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MORPHOLOGY AND ECOLOGY OF THE PARASITIC HYMENOPTERA: ANALYSIS OF THREE MORPHOLOGICAL PARAMETERS AND THEIR RELATIONSHIP TO ENVIRONMENTAL FACTORS

ABSTRACT: In the parasitic Hymenoptera of a dry meadow on limestone and a beech forest on limestone (both near Göttingen, FRG) three morphological parameters were analyzed and related to environmental factors: the relative wing surface, the ovipositor length and the relative length of the hind leg (as a measure of body-compactness). Two coefficients of wing surface and one of body-compactness are developed. Wing surface and length of legs turned out to be allometrically related to the thorax volume of the species. Soil living parasitoids had the relatively largest wings and longest hind legs; parasitoids of the canopy level showed the opposite trend. On the dry meadow many more wingless or short winged species occurred than in the beech wood; these species also reached higher densities. In the fully winged species there were more species with smaller wing surfaces on the dry meadow than in the beech wood. Idiobiontic parasitoids appeared to have much higher proportions of wing reduced species than koinobiontic species. The impact of these differences in morphology on community structure is discussed.

KEY WORDS: Hymenoptera, parasitoids, morphology, wing surface, ovipositor length, flight ability, allometric dependence.

1. INTRODUCTION

The morphology of an animal often reflects some ecological constraints that act in shaping certain morphological parameters (Peters 1983). In the parasitic Hymenoptera, of course, the ovipositor length reflects the necessity of reaching into or at least near the host. Therefore, the length of the ovipositor is in part an

indicator of the host-type or the microhabitat of the host. Other indicators for ecological parameters are the shape and the size of the wings, the relative length of the appendages or the form of the antenna.

Up to now, only very few studies were undertaken relating morphological

and ecological parameters in the Hymenoptera. Most authors dealt with the Hymenoptera in general when constructing density biomass curves (see Currie and Fritz 1993 and literature therein). The body length and its distribution across different habitats and strata had also been studied (Basset and Kitching 1991, Stork and Blackburn 1993, Cyr *et al.* 1997). Zinnert (1969) gave an account on the morphology of ichneumonid larval parasitoids of sawflies. However, studies dealing with all parasitoid species and re-

lating their morphology and ecology are missing.

The aim of the present study is to analyze three important morphological parameters (the wing surface, the body-compactness, and the ovipositor length) of the parasitoid community of two well-studied habitats, a dry meadow on limestone and a beech forest on limestone. It relates these parameters to ecological data and compares the habitats to develop some hypothesis on the constraints shaping the communities.

2. MATERIALS AND METHODS

For the present study the well-known hymenopteran faunas of the Göttingen beech forest and the dry meadow Drakenberg near Göttingen (FRG) were analyzed. Ulrich (1987, 1988, 1998, 1999a) gave detailed accounts of the fauna, the study sites and the sampling program. The Göttingen beech forest is a 120-year old forest on limestone (*Melico-Fagetum* subassociation *Lathyrus vernus*), in which a total of 720 species of Hymenoptera, mainly parasitoids, had been found (Ulrich 1998). The Drakenberg is a dry meadow (*Gentiano Kolerietum*) on a limestone plateau where 475 species were found. Ulrich (1999a) and Hövemeyer (1996) gave detailed descriptions of the study site, the sampling methods, and the fauna.

One middle sized specimen of all of the species was measured, taking the thorax volume (max. length \times max. width \times max height), the total length of the hind leg, the max. length and width of the front wing, and the length of gaster. The length of the valvulae of the ovipositor was also measured, except in those spe-

cies with a totally hidden ovipositor, which were found only in a small number of individuals (to measure the ovipositor length, one would have to destroy these specimen).

The product of max. length \times max width of the wing proved to be a very good estimator of the wing surface WS (Fig. 1):

$$WS [mm^2] = 0.6535 \times (\text{width [mm]} \times \text{length [mm]}). \quad (1)$$

To develop Fig. 1, the wing surface of 15 species of all major superfamilies were measured exactly (raster method after scanning the wings). The good correlation reflects the fact that the overall shapes of the hymenopteran wings are very similar. There are very few exceptions (mainly in the Diapriidae and Encyrtidae) in which lobes or holes at the front side or the tip of the wings appear. The Hymenoptera show a pronounced allometric relationship between thorax volume and wing surface (Figs 2 and 3). The simplest way to measure the relative wing surface of a species and to compare it with others would be to take the dis-

