were the most abundant solitary aculeate Hymenoptera (21 specimen).

The number of sawflies was surprisingly low. Only 30 adults out of 5 species (*Rhogogaster viridis, Pristiphora monogyniae, Pachyprotasis rapae, Macrophya quadrimaculata, Allantus truncatus*, all Tenthredinidae) and 98 larvae were caught. Correspondingly low was the number of sawfly parasitoids: only 1 specimen each of *Olesicampe patellana* and *O. subcallosa* were found, and the large group of sawfly parasitoids Ctenopelmatinae was represented only by one species of *Synomelix* (1 specimen).

96% (455 species) of the Hymenoptera are parasitoids (Table 1, 2). 155 of them attack dipterans, 48 parasitize lepidopterans, 36 coleopterans and 23 other wasps. The high number of parasitoids of Diptera coincides with the respective high number of their potential hosts: mainly Cecidomyiidae, Phoridae, Sphaeroceridae and Fanniidae (Hövemeyer 1996). When the parasitoids are sorted according to host guild it appears that the egg–parasitoids and the parasitoid of miners are the dominant group (47 species each), followed by the parasitoids of ectophytophages (44 species) (Table 2).

It should be kept in mind that the parasitoid guilds have different species–area-relationships (Ulrich 1998). Therefore, the ranking of the guilds does not reflect the real dominance order of the whole meadow but instead the ranking of every respective small part (11 m^2 area sampled by the traps). In the Göttingen beech forest which was studied over a period of 8 years (Ulrich 1998) only

Table 1. Number of parasitoid species of certain host taxa detected at the dry meadow Drakenberg (11 m² sampled) and in the Göttingen beech forest (based on 12 m² sampled area, data from Ulrich 1998).

The numbers of expected species are computed by formulas derived from collector's curves which are given in Ulrich (1998).

Parasitoids of	Drakenberg: Number of species in 11 m² area sampled	Expected No. of species in 11 m² area	Ratio expected No. versus detected No.	Göttingen forest 1982: Detected No. of species in 12 m² area sampled
Arachnida	6	–	–	2
Blattaria	1	–	–	0
Heteroptera	2	–	–	1
Aphidina	13	4	0.31	7
Cicadina	22	5	0.23	6
Coccina	7	–	–	3
Aleyrodina	0	–	–	3
Psocoptera	0	–	–	1
Thysanoptera	1	–	–	–
Planipennia	3	–	–	6
Coleoptera	36	23	0.64	21
Symphyta	3	–	–	4
Apocrita	23	9	0.39	8
Diptera	155	79	0.51	75
Lepidoptera	48	30	0.63	34
Host unknown	135	33	0.24	32
Sum	**455**	**201**	**0.44**	**204**
Other Hymenoptera				
Nest-building species	8			
Phytophagous species	7			
Social species	5			
Total number	**475**			

Table 2. Number of parasitoid species of certain host guilds detected at the dry meadow Drakenberg (11 m² sampled) and in the Göttingen beech forest (based on 12 m² sampled area, data from Ulrich 1998).

The numbers of expected species are computed by formulas derived from collector's curves which are given in Ulrich (1998).

Parasitoids of	Drakenberg: Number of species in 11 m² area sampled	Expected No. of species in 11 m² area	Ratio expected No. versus detected No.	Göttingen forest 1982: Detected No. of species in 12 m² area sampled
Miners	47	23	0.49	24
Gall-makers	35	27	0.77	26
Ectophytophages	44	25	0.57	27
Sap-suckers	30	12	0.40	18
Saprophages	36	22	0.61	17
Mycetophages	24	18	0.75	19
Predators	25	20	0.80	17
Eggs	47	15	0.32	16
Parasitoids	22	8	0.36	7
Xylophages	1	–	–	–
Guild unknown	144	34	0.24	33
Sum	**455**	**201**	**0.44**	**204**

30 % of the species (total number of 669) were detected on an area of 12 m^2 (Table 2) and the ranking of the guilds was different from that of the whole community.

A method for computing the total number of species and to obtain the real ranking order of the guilds is to compute collector's curves (Pielou 1977, Ulrich 1998) which reflect the dependence of the number of newly found species of the area sampled. Table 3 and Figure 1 show such collector's curves for the main parasitoid taxa and guilds. All of the computations resulted in double-log functions of the form:
ln (S) = a +b ln (N), with S: number of newly found species and N: number of eclector; a and b are constants.

The total number of species can be computed by solving the integral

$$S = \int f(x)\, dx\ e^a \times {}^{(b+1)} / (b+1)$$

in the boundaries of N+0.5 and 0.5.

Because all the data stem from one year the results give only the annual species numbers. In contrast to other authors who computed similar curves in forest habitats (Hilpert 1989, Ulrich 1998) nearly all of the curves computed here do not converge to zero. An exception are the egg-parasitoids for which the total number of species per year is 89. Therefore, it is not possible to compute a total number of species per year. Of course, there is an upper limit, but the area sampled is too low to include the very rare species in an adequate manner. Due to this fact Table 3 gives species numbers for upper boundaries of 100 m^2 area (lower density limit of 1 ind. 100 m^{-2} or roughly a total of 100 ind. on the whole meadow in the case of the least abundant species). In total up to 1330 (range of ± one standard deviation: 1161 to 1526, Figure 1) species may be present per year at the Drakenberg. Only 24% of them were actually detected.

