

# Anemophilous pollen in the diet of Syrphid flies with special reference to the leaf feeding strategy occurring in Xylotini (Diptera, Syrphidae)

By

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## Abstract

Anemophilous pollen constitutes an important part of the diet of Syrphidae. Pollen analysis of crop and gut content is a valuable method of tracing the main pollen sources in the food of hoverflies and can be carried out also on material from water-dish-traps. Three groups of syrphids are distinguished: 1. Flower-visiting of grasses and sedges occurs in *Melanostoma*, *Platycheirus* and *Pyrophaena*, 2. flower-visiting of anemophilous trees and shrubs is a major pollen-supply for early-flying syrphids. An example is given with the feeding specializations of three *Melangyna*-species. 3. Feeding on anemophilous pollen precipitated on leaf-surfaces occurs mainly in *Xylota*. Behaviour, pollen-spectra in the gut and feeding structures are discussed.

## 1. Introduction

While the larval biology in the family of the Syrphidae is quite diverse, adult flies show a rather uniform method of feeding – usually visiting flowers and consuming pollen and nectar. At a closer look however, there are specializations mostly at the family or genus level of visited plants e.g. *Cheilosia illustrata* visiting white-flowering Apiaceae (*Heracleum sphondylium* and to a lesser extent *Aegopodium podagraria*) or *Cheilosia albitarsis* visiting the flowers of Ranunculaceae (KORMANN 1983, 1988; STUBBS 1983; SCHMID 1986), and what is more surprising, feeding on anemophilous pollen plays an important role for several specialized syrphid flies.

When recording syrphid flies with coloured water dishes or by netting there are some common species which are not or only rarely seen on flowers of herbaceous plants. Pollen is necessary for normal egg-maturation in female syrphids (STÜRKEN 1964) and therefore the question “what pollen source do they feed on?” immediately arises. The aim of this paper is to contribute to the understanding of pollen feeding of those syrphid imagines which are only rarely observed visiting flowers of herbaceous plants. Apart from feeding mainly on graminoid pollen (for example in our study: *Melanostoma*), two quite different strategies can be distinguished: specialization on anemophilous trees and shrubs, and a completely different method of pollen ingestion without flower-visiting, the leaf-feeding strategy. These phenomena with their ecological implications are the main topic of this paper: there is still a considerable lack of knowledge about these feeding habits, which are not easily recognizable in the field.

## 2. Biology of the studied syrphids

Feeding on graminoid pollen, mainly on Poaceae, but also on Cyperaceae, has been recognized as a specialization in the genus *Melanostoma* and for some *Platycheirus*-species and *Pyrophaena* (VAN DER GOOT & GRABANT 1970; LEEREVELD 1982, 1984). While *Platycheirus*-species occur predominantly in meadows and pastures (BANKOWSKA 1980), *Melanostoma mellinum* and *M. scalare* are more widespread and were abundant in our study of forest vegetation as well. *Melanostoma mellinum* has been shown to feed on Poaceae or Cyperaceae, according to the predominant vegetation, by means of pollen analysis, and SEM-pictures showed that the flies can act as an efficient pollen transport for pollination (LEEREVELD 1982).

In early spring there is a dearth of pollen for overwintering adult hoverflies and for hoverflies which emerge from pupae early and have a short flying period. Pollen is very limited or even lacking by this time in the herb-layer and therefore other pollen sources are used. Syrphids of the genus *Melangyna* probably overwinter as pupae (SSYMANK 1989) and belong to this group with a short early flight period, being only 3–4 weeks with a maximum at the beginning of April in both sexes. Pollen analysis has not yet been applied to early flying syrphids at all and so the role of anemophilous trees and the degree of specialization in feeding remains largely unknown.

*Xylota segnis* and *X. sylvarum* are common species in and near forests, since they have saproxylophagous larvae. The flight period of *Xylota segnis* extends from the beginning of April to October with a peak in early summer, and *X. sylvarum* appears a month later in May flying until September (RÖDER 1990). Flower visiting is very rare. A literature survey of flower visits of *Xylota segnis* and *X. sylvarum* given by DE BUCK (1985), with additional data in KORMANN (1988), again shows the paucity of flower visits. On the other hand *Xylota*-species can frequently be observed on horizontal leaf surfaces, often below or in the vicinity of other flowering plants. The link between the lack of flower visiting and feeding from leaf surfaces in *Xylota* has been made by GILBERT & PERRY (1982) and GILBERT (1985). The huge labella of *Xylota*-species seems ideally suited to acting as a vacuum over leaf surfaces which harbour pollen grains in reasonable high quantities. The mechanism by which they pick up pollen grains almost certainly involves the pseudotracheae (GILBERT 1981b; SCHUHMACHER & HOFFMANN 1982).