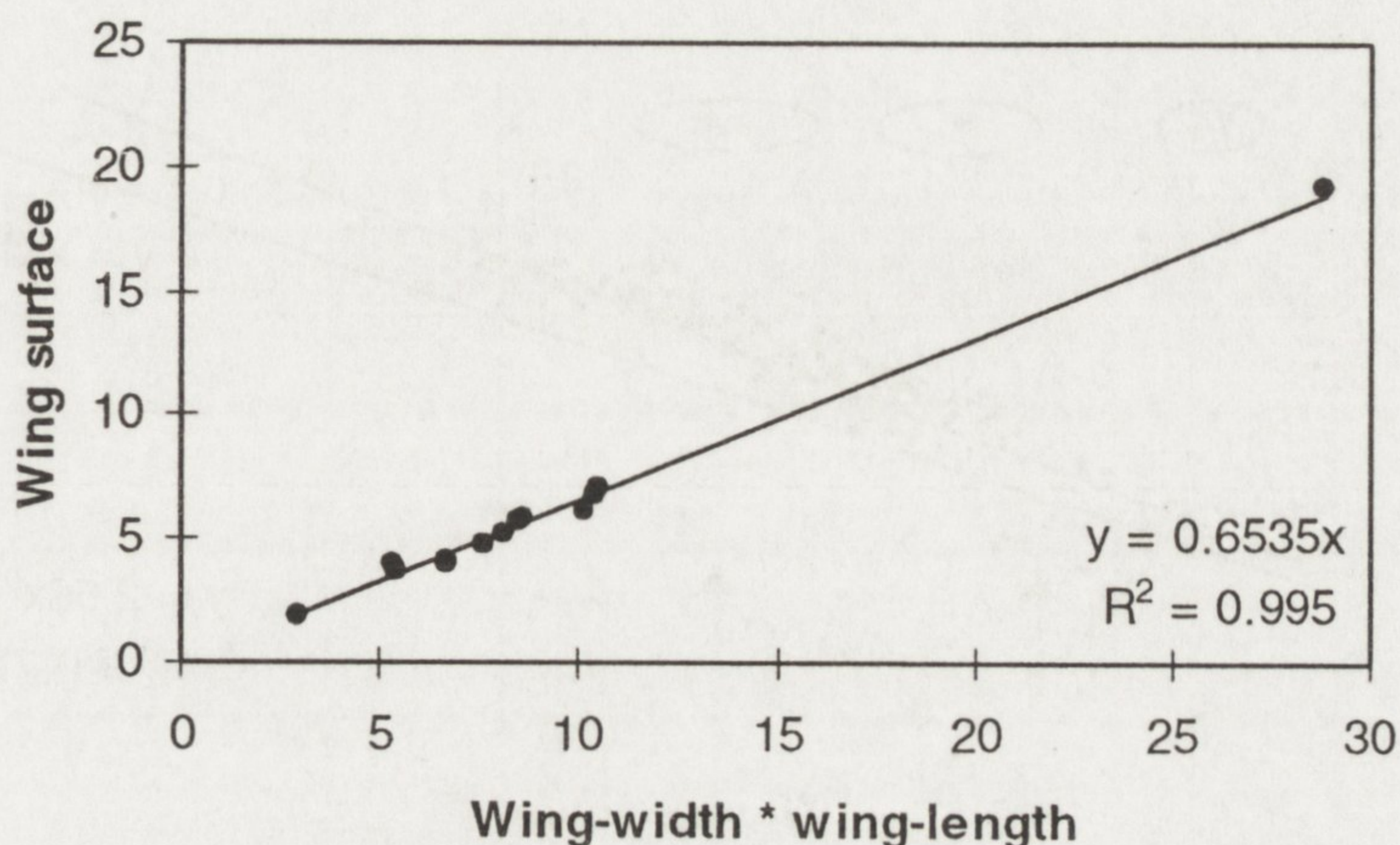


Fig. 1. Dependence of wing surface on product of wing length \times width in 15 hymenopteran species of all major superfamilies. The wings were scanned and the surface measured by a quadrate method. The axe-values are relative measures, R^2 : variance explanation.

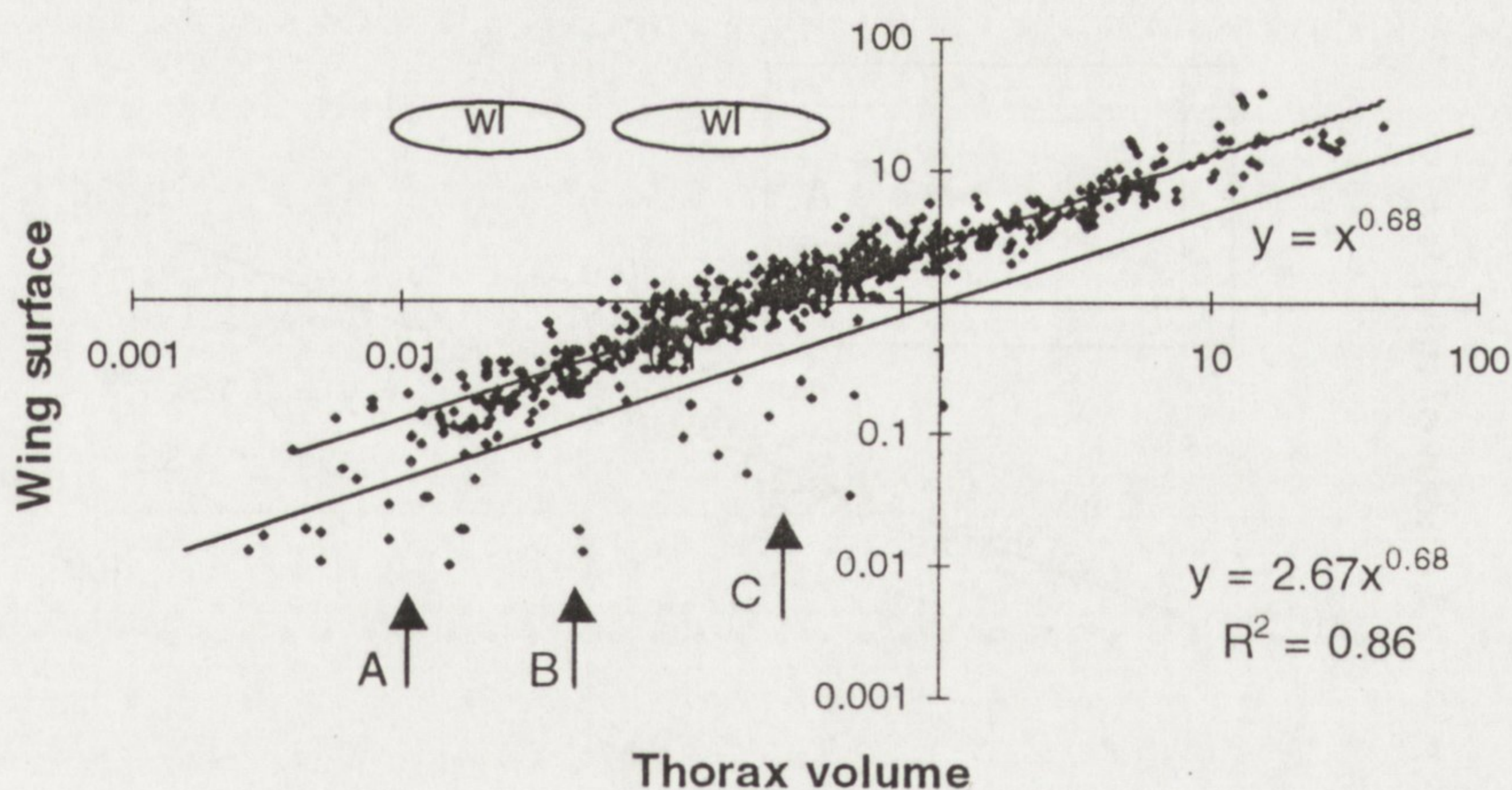


Fig. 2. Thorax volume [mm^3] and wing surface [mm^2] in the Hymenoptera of the beech forest. A, B, C denote the three types of short-winged species, wl marks the size ranges of the apterous species. The lower formula (with variance explanation R^2) refers to the regression of the fully winged species.

The upper formula refers to the lower boundary line for the fully winged species.

tance of the real surface from the one computed with the allometric function (distance A in Fig. 4). Because the real distance is of course strongly dependent of thorax volume, I took the natural logarithm of this distance (denoted as W_A). This procedure has the further advantage that the resulting coefficient is dimensionless. In the case of the parasitoids of

the beech forest this coefficient therefore takes the form:

$$W_A = \ln(\text{wing surface } [\text{mm}^2]) - (\ln(2.6742) + 0.6783 \times \ln(\text{thorax volume } [\text{mm}^3])). \quad (2)$$

In the case of the dry meadow the same coefficient has the form:

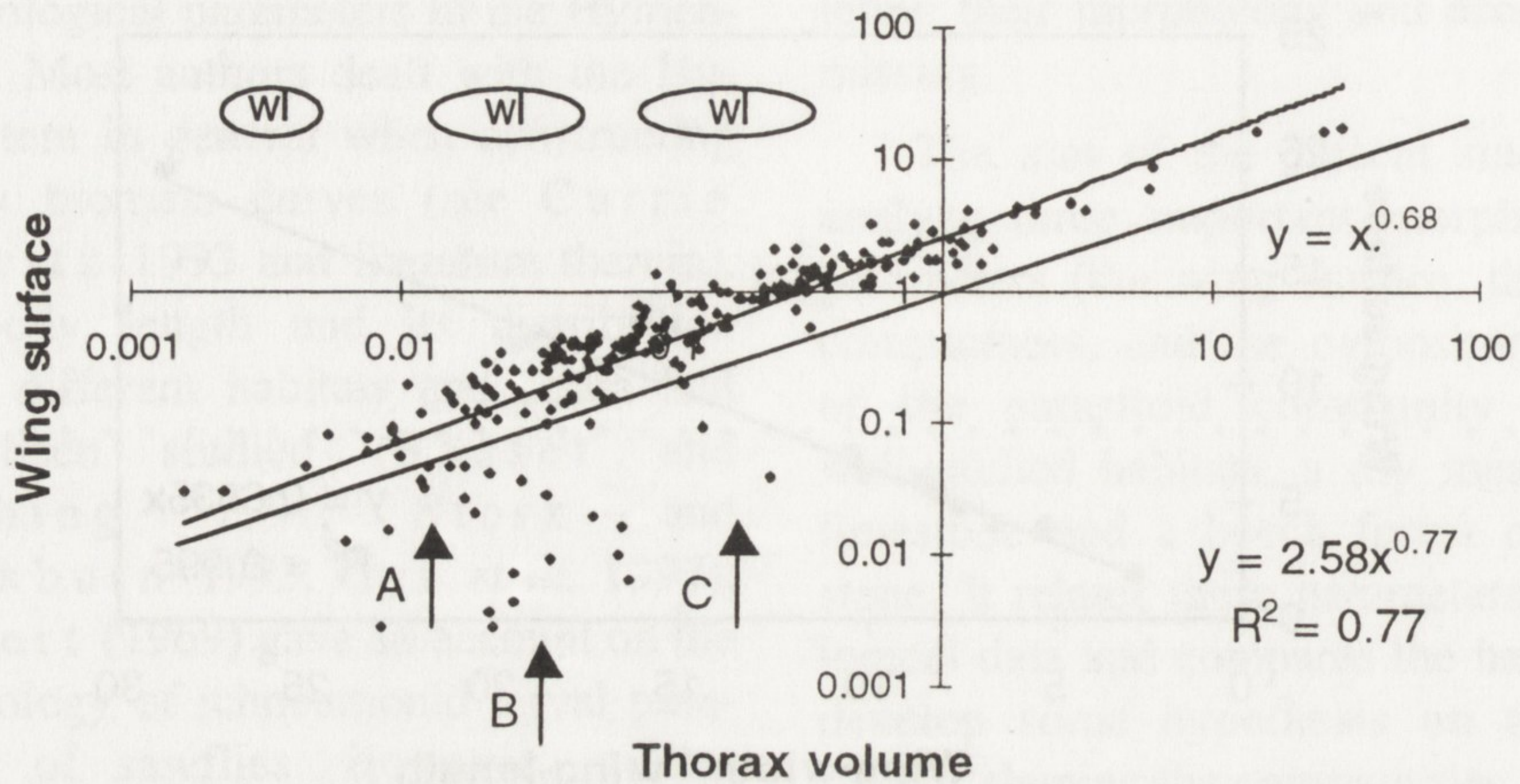


Fig. 3. Thorax volume [mm^3] and wing surface [mm^2] in the Hymenoptera of the dry meadow. A, B, C denote the three types of short-winged species, wl marks the size ranges of the apterous species. The lower formula (with variance explanation R^2) refers to the regression of the fully winged species. The upper formula refers to the lower boundary line for the fully winged species.

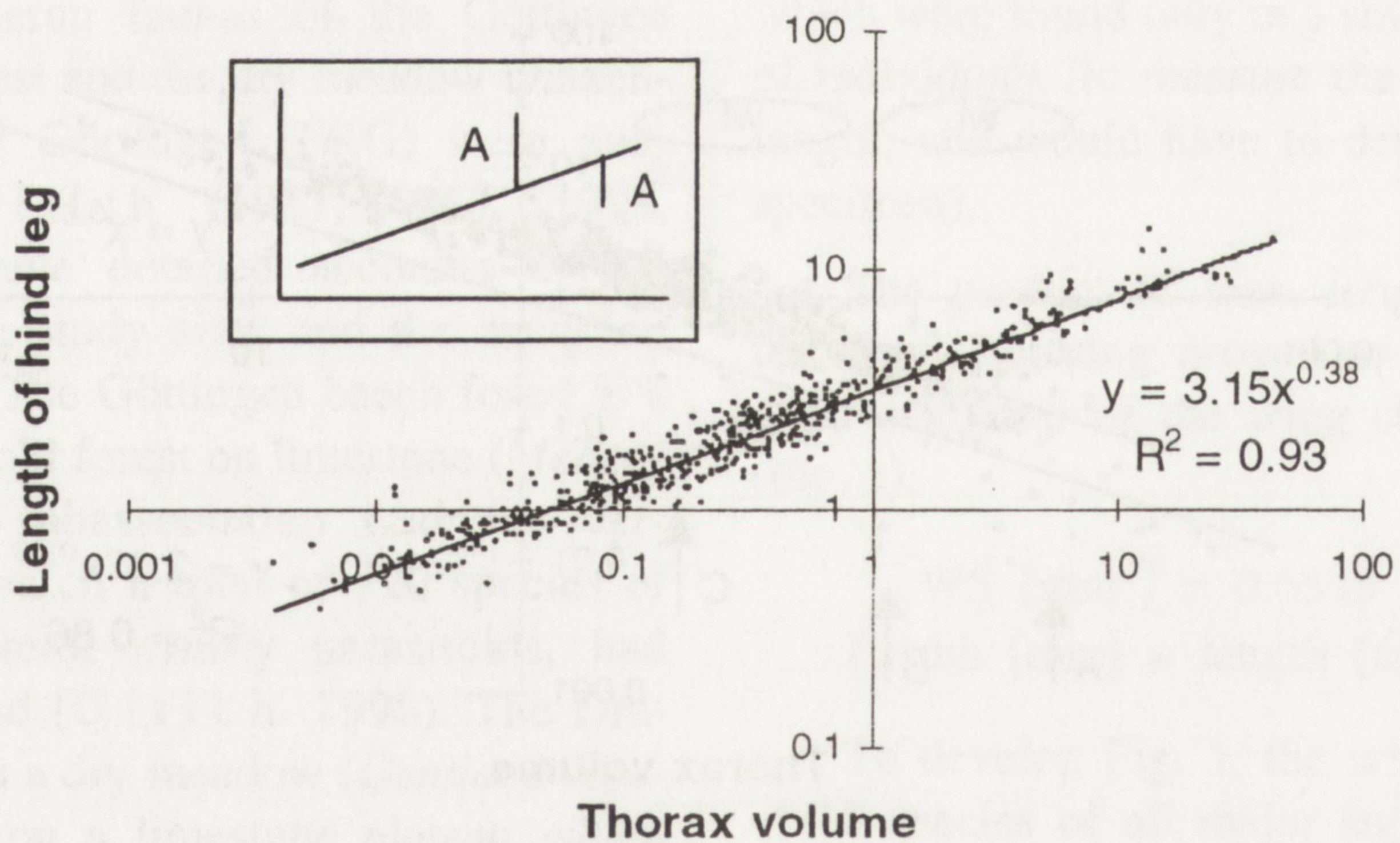


Fig. 4. Dependence of length of hind leg [mm] on thorax volume [mm^3] in the Hymenoptera of the beech forest. A denotes the vertical distance of a data point to the regression line as a measure of relative length of hind leg. Further explanation in the text.