The parasitoids of ectophytophagous

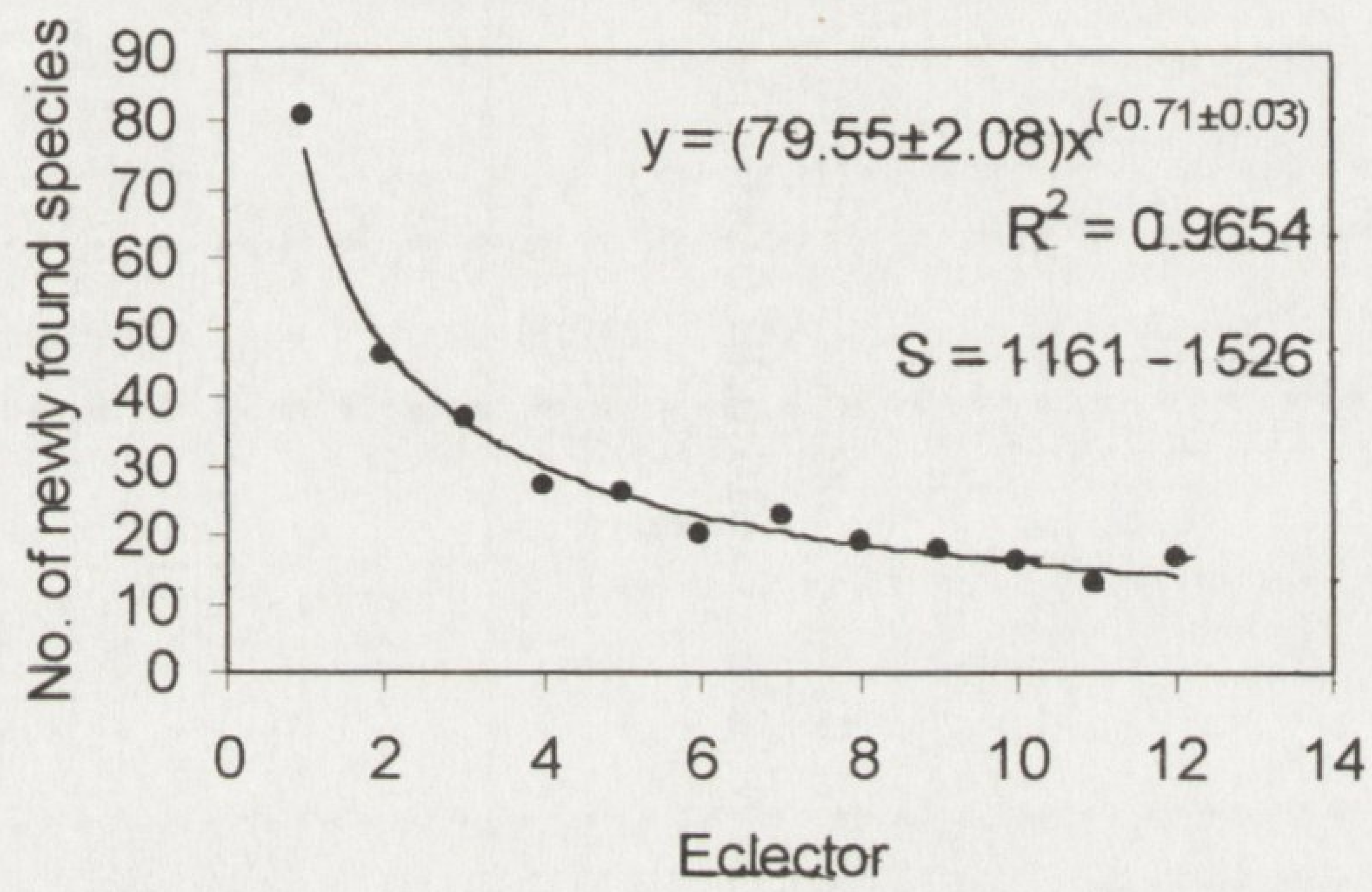

Figure 1. Drakenberg near Göttingen: Number of species found in 1986 with 12 ground-photo--eclectors. Plotted is the number of newly found species against the eclector number. Given are the function fitted to the data and the range of the maximal species number (S) computed with this function; R^2 – variance explanation.

hosts are the most species-rich guild, followed by the parasitoids of miners and myceto- or saprophages. Surprisingly, of the maximal 89 egg-parasitoids nearly half of the species were detected.

A study period of only two years do not allow extinction and immigration rates to be assessed. In the Drakenberg there may be a large species turnover. A comparison between the species found in 1986 and 1988 gives a hint. In 1986 343 species were caught on a sampling area of 3 m^2. In 1988 it was possible to detect only 303 species (8 m^2 area), whereas 543 species were expected on this area. This striking difference indicates that there may be extinction rates of more than 50%.

Annual numbers of species also do not tell how many species can be found if

Table 3. Dependence of the number of newly found species (S) on the area sampled (measured by the number of eclectors (N) used). Data from the most important parasitoid guilds and taxa as well as from the whole parasitoid community.