## 3. Methods

UK field methods have been published elsewhere (GILBERT 1981b, 1985), and were also used in Maine and Oregon (USA). German field studies were carried out with sets of coloured water-dish traps (blue, white, yellow) and 1/2 h standard census walks every 10 days to observe flower visits of syrphids in the years 1986/87 in a mosaic of mesophilous and hygrophilous forests with their accompanying forest cutting and edge communities in the foothills of the Black Forest (Southern Germany). A detailed description of the vegetation is given in SSYMANK (1989, 1991b). The syrphid communities of 14 different sites are described in detail from standard census walks and water-dish traps in SSYMANK (1991a). The abundance of certain syrphid species in the water-dish traps which were not seen flower-visiting at all from the standard census walks was an obvious reason to concentrate further studies on these groups.

In our investigation area in forests, several *Xylota*-species and three *Melangyna*-species were sufficiently abundant in water-dish traps; with only rare records from flowers for these species, we were likely to find preferences for other pollen sources. A hygrophilous beech forest with *Allium*

ursinum-dominance in the herb layer was an ideal place for further observations on leaf-feeding of *Xylota segnis*. Here most of the direct observations were made during the flowering period of *Allium* on 6 days in May 1987.

Pollen analysis of gut-contents was then applied to a selection of syrphid flies and carried out with the method of LEEREVELD (1982), boiling the whole fly in 10% KOH (reduced boiling time of ca. 1–2 min.) and staining with safranin (Merck). After rinsing and dissecting the gut was emptied on a microscopic slide and mounted in glycerine jelly. A pollen herbarium is necessary for identifying the pollen and can be made by directly staining the pollen from anthers with a drop of safranin-solution on a slide and subsequent mounting in glycerine jelly. For determination of the pollen FAEGRI & IVERSEN (1975), MOORE & WEBB (1978) and PUNT (1976ff.) are helpful, but these deal with acetolysed fossil pollen: literature on fresh pollen in glycerine jelly is rare (e.g. ZANDER 1935 for identification of pollen in honey). Pollen identification is not always possible to species level using a light microscope, and especially Poaceae and Asteraceae can usually only be identified to a species group, even taking into account the flowering phenology of plants in the study area. The cited pollen-type refers to the lowest possible level of microscopic distinction using a light microscope.

Pollen precipitation on leaf surfaces was counted under a stereomicroscope and subsequently wiped off with a moist cotton-bud to analyse the percentage of pollen types involved.

In addition to pollen analysis, morphometric data of feeding structures were taken to recognize possible morphometric adaptations to leaf-feeding, using the methods described by GILBERT (1981b, 1985).

Syrphid names follow F. C. THOMPSON'S World Catalogue (held in electronic format at the U.S. National Museum, Washington D.C., USA); plant names follow OBERDORFER (1983).

## 4. Results

### 4.1. The number of flower species visited

A first hint of a specialized feeding behaviour of syrphid flies is a generally low number of plant species recorded during standard census walks. Tab. 1 gives the number of plant species visited according to different authors for some hoverflies. It includes the material from our own research in southern Germany (column F) and Great Britain (Col. G) and shows a group of species (I) with a generally very wide spectrum of flowers visited and (e.g. *Melanostoma mellinum*) and on the other hand a selection of species only rarely seen at flowers. To the latter belong the listed *Melangyna*- and *Xylota*-species, chosen for further investigations.

### 4.2. Flower visiting of grasses and sedges (*Melanostoma*)

The high number of plant species visited in our field studies (s. Tab. 1) for *Melanostoma* shows a very wide spectrum of possible pollen sources. However, specialization for Poaceae and Cyperaceae is evident from the subsequent data on flower visits of *Melanostoma*-species in forest vegetation (SSYMANK 1989). Of 115 recorded visits of *M. mellinum* to 29 plant species, 59% were to Poaceae and a further 17% to Cyperaceae. For 153 visits of *M. scalare* to 38 plant species, the equivalent figures are 65% and 8% respectively. In grass-dominated vegetation types, such as *Molinia arundinacea*-stands, *Melanostoma*-species were the only syrphids recorded.