$$W_A = \ln(\text{wing surface } [\text{mm}^2]) - (\ln(2.5768) + 0.7701 \times \ln(\text{thorax volume } [\text{mm}^3])). \quad (3)$$

The parameters are therefore habitat dependent. In the fully winged Hymenoptera of the beech forest the range of this measurement reaches from -0.9 to 1.3 , at the dry meadow the range is -1.0

to 1.1 . In both cases the mean is nearly 0 . The measurement is independent of thorax volume ($r = 0.001$).

This distance measurement is very suitable to compare species, but to compare guilds (with $W_{A\text{total}} = (\sum W_{A\text{li}})/S$; S : number of species) the measurement has some shortcomings: firstly, when comparing guilds it overemphasizes ex-

treme values; secondly, because there are plus and minus values, the variance is large; thirdly, of course, it is not possible to compare habitats, and fourthly, it is not easy to compute.

A second possibility to measure the relative wing surface is to compute the quotient of wing surface and thorax volume. To linearize the quotient the coefficient takes the form:

$$W_Q = (\text{wing surface [mm}^2\text{]})^{1/2} / (\text{thorax volume [mm}^3\text{]})^{1/3}. \quad (4)$$

Like W_A the coefficient is dimensionless. It is also independent of habitat and easy to measure. But the value is slightly dependent on the thorax volume ($r = -0.09$; $p < 0.01$) and on wing surface ($r = 0.14$; $p < 0.0001$) and may therefore result in a bias towards large or small species. The dependence on wing surface is mainly caused by the ophionine Ichneumonidae (in the beech forest 3 species), which have comparably large wings. After eliminating these three species, the correlation vanished ($r = 0.06$; n.s.). To test whether the correlation between coefficient and thorax volume results in a bias I compared the index values of the upper and lower weighing 10, 20, 30, 50, and 100 species (with and without Ophioninae). In no case did significant differences appear (t-test, all p-values above 0.2). As a further test I compared the coefficient with the previous one. Spearman's rank correlation between the two indices gave a value of 0.998 and 607 of 618 ranks were equal. For the different ecological guilds of the

parasitoids the results of both indices are also nearly identical (Table 4). The second coefficient is therefore suitable to compare many-species-communities.

Hymenoptera differ widely in their overall appearance. There are very slender species with long appendages and a slim body and there are stout ones with short legs and antenna and a rather compact body. The first category is often found in the Braconidae or the ophionine Ichneumonids; the second form is represented by many Ceraphronidae, Pteromalidae or orthocentrine Ichneumonids. A suitable measurement of body-compactness seems to be the relation between hind leg and thorax volume. In the Hymenoptera, the length of the hind leg depends in an allometric manner on the thorax volume (or the weight) (Fig. 4). Again, a simple measurement of body-compactness (BC) is to compute the deviation of the hind leg length of a species from the one derived by the allometric function (like in the case of W_A):

$$BC = \ln (\text{length of hind leg [mm]}) - (\ln (3.1735) + 0.3792 \times \ln (\text{thorax volume [mm}^3\text{]})). \quad (5)$$

(beech forest) and

$$BC = \ln (\text{length of hind leg [mm]}) - (\ln (3.1620) + 0.3820 \times \ln (\text{thorax volume [mm}^3\text{]})). \quad (6)$$

(dry meadow)

The dimensionless coefficient ranges between -0.55 and $+0.72$ with a mean of nearly 0. It is independent of thorax volume.

3. RESULTS

3.1. FLIGHT ABILITY

A lot of hymenopteran species of the Göttingen beech forest and the dry meadow Drakenberg are wingless or short winged. However, because there is an allometric relationship between wing surface and biomass (thorax volume) it is sometimes difficult to judge whether a species is short winged or not. Therefore, in a first step of analysis the exact form of this allometric relationship in the parasitic Hymenoptera was analyzed (Figs 2 and 3).

It appears that the wing surface-thorax volume relationship can readily be described by an exponential function of the form $Y = a X^b$. The exact parameters of the functions differ slightly between the habitats, reflecting the different size distribution (Ulrich 1999c) (Figs 2 and 3).

The function $Y = X^{-0.68}$ marks in both habitats the boundary between full winged and short winged species. On the other hand, there are no species with "too large" wings and the same function, but with an intercept of 10 can be used to describe the upper boundary of wing surface ($Y = 10 X^{-0.68}$). The indices of relative wing surface also allow full winged and short winged species to be separated. All short winged species have index values below -1.1 (coefficient 1), and below 0.9 (coefficient 2). Fully winged species always have values above -1.0 and above 1.0, respectively.

It also appeared that there are no short winged or wingless species with a thorax volume above 1 mm^3 ; that means a biomass above 0.54 mg dry weight. The largest wingless species are some Ichneumonidae of the genera *Gelis* and *Polyaulon* (cocoon or hyperparasitoids), and the

embolemid *Embolemus antennalis* of which the biology is unknown (Lewis and Whitfield 1997). The largest short winged species is also an ichneumonid, *Pleolophus vestigialis* (0.54 mg dry weight), a pupal parasitoid of various dipteran and lepidopteran hosts (Höve-meyer 1995) (Figs 2 and 3).

In both habitats three different types of short winged Hymenoptera can be detected. Type A is represented mostly by very small species (around 0.01 mm^3 thorax volume) mainly of the families Mymaridae and Diapriidae (Tables 1 and 2). Their ratio of wing surface to thorax volume follows the lower boundary line and all of the species compensate their small wing surfaces with long apical hairs. Due to their small size, this combination allows them to fly or, more precisely, to row through the air. Type B is also made up by species of small size (0.01 to 0.1 mm^3 thorax volume), mostly of the families Ceraphronidae, Megaspilidae and Pteromalidae (Tables 1 and 2). In the forest habitat type B species are much less represented than at the open land site. Type C species are small to medium sized (0.1 to 1 mm^3 thorax volume). In this type Ichneumonidae, Diapriidae and Scelionidae dominate and there are more species in the forest than on the meadow (Figs 2 and 3).

These three size classes can also be detected in the wingless species. The size classes of type B and C are well represented in both habitats, whereas wingless Mymaridae or other very small wingless parasitoids are missing in the beech forest (Tables 1 and 2).