Guild	Function	R	p(t)	A	C	S86	S=A+C	% found
Parasitoids of miners	ln (S) = 2.00 – 0.69 ln (N)	0.75	< 0.01	134	52	31	186	17
P. of gall-makers	ln (S) = 1.59 – 0.62 ln (N)	0.52	< 0.01	116	45	29	161	18
P. of ectophytophages	ln (S) = 1.76 – 0.57 ln (N)	0.56	< 0.01	168	65	29	233	12
P. of myceto-/saprophages	ln (S) = 2.64 – 0.88 ln (N)	0.72	< 0.01	132	51	45	183	25
Egg-parasitoids	ln (S) = 2.70 – 1.19 ln (N)	0.66	< 0.01	64	25	35	89	39
Guild unknown	ln (S) = 2.96 – 0.59 ln (N)	0.85	< 0.01	514	–	86	514	17
All parasitoids	ln (S) = 4.38 – 0.71 ln (N)	0.96	< 0.01	1330	–	315	1330	24
Ichneumonidae	ln (S) = 2.14 – 0.44 ln (N)	0.48	= 0.01	425	–	59	425	14
Braconidae	ln (S) = 2.12 – 0.64 ln (N)	0.56	< 0.01	182	–	43	182	24
Chalcidoidea	ln (S) = 3.15 – 0.65 ln (N)	0.90	< 0.01	491	–	94	491	19
Diapriidae	ln (S) = 2.08 – 0.72 ln (N)	0.66	< 0.01	130	–	31	130	24
Ceraphronoidea	ln (S) = 2.12 – 0.84 ln (N)	0.69	< 0.01	89	–	31	89	35

A – Total number of species computed with the functions given (integral over a maximum area of 100 m^2 and 400 eclectors).
C – Correction factor to include the species of which the guild is unknown: C = (A 514) / 1330.
S86 – Number of species found in 1986. S – total number of species expected to occur on 100 m^2 area.
% found – S86 / S. R – Coefficient of determination. p(t) – Value of significance.

one collects longer periods. This so called species pool (Eriksson 1993) of a certain habitat may be very large, and in the case of the parasitic Hymenoptera comprises as many as 3200 species (Ulrich 1998).

How many of these species are indigenous? 391 of the 455 parasitoid species were caught with eclectors that stood in place for more than two weeks and were checked once. These species very probably emerged under the trap and were not caught during the installation. Most if not all of these species should be indigenous. Some of the other 64 species might have been only flower visitors. This means that very probably more than 400 of the 455 species detected are likely to be indigenous and to have their hosts on the meadow.

The number of species with unknown hosts is very high. Roughly 1/3 of all parasitoids belong to this group. This is more than 3 times the ratio of the well studied Göttingen forest (Ulrich 1998). This phenomenon is mostly caused by the high number of species of the taxa Gelinae (50), Encyrtidae (23), Ceraphronidae (24) and Megaspilidae (13), of which we have only a very poor knowledge. Probably most Gelinae attack pupae or egg-cocoons (Kasparjan et al. 1981, Gauld and Bolton 1988), and many Encyrtidae are known to develop in scale insects (Subba Rao and Hayat 1986, Bouček 1988). Ceraphronidae and Megaspilidae are often said to be mostly hyperparasitic (Muesebeck 1979, Dessart 1988) but rearing records are very scarce. Some also attack predatory gnats (Pschorn-Walcher 1956, Gauld and Bolton 1988). Together these 4 taxa account for about 24% of the parasitoid fauna of the Drakenberg.

3.2. ABUNDANCE AND BIOMASS

Table 4 and 5 show that the parasitoid community not only consists of a very large number of species but that these species also have a high abundance. In 1986 the density reached 1120 ind. m^{-2} a^{-1} but declined in 1988 to 335 ind. m^{-2} a^{-1}. This means that many of the species detected up to now have abundances of at least 1 ind. m^{-2} a^{-1} (Table 6).

After sorting to host taxon (Table 4) it appears that the parasitoids of Diptera were by far the most important parasitoid group. They counted for more than 40% of the whole density. Very important are also the wasps that attack plant hoppers (163 ± 12 (1986) and 13 ± 9 (1988) ind. m^{-2} a^{-1}).

Compared to forest habitats where they reach only very low densities (Ulrich 1998) the 6 parasitoids of spiders (mostly of spider eggs: *Aclastus gracilis* and *A. solutus*, *Baeus* sp., *Polyaulon paradoxus*, *Tromatobia ovivora*; or eggs and the egg guarding adults: *Zaglyptus varipes*) reached densities of 56 ± 7 (1986) and 9 ± 4 (1988) ind. m^{-2} a^{-1}. The highest densities were reached by the two spider-egg parasitoids *Baeus* sp. (1986: 55 ind. m^{-2} a^{-1}, 1988: 4 ind. m^{-2} a^{-1}) and *Aclastus gracilis* (3 and 1 ind. m^{-2} a^{-1}) (Table 6).

Judged from the biomass the parasitoids of lepidopterans were the top ranking group (Table 4). In 1986 they emerged with 138 ± 24 and in 1988 with 38 ± 20 mgDW m^{-2} a^{-1}. In both years this was more than half of the whole biomass. These values were caused due to the relatively high abundances of some large

Table 4. Density (ind. $m^{-2} a^{-1}$) and biomass (mgDW $m^{-2} a^{-1}$) of the parasitic Hymenoptera of different host taxa of the dry meadow Drakenberg near Göttingen in 1986 and 1988. StDev: Standard deviation

Taxon	Year							
	1986				1988			
	Density	StDev	Biomass	StDev	Density	StDev	Biomass	StDev
Arachnida	56	7	< 1	< 1	9	4	2	1
Blattaria	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1
Heteroptera	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1
Aphidina	8	4	< 1	< 1	11	7	< 1	< 1
Cicadina	163	12	3	1	13	9	1	1
Coccina	28	4	1	1	1	2	< 1	< 1
Thysanoptera	< 1	< 1	< 1	< 1	< 1	< 1	< 1	< 1
Planipennia	< 1	< 1	< 1	< 1	1	1	< 1	< 1
Coleoptera	78	10	8	1	11	4	2	1
Symphyta	1	1	1	1	< 1	< 1	< 1	< 1
Apocrita	14	2	4	1	6	4	1	1
Diptera	445	44	25	2	138	27	18	4
Lepidoptera	72	6	138	24	16	7	38	20
Host unknown	255	22	14	1	127	29	7	3
Sum	1120	53	194	24	335	42	69	20