Both *Melanostoma*-species occur together but may reduce possible competition since, with exception of *Molinia arundinacea*, there are clear differences in flower visiting. The number of flower visits of *Melanostoma*-species on different grasses in edge communities



Table 2  
Gut content of 26 *Melangyna lasiophthalma*-individuals, caught in different forests in southern Germany

Date	Sex	Gut	Sambucus racemosa	Lonicera xylostema	Alnus glutinosa	Anemone nemorosa	Corylus avellana	Populus tremula	Ranunculus repens	Tussilago farfara	indet- mined	Stellaria nemorum	Dentaria heptaphylla	Salix caprea	Hippophae rhamnoides	Chrysosplenium varia	spores	number of pollen-types
8. 4. 87	f	+	100															1
8. 4. 87	m	+	100															1
8. 4. 87	f	+	99.8		0.2													2
8. 4. 87	f	+	99.8				0.2											2
8. 4. 87	m	+		100														1
8. 4. 87	f	+		100														1
8. 4. 87	f	+		99.8													0.2	4
8. 4. 87	f	+	2.9	59.1		95.5			1.0						37.0			2
8. 4. 87	f	+	4.5						53.2		10.4					0.4		5
8. 4. 87	f	+	36.2			96.0		3.6								0.4		3
11. 4. 86	m	+					100											1
11. 4. 86	m	+	96.6						2.1				1.3					3
15. 4. 86	f	+									10.5							2
15. 4. 86	f	+	89.5								5.2							3
15. 4. 86	f	+	69.6			25.2												3
15. 4. 86	f	+			100													1
15. 4. 86	m	+		58.3														3
15. 4. 86	m	+				75.3			0.4		41.5			0.2				3
15. 4. 86	m	+	0.4				99.0				24.4			0.2				4
15. 4. 86	f	+						96.5	0.9	3.5								2
18. 4. 87	f	+									98.9							2
18. 4. 87	f	+	37.1	45.7		0.3			16.5									6
24. 4. 86	m	+	100															1
24. 4. 86	m	-	100															1
24. 4. 86	m	+	87.2	11.8										1.0	9.0			3
28. 4. 87	f	-	86.9			0.9					4.7						7.5	4
Mean number of pollen types 2.4 ± 1.3																		

From 42 animals dissected 16 (= 38%) had an almost empty gut. Counts have been made on 500 pollen grains. Explanations: Sex: m male, f female. Gut content: - less than 100 pollen grains, (+) gut up to 1/4 filled, + gut 1/4-3/4 filled, ++ gut full of pollen.

Table 3  
Gut content of 11 *Melangyna quadrimaculata*-individuals, caught in different forests in southern Germany

Pollen-types (%)											number of pollen types	
Date	Sex	Gut	Anemone nemorosa	Sambucus racemosa	Alnus glutinosa	Populus tremula	Corylus avellana	Carpinus betulus	Lonicera xylosteum	Fagus sylvatica		varia
8. 4. 87	f	++	99.2		0.6						0.2	3
8. 4. 87	f	+	99.0		1.0							2
8. 4. 87	f	++	100.0									1
8. 4. 87	f	-			100.0							1
11. 4. 86	m	++	100.0									1
11. 4. 86	f	+			2.0		73.2	4.4	19.5	1.0		5
15. 4. 86	f	++	85.8		14.2							2
15. 4. 86	f	++	0.4	99.6								2
15. 4. 86	f	+				99.8						2
21. 4. 86	f	+	100.0									1
21. 4. 86	f	++	99.9								0.1	2
Mean number of pollen types $2 \pm 1$												

From 19 animals dissected 8 (= 42%) had an almost empty gut. Counts have been made on > 500 pollen grains. Explanations see Tab. 2.

obviously feeds on one plant until the gut is completely full. The flies were caught in traps in vegetation units where no *Alnus* occurs, and therefore minimum flight distances would have to have been between 250 and 400 m.

For *Melangyna lasiophthalma*, standard census walks showed most observations on *Anemone nemorosa*, but pollen analysis revealed a wide spectrum of pollen feeding on trees and shrubs (Tab. 2). The mean number of pollen types present was 2.4, with one main pollen type representing usually more than 70% of the gut content. The main pollen types were *Sambucus racemosa* and *Lonicera xylosteum*, both in 25% of the individuals dissected, *Alnus glutinosa* and *Anemone nemorosa* each in 17%. *Melangyna lasiophthalma* clearly shows a specialization for pollen of the tree and shrub layers.