There are interesting ecological differences between the members of the

Table 1. Apterous and brachypterous species of parasitic Hymenoptera from the beech forest.
The types of short-wingedness (A, B, C) are the same as in Fig. 2.

Species	Family	Guild	No. of species	% total fauna	Species	Stratum	No. of species	% total fauna
Brachypterous					Brachypterous			
Type A	Mymaridae	Egg-parasitoids	10	1.5	Type A	Canopy	3	0.5
	Diapriidae	Parasitoids of saprophages	2	0.3		Herb layer	3	0.5
	Megaspilidae	Unknown	1	0.2		Soil	3	0.5
						Unknown	4	0.6
Type B	Megaspilidae	Unknown	1	0.2	Type B	Unknown	3	0.5
	Ceraphronidae	Unknown	2	0.3				
Type C	Scelionidae	Egg-parasitoids	4	0.6	Type C	Canopy or herb layer	0	0.0
	Diapriidae	Parasitoids of saprophages	2	0.3		Soil	6	0.9
	Pteromalidae	P. of mycetophages	1	0.2		Unknown	5	0.8
	Diapriidae	P. of mycetophages	3	0.5				
	Ichneumonidae	P. of ectophytophages	1	0.2				
Apterous	Scelionidae	Egg-parasitoids	1	0.2	Apterous	Canopy or herb layer	1	0.2
	Braconidae	P. of sap-suckers	1	0.2		Soil	4	0.6
	Diapriidae	P. of mycetophages	1	0.2		Unknown	7	1.1
	Ichneumonidae	P. of predators	1	0.2				
	Ichneumonidae	Hyperparasitoid	1	0.2				
	Megaspilidae	Unknown	1	0.2				
	Ceraphronidae	Unknown	2	0.3				
	Pteromalidae	Unknown	1	0.2				
	Embolemidae	Unknown	1	0.2				
	Ichneumonidae	Unknown	2	0.3				

Table 2. Apterous and brachypterous species of parasitic Hymenoptera from the dry meadow. The types of short-wingedness (A, B, C) are the same as in Fig. 3.

Species	Family	Guild	No. of species	% total fauna	Species	Stratum	No. of species	% total fauna
Brachypterous					Brachypterous			
Type A	Mymaridae	Egg-parasitoids	5	1.7	Type A	Herb layer	5	1.7
	Scelionidae	Egg-parasitoids	1	0.3		Soil	3	1.0
	Diapriidae	Parasitoids of saprophages	2	0.7		Unknown	3	1.0
	Aphelinidae	P. of sap-suckers	1	0.3				
	Eupelmidae	Hyperparasitoid	1	0.3				
	Ceraphronidae	Unknown	1	0.3				
Type B	Scelionidae	Egg-parasitoids	1	0.3	Type B	Herb layer	4	1.4
	Charipidae	Hyperparasitoid	1	0.3		Soil	1	0.3
	Eulophidae	P. of miners	1	0.3		Unknown	8	2.8
	Pteromalidae	P. of miners	2	0.7				
	Diapriidae	P. of mycetophages	1	0.3				
	Megaspilidae	Unknown	2	0.7				
	Ceraphronidae	Unknown	5	1.7				
Type C	Encyrtidae	P. of sap-suckers	1	0.3	Type C	Herb layer	1	0.3
	Diapriidae	P. of saprophages	2	0.7		Soil	2	0.7
Apterous	Scelionidae	Egg-parasitoids	1	0.3	Apterous	Herb layer	2	0.7
	Mymaridae	Egg-parasitoids	2	0.7		Soil	2	0.7
	Braconidae	P. of miners	1	0.3		Unknown	6	2.1
	Ichneumonidae	P. of predators	1	0.3				
	Ichneumonidae	Unknown	3	1.0				
	Megaspilidae	Unknown	2	0.7				

above defined types (Tables 1 and 2). Type A contains mostly egg-parasitoids (77% in the beech forest and 55% at the dry meadow) and parasitoids of saprophagous Diptera (15 and 18%). The ecology of the type B species is to a large extent unknown (100 and 54%), and in type C soil living parasitoids of mycetophages and saprophages dominate (55 and 67%). In general the species composition on the dry meadow appears to be more diverse; in the beech forest the types are ecologically more clearly defined.

In the beech forest most of the short winged or wingless species are soil living (Tables 1 and 2). 13 out of 39 species (33%) find their hosts at the soil, and only 7 (18%) in the canopy or herb layer. The highest percentage of canopy or herb layer living species occur in the morphologically short winged, but functionally full winged species of type A. On the dry meadow this trend reverses. More short winged or wingless species are confined to the herb layer (12 species; 32%) than to the soil (8; 22%).

In the full winged species of both habitats there is a negative gradient in relative wing surface from the soil towards the canopy region (Table 3). The parasitoid species living in the canopies of the trees have relatively smaller wings than the species at the soil. The species which find their hosts in the herb layer take an intermediate level. The difference between the canopy species and the soil / herb layer species appeared to be statistically highly significant (U-test both p -values below 0.01).

There are also differences in wing surface between the parasitoid guilds. Parasitoids of saprophages, mycetophages, and miners have comparably large wings (Table 4). On the other hand, egg-parasitoids and parasitoids of predatory arthropods have relatively small wing surfaces. The other guilds do not differ from the mean.

Table 3 shows that there are striking differences between the open land site and the forest. At the dry meadow 13% of all species are short winged or wingless, in the beech forest only 6%. Espe-

Table 3. Differences in wing-surface of the hymenopteran parasitoid species in the Göttingen beech forest and the dry meadow. Significant differences (U-test) between the two habitats are marked with *: $p(U) < 0.05$, **: $p(U) < 0.01$, and ***: $p(U) < 0.001$. W_Q refers to the second coefficient of wing surface (Formula 4). The types of short-wingedness (A, B, C) are the same as in Figs 2 and 3.

Flight ability	Dry meadow			Beech forest		
	No. of species	% total fauna	W_Q	No. of species	% total fauna	W_Q
Normal						
Soil	57	19.7	1.69	194	29.6	1.81*
Herb layer	122	42.1	1.59	49	7.5	1.77***
Canopy	—	—	—	81	12.3	1.623
Type A	11	3.8		13	2.0	
Type B	13	4.5		3	0.5	
Type C	3	1.0		11	1.7	
Apterous	10	3.4		12	1.8	
All brachypterous or apterous species	37	12.8		39	5.9	

Table 4. Differences in wing surface (W_A , W_Q), body-compactness (BC) and ovipositor-length in different parasitoid guilds of the beech forest. *: $p(U) < 0.05$, **: $p(U) < 0.01$, ***: $p(U) < 0.001$, ****: $p(U) < 0.0001$. The significance level refers to differences from the mean. The species with unknown guild were taken as a null model for this mean and the guilds were tested against this null model guild. In the case of the wing surface only the fully winged species are included. W_A and W_Q refer to the first and second coefficient of wing surface (Formulas 2 and 4). The body-compactness BC was calculated with Formula 5.