Table 5. Density (ind. $m^{-2} a^{-1}$) and biomass (mgDW $m^{-2} a^{-1}$) of the parasitic Hymenoptera of different host guilds of the dry meadow Drakenberg near Göttingen in 1986 and 1988. StDev: Standard deviation

Guild	Year							
	1986				1988			
	Density	StDev	Biomass	StDev	Density	StDev	Biomass	StDev
Miners	200	20	9	1	24	13	1	1
Gall-makers	324	44	9	1	49	17	1	1
Ectophytophages	23	3	138	24	15	7	38	20
Sap-suckers	39	6	1	< 1	16	11	1	1
Saprophages	30	4	1	< 1	31	12	2	1
Mycetophages	26	5	3	1	35	10	11	4
Predators	16	2	5	1	10	4	3	2
Eggs	279	17	3	< 1	24	6	2	1
Xylophages	2	1	< 1	< 1	< 1	< 1	< 1	< 1
Parasitoids	14	2	4	1	6	4	1	1
Guild unknown	167	12	20	2	126	29	9	3
Sum	1120	53	194	24	335	42	69	20

Table 6. Abundance (ind. $m^{-2} a^{-1}$) and biomass (mgDW $m^{-2} a^{-1}$) of important parasitoid species of the dry meadow Drakenberg.

Species	Year			
	1986		1988	
	Ind. $m^{-2} a^{-1}$	mgDW $m^{-2} a^{-1}$	Ind. $m^{-2} a^{-1}$	mgDW $m^{-2} a^{-1}$
Aclastus gracilis	3 ± 3	2 ± 2	1 ± 1	< 1
Anaphes sp.	21 ± 7	< 1	38 ± 12	< 1
Arthrolytus sp.	97 ± 19	11 ± 2	< 1	< 1
Baeus sp.	55 ± 7	< 1	4 ± 2	< 1
Basalys nr. *cymocles*	11 ± 3	< 1	10 ± 10	< 1
Basalys parva	4 ± 1	< 1	< 1	< 1
Belyta depressa	3 ± 1	< 1	21 ± 5	1 ± 1
Blacus ruficornis	3 ± 1	< 1	4 ± 2	< 1
Callitula pyrrhogaster	22 ± 3	< 1	11 ± 13	< 1
Ceraphron sp.	19 ± 2	1 ± 1	56 ± 16	2 ± 1
Chasmodon apterus	3 ± 1	< 1	< 1	< 1
Coelichneumon desinatorius	7 ± 2	61 ± 14	1 ± 1	10 ± 11
Gonatocerus sp.	23 ± 4	< 1	< 1	< 1
Litus cynipseus	14 ± 5	< 1	1 ± 1	< 1
Ooctonus hemipterus	6 ± 1	< 1	< 1	< 1
Ooctonus vulgatus	34 ± 4	< 1	2 ± 2	< 1
Phygadeuon trichops	5 ± 1	3 ± 1	2 ± 2	1 ± 1
Platygaster sp.	269 ± 41	8 ± 1	35 ± 15	1 ± 1
Polynema fumipenne	15 ± 4	< 1	2 ± 2	< 1
Synopeas sp.	35 ± 15	< 1	< 1	< 1

Ichneumonidae (*Diphyus palliatorius, Coelichneumon desinatorius, Pimpla* spp.) and Rogadinae (*Rogas* spp.). The biomass of the other groups was comparably low.

The parasitoid guilds with the highest abundance were the egg-parasitoids and the parasitoids of gall-makers and mining insects (Table 5). In 1986 each of these 3 guilds counted for roughly 20% to 30% of the parasitoid community. In 1988 this value declined to 7 to 14%, whilst the portion of the ground-living parasitoids of mycetophagous and saprophagous Diptera doubled (roughly 10% each).

Egg-parasitoids are small animals, so their total biomass was only 2 to 3 mgDW m^{-2} a^{-1} (Table 5). On the other hand, the much less abundant parasitoids of ectophytophagous lepidopterans and coleopterans emerged with a total biomass of 138 (1986) and 38 (1988) mgDW m^{-2} a^{-1}. In both years this was more than half the biomass of the whole parasitoid community.

4. DISCUSSION

Most of the studies on the species composition of the parasitic Hymenoptera have been done in forests or coastal areas. Each of these studies revealed that the parasitoids are the most diverse and species-rich group of insects. Janzen and Pond (1975), Thiede (1975), Moran and Southwood (1982), Ulrich (1987, 1998) and Hilpert (1989) showed that in open grasslands as well as in woods the parasitic wasps count for more than 1/3 of all insect species. The high species number reported in this study also points to this conclusion.