In the third species, *Melangyna quadrimaculata*, according to pollen analysis about half of the individuals had fed mainly on pollen of *Anemone nemorosa*, and the other half on different shrubs and trees, being mostly anemophilous (Tab. 3). Other herbs are missing from the diet simply because they were only just beginning to flower: *Anemone nemorosa* is the only dominant flowering herb in these meso-hygrophilous beech-forests in mid-April.

#### 4.4. Leaf-feeding (*Xylota*)

In our study only one flower visit of *Xylota segnis* on *Allium ursinum* was observed, while in the same collecting period 4171 individuals of *X. segnis*, 580 of *X. nemorum* and

239 of *X. sylvarum* were caught in water dishes, representing together 25% of all syrphidae (SSYMANK 1991a).

As mentioned above, direct observations have been done mainly in a beech-forest with *Allium ursinum* in the herb layer in May 1987. *Allium ursinum* was in full flower, and its leaves covered about 80–90% of the herb layer in the study plot, with both *Pulmonaria obscura* and young *Acer pseudoplatanus* each covering about 5%. On six days between 10. 5. and 30. 5. 1987 with a total of 285 min. observation time, concentrating on leaf-feeding syrphids, 21 *Xylota segnis* individuals were recorded. They visited usually 2–3 *Allium* leaves one after another before they flew a longer distance out of reach of further observation. Feeding on *Acer pseudoplatanus*-leaves was observed only twice, and on *Pulmonaria obscura* one *Xylota segnis* female landed for a short time without any leaf-feeding. In the other study plots in the foothills of the black-forest during standard census walks, *Xylota segnis* was only seen twice feeding from leaves (of *Tussilago farfara* under flowering *Cirsium arvense* on a roadside-margin).

Close observation of *Xylota segnis* on the leaf surfaces of *Allium ursinum* and *Acer pseudoplatanus* showed that proboscis action and walking along leaf veins occurred more often than on the smooth surfaces of the lamina. Along the veins, pollen aggregations of *Allium*-pollen ( $12 \pm 3$  grains) and *Picea*-pollen from nearby *Picea*-stands accumulate to about double the amount on the lamina. Pollen density on leaf surfaces in May 1987 on the smooth lamina of *Allium ursinum* and *Acer pseudoplatanus* leaves was 60–70 pollen aggregations per  $\text{cm}^2$ , while on the surface along veins there were 100–130 aggregations/ $\text{cm}^2$ . Rough and hairy leaves, like *Pulmonaria obscura*, had an equal distribution of pollen aggregations.

The percentage of pollen types on leaf-surfaces is the same as in the gut content of *Xylota* individuals seen feeding on it. For example, 98.5% of pollen on *Allium ursinum*-leaves was of *Allium*, and this pollen made up 98.6% of pollen in the gut of one *Xylota segnis* female caught feeding on these leaves; even the minor components (anemophilous pollen) correspond. Deformed pollen and fungus-spores were rare in the gut, but often there were bits of leaf epidermal structures and phylloplane mites (mostly Eriophyidae).

The example of *Xylota segnis* given is very instructive since the predominant pollen type in the gut, here *Allium ursinum*, does not imply flower visiting of this plant at all. In the course of the year the diet of both *Xylota segnis* and *X. sylvarum* is mostly anemophilous pollen. A typical table of pollen analysis of the gut content in summer is given for *Xylota sylvarum* (Tab. 4).

The leaf-feeding *Xylota sylvarum* had a high mean number of pollen types present in the gut with 4.8 (for flower-visiting species this is usually well below 4.0). The anemophilous Poaceae, *Urtica dioica* and *Rumex sanguineus* were the main pollen types in 70% of the dissected flies that had eaten pollen. However *Impatiens glandulifera* played a major part in the diet in places of wetter forest cuttings, where this plant dominated in late summer to autumn.

A broader survey of the Xylotini in different places (Tab. 5) suggests that the leaf-feeding method is characteristic for the genus *Xylota*<sup>1</sup> while its close relative *Chalcosyrphus* probably feed from flowers as in other syrphids. This is true for european data as well as for data from the USA, where the number of observations from standard census walks is 139

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<sup>1</sup>) *Xylota coeruleiventris* is an exception and does visit flowers; further investigations on this point are necessary.

leaf-feeding and 7 flower-feeding for *Xylota*, but 1 leaf-feeding vs. 5 flower-visits for *Chalcosyrphus* (chi-sq. = 49,  $p < 0.001$ ). Morphometric measurements on the feeding structures show that *Xylota*-species have a higher pseudotracheal density ( $43.1 \pm 2.5/\text{mm}$ ) than *Chalcosyrphus*, where there are only  $37.8 \pm 2.9$  mm (test of difference,  $F_{1,25} = 25.3$ ,  $p < 0.001$ ).