Parasitoids of	Number of species	Mean length of ovipositor [mm]	BC	W_A	W_Q
Sap-suckers	33	0.24±0.17****	0.04	0.02	1.65±0.27
Egg-parasitoids	45	0.29±0.31**	0.08	-0.22*	1.48±0.38*
Saprophages	63	0.47±0.31**	0.09***	0.33****	1.94±0.35****
Gall-makers	68	0.52±0.85*	-0.09***	-0.03	1.60±0.18
Miners	55	0.72±0.69	-0.05	0.17****	1.78±0.27****
Mycetophages	82	0.97±1.08	0.07***	0.24****	1.85±0.23****
Predators	41	0.83±0.62	0.002	-0.06	1.59±0.20
Guild unknown	133	0.86±0.75	-0.06	-0.04	1.62±0.30
Hyperparasitoids	37	0.99±0.78	0.00	0.024	1.66±0.23
Ectophytophages	108	1.76±1.81**	0.002	-0.002	1.63±0.32
Xylophages	4	2.29±2.49	0.02	0.063	1.68±0.14
All species	669	1.00±1.130	0.003	-0.035	1.69±0.30

cially marked is this difference in the type B species. Additionally, in the normal winged species there are also more species with relatively small wing surfaces (Table 3). For the parasitoids living at the soil as well as for the species of the herb layer coefficient 2 (coefficient 1 is not applicable) of wing surface gives significantly lower values in the case of the meadow. The relatively smaller wing surfaces of the dry meadow species also explain the lower intercept of the wing surface – thorax volume regression in Fig. 3.

The total number of wingless parasitoid species in Europe is around 150 and there are probably around 400 to 600 short winged species (Types B and C only) (see Ulrich 1999b for details concerning the method of counting). Therefore, between 550 and 750 hymenopteran parasitoid species (3.4% to 4.7% of the total European fauna) have reduced wings. The dry meadow under

study has therefore between two to three times the expected number of species with reduced wings (9.0%). The beech forest, on the other hand, does not deviate from expectation (4.0%).

The beech forest and the dry meadow differ not only in the number of short winged species, but also in their densities (Table 5). At the open land site the wingless species reach the three-fold density of the forest habitat, and the type B and C species even 50-fold abundances. In the type A species (mostly Mymaridae) *Litus cynipseus* accounts for a large part of the total density in the beech forest and on the meadow. Not counting this species the abundance of the type A species is more than two times the value of the beech forest. But the percentage of the total abundance of the type A species is nearly equal in both habitats, whereas the other types of short winged species reach a much higher percentage of the total density on the dry meadow. In

Table 5. Mean densities (ind. m⁻²) of the short winged or wingless hymenopteran parasitoids of the beech forest and the dry meadow. The types of short-wingedness (A, B, C) are the same as in Fig. 2 and 3.

Flight ability	Beech forest		Dry meadow	
	Density	% of total mean density	Density	% of total mean density
Type A	51	11.8	81	11.1
without <i>Litus cynipseus</i>	35	8.1	73	10.0
Type B	<1	<0.5	45	6.2
Type C	<1	<0.5	1	0.1
Apterous	4	0.9	38	5.2
Normal winged species	376	87.2	563	77.3

total, in the beech forest the short winged or wingless species account for 13% of the total mean density; on the meadow they reach 23%.

The percentages of short winged egg-parasitoids is higher (2.2 to 3.3%) (Tables 1 and 2) on the meadow than in the forest which indicates a higher percentage of potential hosts. The parasitoids of soil living saprophages or mycetophages take roughly the same percentage in both habitats but brachypterous parasitoids of sap-suckers are also more abundant on the meadow (0.2 to 0.7%) again indicating higher numbers of hosts, mostly various Rhynchota, which indeed reach higher abundances in open habitats. The most striking difference is the high percentage of short winged or wingless Ceraphronoidea on the meadow

(3.4%). In the forest this group only reaches 1.2%. The dry meadow is therefore richer in species of ecological groups and taxa which contain high percentages of short winged species, especially parasitoids of sap-suckers, egg-parasitoids, and Ceraphronoidea of which the ecology is mostly unknown. This fact may also explain the observed pattern.

The flight ability is not equally distributed between the idio- and the koinobiontic species (that means between species which kill or paralyze their hosts immediately and parasitoids which do not) (Table 6). Although there are fewer idiobiontic species, many more of them are wingless or short winged. This trend is apparent in both habitats and in all of the four types. At the dry meadow there

Table 6. Flight ability and parasitoid type (koino- versus idiobiontic) of the parasitic Hymenoptera of the beech forest and the dry meadow. The types of short-wingedness (A, B, C) are the same as in Figs 2 and 3.

Flight ability	Dry meadow			Beech forest		
	Idiobiontic	Koinobiontic	Unknown	Idiobiontic	Koinobiontic	Unknown
Normal	80	127	45	197	350	70
Type A	9	0	2	12	0	1
Type B	2	2	9	0	0	3
Type C	1	1	1	8	3	1
Apterous	7	1	2	6	1	5

are 19 idiobiontic and 4 koinobiontic species with reduced wings; in the beech forest the relation is even more extreme (26 to 4). The short winged species with unknown biology (Tables 1 and 2) come mostly out of the families Ceraphronidae

(genus *Ceraphron*), Megaspilidae (genus *Conostigmus*), Pteromalidae, and Ichneumonidae. Probably, most of these species are also idiobiontic (Gauld and Bolton 1988).

3.2. LENGTH OF OVIPOSITOR

Parasitic Hymenoptera differ extremely in the length of the ovipositor. Parasitoids of endophytophages or concealed hosts have often very long ovipositors, whereas species which lay their eggs on exposed hosts have normally short ovipositors. Table 4 shows that there are clear differences in ovipositor length between the parasitoid guilds. Egg-parasitoids, and the parasitoids or saprophages and of sucking insects have, on average, the smallest ovipositors. Medium sized ones have parasitoids of miners, gall-makers, mycetophages, predators and the hyperparasitoids. Very large

ovipositors are found in the parasitoids of ectophytophages and, of course, of xylophages.

In the beech forest there are also significant differences between the strata. Species which find their hosts in the canopy or at the soil have longer ovipositors than species confined to the herb layer (Table 7). Between the habitats no significant differences could be detected. As a comparison Table 7 also gives the mean thorax volume of the species. The data show that the differences in ovipositor length are not correlated with differences in thorax volume.

Table 7. Differences in ovipositor length [mm], thorax volume ThV [mm³], and body-compactness BC between different strata in the beech forest and the dry meadow. S: Number of species. Significance values refer to the U-test. The body-compactness BC was calculated with Formula (5).