The fact that more than twice the number of species occur at the Drakenberg than in a comparable area of the Göttingen beech forest lead to the conclusion that open dry habitats are more species rich than forests. To substantiate this hypothesis quantitative samplings over a longer period are necessary. At present only rough assessments can be made. Tables 2 and 7 compare the expected numbers of species (as obtained by collector's curves) at the Drakenberg and in the Göttingen forest. Striking differences appear. In all of the guilds many more species were found on the dry meadow than in the beech forest. This trend is especially pronounced in the parasitoids of miners, sap-suckers, and in the egg- and hyperparasitoids. Only the parasitoids of mycetophagous Diptera and of predators have comparable numbers of species on the meadow and in the beech forest. These differences are best seen if one refers the species number to one m^2 of sampled area (Table 7). In total 3 times more species were found on every m^2 of the dry meadow than in the beech forest. There are 5 times more egg-parasitoids and 2.67 times more parasitoids of ectophytophages. But there are nearly equal numbers of parasitoids of gall-makers. If larger areas are sampled these factors also get larger (Table 7). On a 10 m^2 area 3.05 times more species can be collected at the Drakenberg and on 50 m^2 even 3.53 times more. This means that the species-area-relationships of the dry meadow have not only higher ordinate crossings but also actually higher slopes. On the basis of 2 sampling years it is not possible to compute adequate collector's curves to compare the slopes in detail, but it seems to be a general trend in all of the guilds. This finding is sustained by the fact that the collector's curve of the Drakenberg do not converge to zero as it is the case in forest habitats (Hilpert 1989, Ulrich 1998).

As already mentioned, up to now there has been no complete study on the species numbers and abundances of the parasitic Hymenoptera of dry grassland areas. Due to this gap in our knowledge, I have chosen the studies made upon the parasitoid fauna of open sand dunes for a comparison with my data. The main reason was that they are comparable to open xerophytic habitats in respect of the floral diversity and microclimatic parameters. Table 8 shows the results of three studies on dune biotops.

Ichneumonidae: Horstmann (1988) reported totals of 323 and 320 species of Ichneumonidae found on two small islands in the North Sea. At the Drakenberg I found only 102. But Table 3 indicates a total of 425 species per year. This number coincides quite well with the data of Horstmann and shows that there may be comparable numbers of Ichneumonidae in open dry habitats.

A striking difference between the two North sea islands and my meadow is in the occurrence of parasitoids of Lepidoptera. On the dunes roughly 40% of all Ichneumonidae attack Lepidoptera, whereas on the Drakenberg only 25% do so. The same fact holds for the parasitoids of the also phytophagous tenthredinid larvae. Overrepresented, on the other hand, are the wasps that attack brachycerous Diptera (mostly the pupae).

Chalcidoidea: I found only 25 species of Eulophidae whereas Copland and Askew (1977) reported 54 species in a sand dune area and Vidal (1988) collected 94 and 81 species on two small

Table 7. Comparison of the species numbers of the Göttingen beech forest and the dry meadow of the present study. Data obtained by the collector's curves in Table 3 and Ulrich (1998). Drakenberg factor: number of species at the dry meadow / species number in the beech forest.

	Number of species expected on								
	1 m²			10 m²			50 m²		
Guild	Drakenberg	Göttingen beech forest	Drakenberg Factor	Drakenberg	Göttingen beech forest	Drakenberg Factor	Drakenberg	Göttingen beech forest	Drakenberg Factor
Parasitoids of miners	19	8	2.38	56	22	2.54	104	31	3.36
P. of gall-makers	13	11	1.18	43	26	1.64	87	38	2.28
P. of ectophytophages	16	6	2.67	56	24	2.35	122	47	2.60
P. of myceto-/saprophages	32	18	1.78	75	38	1.96	113	65	1.74
Egg-parasitoids	30	6	5.00	51	15	3.37	61	21	2.89
Guild unknown	52	10	5.20	179	32	5.60	378	58	6.52
All parasitoids	195	65	3.00	598	196	3.05	1140	323	3.53

Table 8. Comparison of the results of various studies about parasitic Hymenoptera living in open sandy habitats with the data of the present study.

Habitat	Parasitoid group	Author	Number of species	Numbers of species of the present study
Island of Memmert (dunes with a mixed vegetation)	Ichneumonid parasitoids of	Hortstmann 1988		
	Arachnida		15	5
	Planipennia		5	2
	Coleoptera		13	3
	Nematocera		38	9
	Brachycera		51	22
	Lepidoptera		132	26
	Terebrantes		17	15
	Symphyta		15	3
	all Ichneumonidae		323	102
	Eulophidae	Vidal 1988	81	25
Island of Mellum (dunes with a mixed vegetation)	Ichneumonid parasitoids of	Hortstmann 1988		
	Arachnida		18	5
	Planipennia		6	2
	Coleoptera		15	3
	Nematocera		36	9
	Brachycera		56	22
	Lepidoptera		125	26
	Terebrantes		15	15
	Symphyta		13	3
	all Ichneumonidae		320	102
	Eulophidae	Vidal 1988	94	25
Whiteford Burrows		Copland and Askew 1977		
	Pteromalidae		87	45
(maritime sand dunes)	Eulophidae		54	25
	Encyrtidae		30	21
	Eurytomidae		14	4
	Torymidae		13	2
	Chalcidoidea (except Mymaridae)		212	108
	Mymaridae		–	24

North Sea islands. From the data of Table 3 one can infer a total number of 109 species at the Drakenberg, a value which also equals the species numbers in other dry habitats. Leaving the Mymaridae aside, Copland and Askew found 212 species of Chalcidoidea, twice the species number of the Drakenberg (106). But in this case the data of Table 3 give a much higher annual number of species (491).

Quantitative data about biomass and abundance of the parasitoids are also rare. Thiede (1975), in a study of a spruce forest, found between 66 and 600 ind. m^{-2} a^{-1}, Hilpert (1989) reported densities between 410 and 518 ind. m^{-2} a^{-1} for a mixed leaf forest and my samplings in a beech forest on limestone (Ulrich 1987, 1998) revealed abundances between 123 and 1078 ind. m^{-2} a^{-1}. The abundances presented here (335 and 1120 ind. m^{-2} a^{-1}) lie at the upper limit of this range. The density in 1986 is the highest one reported up to now. The average density of the Drakenberg is 1.66 times the value of the Göttingen beech forest (728 to 431 ind. m^{-2} a^{-1}).