Table 4  
Gut content of 32 *Xylota sylvarum*, caught in different forests in southern Germany

Pollen-types %												
Date	Sex	Gut	Poaceae; small	<i>Impatiens glandulifera</i>	<i>Urtica dioica</i>	<i>Rumex sanguineus</i>	<i>Cirsium</i> -type	Poaceae; big	<i>Zea mays</i>	<i>Ranunculus</i> -type	<i>Rubus-fruticosus</i>	Hordeum
10. 7. 86	f	(+)			93.9		4.5					
10. 7. 86	m	(+)			0.2		99.0					
21. 7. 87	f	+	100.0									
21. 7. 87	f	++	98.2		1.8							
21. 7. 87	f	++	88.2		3.7					0.5	0.5	
21. 7. 87	m	+	0.8		96.5	0.2	0.2	1.1		0.2		
21. 7. 87	f	+	34.2		51.5			13.5				
21. 7. 87	m	+					2.0			60.1		
21. 7. 87	m	+	2.2		0.3		4.4				63.2	
31. 7. 87	f	+			82.4		10.4		0.2			
31. 7. 87	f	++	0.2		50.3		47.4		0.2			
21. 8. 87	f	++	99.4					0.4				
21. 8. 87	f	++	99.2									
21. 8. 87	f	++	98.5					1.0	0.2			
21. 8. 87	f	+	90.9					8.9				0.2
21. 8. 87	f	+		100.0								
21. 8. 87	f	++		96.7								
21. 8. 87	m	(+)	0.2	60.8	38.1							
21. 8. 87	f	+		2.3	45.7				51.8			
21. 8. 87	m	+	1.9	12.8	2.9	67.5	0.2	6.9				4.7
21. 8. 87	f	++	13.6		0.4			60.1				24.6
21. 8. 87	f	+		30.1	0.4			0.2	67.2			
1. 9. 87	m	++	60.1	29.8	4.6	5.1						0.4
1. 9. 87	m	+		98.0	0.6	1.4						
1. 9. 87	f	+		98.0	0.6	1.2	0.2					
1. 9. 87	m	+	97.8				2.0					
1. 9. 87	m	(+)		96.9	0.4			0.2				
1. 9. 87	m	+	0.2	48.4	8.4	25.2	9.8	2.9			0.2	
1. 9. 87	m	+	3.3	96.3	0.4							
1. 9. 87	m	+		8.4	91.4	0.2						
1. 9. 87	m	++				99.7		0.2				0.1
1. 9. 87	f	+				97.3		2.7				

From 38 animals dissected 6 (= 15%) had an empty gut. Counts have been made on > 500 pollen grains.



5. General discussion

The number of plant species visited and even knowledge of the relative proportions of flowers visited are not always suitable for proof of specialization in feeding for at least three major reasons: first, the number of plant species visited is locally dependent on the

Plantago lanceolata	Erigeron-type	Heracleum sphondylium	Chenopodiaceae	Dryopteris-spores	Lotus	Solanum dulcamara	Tilia	Eupatorium cannabinum	Impatiens noli-tangere	Stellaria nemorum	Achillea-type	Typha latifolia	varia	spores	number of pollen-types
							1.6								3
							0.2				0.2		0.4		6
															1
															2
0.2					5.4	1.0								0.5	8
		1.1												0.2	8
									0.6					0.3	5
					37.3							0.2	0.4		5
	0.3											26.9	2.5	0.3	9
								0.2	1.8				5.5		6
0.2	0.9												0.4	0.5	8
														0.2	3
				0.2										0.6	3
													0.2	0.2	5
															3
															1
		0.2	2.8												5
	0.7												0.3		5
			0.1							0.1			0.2		5
1.5										0.3			1.3		10
0.4				0.4				0.4							8
											0.6		1.6		8
															5
															3
															4
													0.2		3
	2.5														4
	4.1	0.2												0.5	10
															3
															3
															3
															2
Mean number of pollen types $4.8 \pm 2.5$															

For Explanations see Tab. 2.

phenology of flowering and the richness of the vegetation; second, standard census walks do usually not cover all vegetation types within reach of a particular syrphid species and do not include the flowering shrubs and trees, as these flowers are too high up for direct observation; and third, the number of flower records is influenced by the abundance of