Stratum	S	Mean length of ovipositor	BC	ThV
Beech forest				
Tree crowns	81	1.21±1.52	Crown-herb: -0.09 p (U) < 0.01	Tree-herb: 1.06±2.16 p (U) = 0.07
Herb layer	49	0.51±0.44	Ground-herb: -0.02 p (U) < 0.01	Ground-herb: 1.71±3.34 p (U) < 0.01
Ground	194	0.95±1.05	Ground-tree: 0.07 n.s.	Ground-tree: 1.92±5.38 p (U) < 0.001
Dry meadow				
Herb layer	122	0.63±0.70	Ground-herb: -0.001 n.s.	Ground-herb: 0.57±2.84 p < 0.05
Ground	57	0.69±0.73	0.06	1.02±3.86

3.3. RELATIVE LENGTH OF THE APPENDAGES

The parasitic Hymenoptera of the beech forest differ widely in the relative length of the appendages (Table 4). The

parasitoids of soil living mycetophagous or saprophagous insect larvae or pupae have the relatively longest hind legs.

It may be that these legs are used for digging or jumping. On the other hand, the parasitoids of gall-makers are the stoutest species; that means they have comparably short hind legs. All other guilds do not differ from the mean.

There is an interesting relationship between body-compactness and wing surface (Fig. 5). With the exception of the egg-parasitoids, which mostly have small wings but long hind legs, a positive correlation between both variables turns up. Slender species have also relatively large wings; short legged species have

comparably small wing surfaces. The relationship is not size dependent because both indices are independent of the thorax volume of the species. But the data indicate a relationship with the stratum (Table 7). Parasitoids of the crown region were found to have the relatively shortest hind legs, parasitoids with hosts at the soil have the longest ones, and herb layer species take a middle range. This trend is the same as in the relative wing surface (Table 3) and in mean thorax volume (Table 7), indicating that the stratum may play a crucial role in shaping the communities concerning morphological traits.

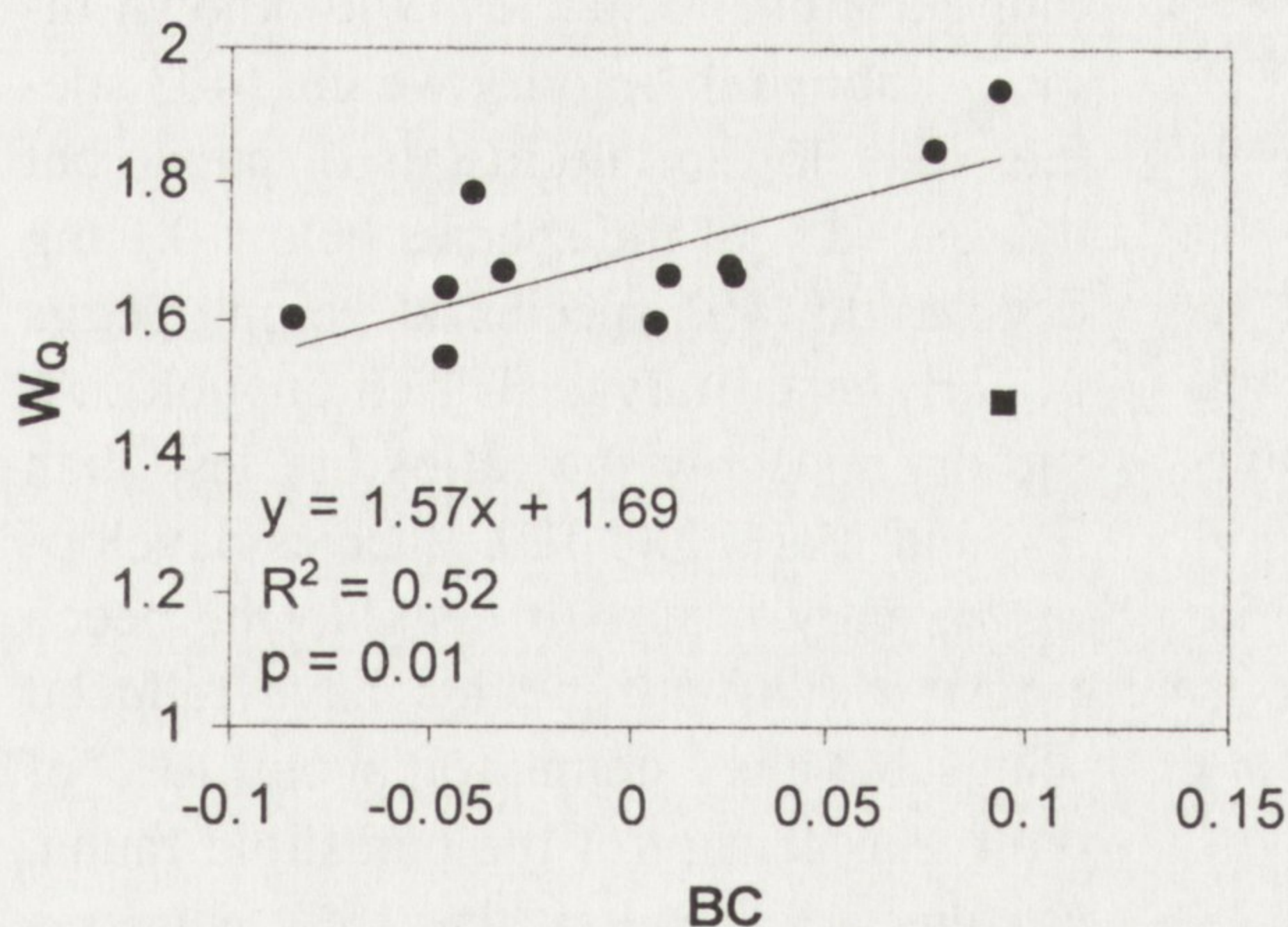


Fig. 5. Relation between body-compactness (coefficient BC) and relative wing length (coefficient W_Q) in different parasitoid guilds of the beech forest. The data point marked by a ■ refers to the egg-parasitoids, which are not included in the regression. R^2 : variance explanation; p : significance level.

4. DISCUSSION

Ever since Hutchinson (1959) ecologists were interested in the relationship between morphology and ecology. Most work had been done in defining niche dimensions and limits of co-existence using morphological parameters (e.g. Hutchinson 1959, Horn and May 1977, Abrams 1983, McNally 1988). It focused on competition as a morphology-shaping – and therefore

community-shaping – factor. The present work takes a different, and much more seldom, approach. It compares different ecological guilds of parasitic Hymenoptera of two habitats and shows that there are differences concerning morphological parameters. These parameters do not concern direct adaptations to certain hosts or mate finding such as the shape of the exodont mandible in alysiine Braconidae

(to crack the puparium of the dipteran hosts) or various enlargements of antenna of many Encyrtidae, Eulophidae and other families (to harbor more sensilla). With the exception of ovipositor length they also can not be related directly to constraints resulting from guild membership. The differences found deserve therefore more general ecological or environmental explanations. On the other hand, these differences influence the structure of the parasitoid communities.