Only Thiede (1975) and Ulrich (1998) provided data on the biomass of parasitoid communities. Judged by the means the parasitoids of the semixerophytic meadow emerge roughly with twice the biomass (132 mgDW m^{-2} a^{-1}) of the two forest habitats (68 mgDW m^{-2} a^{-1} in the beech forest and 59 mgDW m^{-2} a^{-1} in the spruce forest).

On the basis of these results it seems that open dry areas not only have more than twice the number of species of parasitic Hymenoptera than forest habitats but that abundance and biomass also takes roughly the double value.

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5. SUMMARY

In 1986 and 1988 the hymenopterous fauna of a semixerophytic meadow on limestone near Göttingen (FRG) was studied using ground-photo-eclectors.

A total of 4982 specimens belonging to 475 different species were collected (Tables 1, 2, 3). Extrapolations from double-log functions revealed that there may be as many as 1330 parasitoid species present per year (Figure 1). This number is significantly higher than that of a nearby beech forest (Table 7), but may be comparable to species numbers in open sand dune habitats (Table 8).

455 of the 475 species were parasitoids. 155 of them attack Diptera, 48 Lepidoptera, 36 beetles, 23 wasps, 22 plant hoppers and 13 aphids (Table 1). The other arthropod groups support only a minor number of species. 47 of the species are egg-parasitoids and parasitoids of miners, ectophytophages count for 44 of the wasp species. But only 69% of the species could be sorted according to their biology; for 144 species no hosts are known (Table 2).

The abundance of the wasp fauna was rather high (1120 ± 53 ind. m^{-2} a^{-1} (1986) and 335 ± 42 ind. m^{-2} a^{-1} (1988) (Tables 4, 5,6). Most abundant were the parasitoids of miners, gall-makers and the egg-parasitoids. Compared to the high abundance the biomass was low. In 1986 the wasps weighed a total of 194 ± 24 mgDW m^{-2} a^{-1} and in 1988 only 69 ± 20 mgDW m^{-2} a^{-1}. The parasitoids of ectophytophagous Lepidoptera and Coleoptera counted for more than half of the whole biomass.

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Appendix. Alphabetical list of the Hymenoptera and the number of individuals (N) collected on the dry meadow Drakenberg near Göttingen (FRG).

Species	N
Aclastus gracilis	24
Aclastus solutus	1
Aclista TD1	1
Aclitus TD1	2
Acrolyta rufocincta	1
Aleiodes TD1	15
Allantus truncatus	6
Alloea ?contracta	13
Allotropa TD1	11
Alloxysta ?cursor	2
Alloxysta TD1	36
Alloxysta TD2	17
Alloxysta TD3	2
Alomya debellator	2
Alysiini TD1	1
Amblyaspis TD1	39
Amblyaspis TD2	10
Amblyaspis TD3	2
Anagrus TD1	126
Anagrus TD2	125
Anagrus TD3	65
Anaphes TD1	12
Anaphes TD2	96
Anaphes TD3	3
Anaphes TD4	11
Anaphes TD5	6
Anaphes TD6	19
Anaphes TD7	5
Anaphes TD8	14
Andrena TD1	2
Andrena TD2	1
Aneurhynchus TD1	1
Anopedias TD1	1
Anoplius viaticus	1
Anteon TD1	2
Anteris TD1	1
Apanteles TD1	24
Apanteles TD2	20
Aphaereta ?tenuicornis	1
Aphaereta major	29
Aphanogmus TD1	2
Aphanogmus TD10	3
Aphanogmus TD11	2
Aphanogmus TD12	1
Aphanogmus TD14	2
Aphanogmus TD2	11
Aphanogmus TD3	6
Aphanogmus TD4	33
Aphanogmus TD5	1
Aphanogmus TD6	2
Aphanogmus TD7	20
Aphanogmus TD8	7
Aphanogmus TD9	2
Aphelinus abdominalis	6
Aphelinus asychis	2
Aphelinus TD1	5
Aphelopus melaleucus	3
Aphelopus serratus	1
Aphidius ?uzbekistanicus	57
Aphytis TD1	69
Aphytis TD2	3
Arthrolytus TD1	251
Arthrolytus TD2	1
Asaphes suspensus	2
Ascogaster abdominator	13
Asobara tabida	1
Aspilota TD1	4
Aspilota TD"2"	13
Aspilota TD3	1
Aspilota TD4	4
Aspilota TD5	69
Aspilota TD6	4
Aspilota TD7	1
Astiphromma mandibulare	1
Atractodes TD1	3
Baeus TD1	253
Basalys abrupta	8
Basalys ciliaris	1
Basalys longipennis	2
Basalys nr. cymocles	108
Basalys parva	15
Basalys TD2	4
Basalys TD4	2
Basalys TD5	2
Basalys TD7	6
Basalys TD8	1
Basalys TD9	1
Basalys tripartita	3
Belyta depressa	132
Blacus ambulans	19
Blacus exilis	1
Blacus humilis	13
Blacus ruficornis	35
Blacus TD1	2
Blacus TD2	1
Blastothrix TD1	1
Blastothrix TD2	19
Brachygaster minuta	2
Bracon TD1	11
Bracon TD3	3
Bracon TD4	3
Bracon TD5	1
Bracon TD6	6
Bracon TD7	1
Bruchophagus TD1	9
Callitula pyrrhogaster	161
Campoletis zonatus	3
Camptoptera papaveris	1
Centistes cuspidatus	6
Ceranisus menes	1
Ceraphron TD1	476
Ceraphron TD10	3
Ceraphron TD11	1
Ceraphron TD2	10
Ceraphron TD3	20
Ceraphron TD4	4
Ceraphron TD5	40
Ceraphron TD6	6
Ceraphron TD7	43
Ceraphron TD8	36
Ceraphron TD9	3
Charitopes clausus	3
Chasmodon apterus	10
Chelogynus ephippiger	18
Chelogynus TD1	1
Chelonus TD1	3
Chlorocytus longiscapus	1
Chlorocytus TD1	1
Chorebus ?stilifer	2
Chorebus leptogaster	1
Chorebus nerissa	3
Chorebus petiolatus	3
Chorebus senilis	9
Chorebus TD1	2
Chorebus TD2	1
Chorebus TD3	3
Chrysocharis TD1	2
Cinetus TD1	1
Cirrospilus vittatus	1
Cleonymus TD1	3
Cleruchus TD1	5
Coelichneumon desinatorius	23
Coelinius gracilis	16
Conostigmus TD1	26
Conostigmus TD10	32
Conostigmus TD2	12
Conostigmus TD3	10
Conostigmus TD4	5
Conostigmus TD5	4
Conostigmus TD6	7
Conostigmus TD7	2
Conostigmus TD8	1
Cremnodes atricapillus	1
Cryptopimpla errabunda	1
Cryptus TD1	1
Cyclolabus nigricollis	1

Species	N
Cymodusa leucocera	1
Cyrtogaster vulgaris	8
Dacnusa ?dryas	1
Dacnusa faroeensis	1
Dacnusa TD1	4
Dacnusa TD2	1
Dapsilarthra rufiventris	1
Dendrocerus ?laticeps	1
Dendrocerus dubiosus	1
Dendrocerus halidayi	1
Dibrachys boarmiae	1
Dibrachys cavus	5
Dicaelotus pictus	1
Dichrogaster aestivalis	2
Diglyphus crassinervis	1
Diphyus palliatorius	1
Diplazon laetatorius	2
Disorygma depile	1
Doliphoceras TD1	5
Dryinus TD1	1
Encyrtidae TD1	3
Encyrtidae TD10	1
Encyrtidae TD11	1
Encyrtidae TD12	1
Encyrtidae TD13	1
Encyrtidae TD14	1
Encyrtidae TD15	1
Encyrtidae TD2	3
Encyrtidae TD4	5
Encyrtidae TD5	3
Encyrtidae TD6	1
Encyrtidae TD7	22
Encyrtidae TD8	38
Encyrtidae TD9	16
Entomacis TD1	2
Entomacis TD2	1
Ephedrus TD1	4
Ephedrus TD2	1
?Ephedrus TD3	3
Epitomus infuscatus	4
Ericydnus TD1	2
?Ericydnus TD2	21
Ethelurgus sodalis	2
Eupelmus TD1	1
Eupteromalus hemipterus	21
Eurytoma collaris	1
Eurytoma TD1	2
Eusterinx TD1	3
Eustochus atripennis	1
Exallonyx brevicornis	2
Exallonyx confusus	2
Exallonyx ligatus	11
Exallonyx longicornis	4
Exallonyx microcerus	3
Exallonyx nixoni	7
Exallonyx pallidistigma	1
Exallonyx quadriceps	7
Exallonyx subserratus	3
Exallonyx trichomus	1
Formica rufa	5
Gastrancistrus TD1	2
Gelinae TD1	1
Gelinae TD12	1
Gelinae TD2	1
Gelinae TD25	1
Gelinae TD26	1
Gelis brassicae	2
Gelis TD1	13
Gelis TD2	1
Gelis TD3	10
Gelis TD4	2
Gelis TD5	1
Gelis TD7	1
Gelis TD9	2
Gonatocerus TD1	87
Gryon TD1	8
Gryon TD2	1
Habrocytus TD1	1
Habrocytus TD2	4
Habrocytus TD3	1
Habrocytus TD4	1
Hemigasterini TD1	1
Hemigasterini TD2	1
Hemigasterini TD3	3
Hemigasterini TD4	1
Hemigasterini TD5	1
Hemigasterini TD6	1
Hemigasterini TD7	7
Hemigasterini TD8	12
Hemiptarsenus fulvicollis	37
Hemiptarsenus TD1	6
Heterischnus truncator	1
Homoporus TD1	1
Homotherus locutor	1
Hoplismenus albifrons	1
Hormius similis	6
Ichneumoninae TD10	3
Idiolispa analis	1
Inostemma TD1	2
Inostemma TD2	2
Iphitrachelus lar	1
Ismarus rugulosus	1
Kleidotoma psiloides	25
Kleidotoma TD1	1
Kleidotoma TD2	2
Kleidotoma TD3	6
Lagynodes pallidus	32
Lasius flavus	82
Leptacis tipulae	6
Lipolexis TD1	24
Lissonota TD1	4
Lissonota TD2	3
Lissonota TD3	1
Lissonota TD4	1
Lissonota TD5	1
Lissonota TD6	2
Litus cynipseus	79
?Lyka TD1	1
Macrocentrus infirmans	2
Macrocentrus linearis	1
Macroglenes bouceki	1
Macroglenes chalybea	1
Macroglenes penetrans	1
Macroneura vesicularis	1
Macrophya quadrimaculata	3
Mastrus deminuens	2
Megastylus TD1	6
Meraporus graminicola	19
Merostenus excavatus	3
Mesochorus thoracicus	2
Mesochorus vitticollis	2
Mesopolobus TD1	1
Metaphycus TD1	1
Microctonus TD1	3
Microgaster ?tibialis	2
Microplitis calcaratus	4
Microplitis mediator	2
Microplitis TD1	1
Miscogaster maculata	14
Mymar pulchellum	2
Myrmica rubra	390
Myrmica ruginodis	1
Necremnus ?folia	1
Olesicampe patellana	1
Olesicampe subcallosa	1
Oligosita TD1	1
Omphale TD1	16
Omphale TD2	2
Omphale TD3	1
Omphale TD4	3
Omphale TD5	7
Omphale TD6	9
Ooctonus hemipterus	21
Ooctonus TD1	1
Ooctonus vulgatus	97
Opius pallipes	1
Opius TD1	1
Opius TD2	2
Opius TD3	2
Opius TD4	1
Orthocentrus TD1	29
Orthocentrus TD2	6