The first finding that needs explanation is the difference in flight ability between the open land site and the forest habitat. Similar findings were made by Brown and Southwood (1983, 1987) and Brown (1985) who reported higher proportions of apterous or brachypterous herbivorous insect species in mid successional stages of grasslands. W a l o f f (1983) reported a reduced wing polymorphism in arboreal phytophagous Hemiptera. W a l o f f (1983) and B r o w n (1985) explained their findings with the more uniform distribution of resources during successional stages. While such an argument may be applicable to phytophages for the parasitoids two other explanations seem to be more plausible.

A first explanation involves the much more dense herb layer of the dry meadow in comparison to the beech forest. This also leads to a higher density of spiders (Stippich 1986, Ulrich unpubl.), which causes a high pressure by enemies on flying insects. K a j a k (1978) found that up to 38% of all emerging insects in a Polish grassland were caught by spiders. Insects may overcome this pressure by reducing their wing surface and by a higher percentage of apterous or brachypterous species in the community.

Stronger winds at open land sites may also cause a trend towards wing reduction. Short winged species do run a lower risk of being drifted away, an argument frequently used to explain the many wingless insect species on islands (K r e b s 1985).

The data presented here suggest that the forest habitat has just the proportion of species with reduced wings that is expected taking the total European hymenopteran fauna as a base. However, the dry meadow "accumulates" apterous or brachypterous species. These parasitoid species also reached comparably higher densities than the fully winged species and are (due to their smaller size, cf. Figs 2 and 3) more often parasitoids of eggs or early instar larvae. In the forest more than 95% of the species (with known biology) above 0.1mg dry weight (403 species) develop in late instars or pupae but at least 15% of the species below 0.1 mg dry weight (291 species) develop in eggs or early instar larvae (Ulrich unpubl.). At the dry meadow the ratios are less than 3% and more than 12% species developing in early instars or eggs. In the beech forest 6% of all species have reduced wings but they count for about 13% of the mean density of the parasitoid fauna. On the dry meadow the 13% wing reduced parasitoid species even have a proportion of 23% of total density. Taking into account that ground-photo-eclectors may not catch apterous species quantitatively their proportions of total density may even be higher. Therefore, apterous or brachypterous parasitoids consume a large amount of available resources. This may also have an influence on abundance and frequency of larger species which develop in later developmental stages of their hosts. Idiobionts do not discriminate as much as koinobionts whether a host is already parasitized or not. Among them

there is a high proportion of facultative hyperparasitoids and many of the species are rather polyphagous (Askew and Shaw 1986). Thus, competition with brachypterous species may be more strong for koinobiontic larval parasitoids (which frequently also lay their eggs in early instar larvae or eggs) than for the idiobionts. Such higher competition would result in a higher proportion of idiobiontic species on the dry meadow. This is indeed the case. In the beech forest of the fully winged species below 0.1 mg dry weight the quotient of idiobionts to koinobionts is 0.74, of the species above 0.1 mg dry weight 0.42, and in total 0.53. That means 34% of the beech forest species are idiobiontic. At the dry meadow the same quotients are 0.9, 0.52 and 0.7, thus 41% of the dry meadow parasitoids are idiobiontic (Ulrich 1999d).

Reduction of wings limits the ability of dispersal. It is therefore no surprise that several studies reported a higher number of apterous species in stable environments compared with ephemeral or unstable habitats (Johnson 1969, Harrison 1980 and literature therein). On first sight, the higher number of wing reduced species in a mid successional dry meadow in comparison to an old stable forest habitat is thus surprising. One may speculate that there is a counterbalance between the need to disperse and the benefits of being apterous. However, more data from other habitats are necessary to sustain such a speculation.

The present study demonstrates that there are markedly differences in morphological parameters between ecological guilds. In the case of the ovipositor length this is of course the expected result. Parasitoids of exposed sap-suckers or of eggs do not need as large ovipositors as parasitoids of large ectophy-

tophages or xylophages. However, the differences in body-compactness and wing surface do not have such an obvious explanation. Interesting is also that both parameters are to a certain extent connected. Parasitoids of mycetophages and saprophages are rather slender and have larger wings, parasitoids of gall makers are rather stout, small winged species. I am not aware of any other study that measured morphological parameters in relation to ecological guilds, but it would be interesting to see whether these trends also hold for the hosts of the parasitoids.

One of the most interesting results of the present study is the high proportion of idiobiontic species with reduced wings. It seems that egg-, pupal- and ectoparasitoids are more prone becoming wingless than larval endoparasitoids. This result can only partly be explained by the different distribution of the host types between the strata. Of course, larvae are more abundant in the canopy or herb layer (where fewer short winged species occur), whereas many species pupate in the soil. But if one looks at the soil living species only, the trend is still apparent. Of the 18 species with reduced wings (both habitats) 13 are idiobiontic and only 5 koinobiontic ($\text{CHI}^2: p < 0.001$). This result means that a life history trait in larval development may influence a morphological parameter in the adults. Further studies in other habitats are needed to explain the phenomenon in detail.

The large amount of data, morphologic, ecologic and phenologic, available for the parasitoid species of the Göttingen beech forest and the dry meadow Drakenberg raise the question whether it may be possible to predict the biology of the species by a combination of all these data. For this purpose I undertook a regression and cluster analysis combining

all the available data to predict the host guild, host taxon, stratum and parasitoid type (idio- or koinobiontic). In the cases of host guild and host type the regression analysis resulted in highly significant functions (all p-values below 0.001) with degrees of variance explanations above 0.9 (data not shown). For the host taxon it was not possible to derive such functions. But in the test of predicting the biology of the species the success rate in predicting the parasitoid guild was only 27%. Although this rate is by far more than would be expected by chance (10%) it is of course much too low to be reliable. Similar low performance came up

in predicting host stratum and parasitoid type. The functions performed better in predicting parasitoids of myceto- or saprophages but could not separate parasitoids of phytophagous insects.

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5. SUMMARY

In the parasitic Hymenoptera of a dry meadow on limestone and a beech forest on limestone (both near Göttingen, FRG) three morphological parameters were analyzed and related to environmental and ecological factors: the relative wing surface, the ovipositor length and the relative length of the hind leg (as a measure of body-compactness).

Two indices of wing surface and one of body-compactness are developed (Figs 1 and 4).

Wing surface and length of legs turned out to be allometrically related to the thorax volume of the species (Figs 2 and 3). Body compactness and relative wing surface were correlated (Fig. 5).

Soil living parasitoids had the relatively largest wings and longest hind legs; parasitoids of the

canopy level showed the opposite trend (Tables 3, 4, 6 and 7). Differences also appeared between parasitoid guilds.

On the dry meadow many more wingless or short winged species occurred than in the beech wood (Tables 1 and 2); these species also reached higher densities (Table 5). In the fully winged species there were more species with smaller wing surfaces on the dry meadow than in the beech forest.

The number of species with reduced wings was not equally distributed between koinobiontic and idiobiontic species. (Table 5). Idiobionts (mainly pupal, ecto- and egg-parasitoids) appeared to be much more prone becoming brachypterous or apterous than koinobionts (mostly larval endoparasitoids).

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