Species	N
Exallonyx minor	3
Osmia TD1	1
Oxybelus uniglumis	1
Oxylabis thomsoni	2
Pachyprotasis rapae	9
Panstenon oxylus	3
Pantoclis ?ruralis	1
Pantoclis leviventris	7
Pantolyta TD1	13
Pantolyta TD2	10
Pantolyta TD3	8
Pediobius TD1	127
Pediobius TD2	2
Pentapleura pumilio	4
Peristenus ortholyti	1
Peristenus TD1	1
Phaenoglyphis TD1	2
Phaenoglyphis TD2	3
Phaneroserphus calcar	18
Phrudus devectivus	1
Phygadeuon ?trichops	23
Phygadeuon TD12	2
Phygadeuon TD14	1
Phygadeuon TD15	1
Phygadeuon TD16	1
Phygadeuon TD17	1
Phygadeuon TD18	1
Phygadeuon TD19	4
Phygadeuon TD2	1
Phygadeuon TD20	1
Phygadeuon TD21	1
Phygadeuon TD3	3
Phygadeuon TD4	1
Phygadeuon TD9	1
Piestopleura TD1	1
Pimpla instigator	1
Pimpla melanacrias	9
Pimpla TD2	1
Platygaster TD1	15
Platygaster TD2	1104
Platygaster TD3	17
Platygaster TD4	2
Platygaster TD5	1
Platygaster TD6	1
Platygaster TD7	3
Platylabus iridipennis	1
Platystasius TD1	1
Polyaulon paradoxus	9
Polynema fumipenne	62
Polynema TD1	10
Polynema TD2	6
Polynema TD3	1
Polynema TD4	2
Praon "volucre"	37
Lasius niger	137
Priocnemis perturbator	5
Pristiphora ?monogyniae	1
Probles neoversutus	1
Probles TD1	2
Proclitus TD1	1
Psilocera ?obscura	16
Pteromalinae TD2	14
Pteromalinae TD4	1
Pycnocryptus director	1
Rhogogaster viridis	11
Rhoptromeris eucera	17
Rhynchopsilus apertus	6
Rogas TD1	6
Rogas TD2	6
Rogas TD3	3
Rogas TD4	1
Scelio vulgaris	1
Seladerma TD1	4
Seladerma TD2	1
Semiotellus mundus	3
Semiotellus TD1	1
Semiotellus TD2	3
Spaniopus TD1	1
Sphegigaster flavicornis	4
Spilomena troglodytes	1
Stenodontus marginellus	1
Stenomacrus TD1	139
Stenomacrus TD2	5
Stenomalina ?dives	2
Stenomalina muscarum	6
Stenomalina TD1	1
Stenomalina TD2	4
Stilbobs abdominalis	1
Stilpnus blandus	4
Subprionomitus TD1	2
Sussaba cognata	1
Sussaba flavipes	7
Sympiesis sandani	11
Synacra brachialis	32
Synomelix TD1	1
Synopeas decurvatus	3
Synopeas TD2	77
Synopeas TD3	1
Synopeas TD4	3
Telenomus TD1	5
Telenomus TD3	1
Tetramesa flavicollis	30
Tetrastichus TD1	6
Tetrastichus TD10	1
Tetrastichus TD11	2
Tetrastichus TD2	41
Tetrastichus TD3	5
Tetrastichus TD4	10
Orthocentrus TD3	2
Tetrastichus TD8	181
Tetrastichus TD9	1
Theroscopus hemipterus	5
Theroscopus TD1	4
Theroscopus TD2	2
Torymus TD1	16
Torymus TD2	1
Toxares TD1	5
Tretoserphus laricis	1
Triaspis TD1	1
Trichacis pisis	4
Trichacis TD1	8
Trichacis TD2	1
Trichogramma TD1	12
Trichomalus TD1	2
Trichomalus TD2	3
Trichomalus TD3	2
Trichomalus TD4	0
Trichopria ?alifera	1
Trichopria ?melanopa	1
Trichopria aequata	20
Trichopria alienus	1
Trichopria minor	5
Trichopria verticilliata	8
Trimorus TD1	18
Trimorus TD2	6
Trimorus TD3	7
Trimorus TD5	1
Trimorus TD6	6
Trimorus TD7	1
Trimorus TD8	1
Trioxys "pallidus"	22
Trioxys TD2	1
Tromatobia ovivora	3
Trybliographa TD1	16
Trybliographa TD2	1
Vulgichneumon suavis	15
Woldstedtius biguttatus	2
Zaglyptus varipes	1
Zygota ?fossulata	2
Zygota soluta	1
Zygota TD1	2
Zygota TD2	1
Zygota TD3	1