Table 5  
Summary of field data on Xylotini from UK and USA

Species	Place	N	Crop	Gut	Nem	L	P/N	Other	PS
<i>Xylota</i>									
<i>annulifera</i> BIGOT	Me	2f	0.0	0.0	0	1	0	1	46.6
<i>atlantica</i> SHANNON	Me	0	—	—	—	2	0	0	—
<i>barbata</i> LOEW	Ore	2m3f	2.2	1.8	1	1	1	3	45.3
<i>confusa</i> SHANNON	Me	2m3f	2.0	1.0	0	11	1	0	39.7
	Ore	2f	3.0	3.0	0	2	0	0	44.6
<i>flavifrons</i> WALKER	Me	1m	1	1	0	0	1	0	37.1
<i>hinei</i> CURRAN	Me	4m1f	1.2	1.0	0	1	0	4	42.0
<i>loveti</i> CURRAN	Ore	1f	3	3	0	1	0	0	41.7
<i>naknek</i> SHANNON	Me	1m2f	0.0	1.0	0	1	0	2	42.4
<i>quadrinaculata</i> LOEW	Me	1m3f	0.5	1.2	1	1	0	3	44.1
	Ore	1m	2	3	0	1	0	0	42.6
<i>raineri</i> SHANNON	Ore	3f	3.0	3.0	0	0	2	1	45.7
<i>segnis</i> L.	Me	1f	—	—	1	1	0	1	44.9
	UK	10m10f	1.8	2.1	1	87	2	0	46.5
<i>subfasciata</i> LOEW	Me	2m1f	0.3	0.0	0	1	0	2	41.5
<i>sylvarum</i> L.	UK	3m9f	1.3	1.6	0	25	0	3	43.8
<i>tuberculata</i> CURRAN	Me	1f	3	3	0	0	0	1	41.5
n.sp. 78-3 THOMPSON	Me	2m	0.0	0.0	1	1	0	1	43.4
sp.	Me	—	—	—	—	2	0	0	—
<i>Chalcosyrphus</i>									
<i>anthreas</i> WALKER	Me	1m	3	3	0	0	0	1	37.8
<i>curvaria</i> CURRAN	Me	1m	0	0	0	0	0	1	37.9
<i>flexus</i> CURRAN	Ore	1f	3	3	0	1	0	0	40.0
<i>nemorum</i> FABR.	Me	3m2f	1.8	2.6	0	0	1	0	39.4
	Ore	1m	3	3	0	0	0	1	39.8
<i>nigromaculata</i> JONES	Ore	3f	2.7	1.3	0	0	1	0	34.5
<i>libo</i> WALKER	Me	1m1f	3.0	3.0	0	0	0	2	31.4
<i>pigra</i> FABR.	Ore	3m	2.0	2.3	0	0	0	3	41.5
<i>plesia</i> CURRAN	Me	1f	3	3	0	0	1	0	37.5
<i>vecors</i> O. S.	Me	3m1f	0.8	0.8	0	0	2	2	38.4
<i>Brachypalpus</i>									
<i>oarus</i> WALKER	Me	1m	1	1	0	0	1	0	29.6

Abbreviations:

Place:	Me Maine. USA; Ore Oregon. USA; UK Cambridge. UK
N	Number dissected; f female. m male
Crop, Gut:	mean pollen score of contents from 0 (none) to 3 (packed)
Nem	number with haemocoel nematodes
L	number seen leaf-feeding
P/N	number visiting flowers (taking up nectar/pollen)
Other	number seen flying or resting
PS	number of pseudotracheae per mm length of the labellum

species. Therefore, it is always necessary to assess the abundance of flower flies with a second method (Malaise or water-dish traps) and to control apparent specializations by analysing the crop and gut contents. A good example in our studies is *Melangyna lasiophthalma*, where 11 of 12 visits were observed on *Anemone nemorosa*, while subsequent pollen analysis showed a specialization for different trees and shrubs!

The data we have presented show clearly the importance of anemophilous pollen for syrphid diets. Numerous species of syrphids appear to prefer to feed upon such pollens. The plesiomorphic (ROTHERAY & GILBERT 1989) *Melanostoma*- and *Platycheirus*-species (Syrphinae) are well-known for feeding from wind-pollinated flowers on several continents (CLIFFORD 1964; STELLEMAN & MEEUSE 1976; HOLLOWAY 1976; STELLEMAN 1984 and LEEREVELD 1982, 1984). The role of these species in pollination itself still needs further investigation. It is possible that both *Melanostoma*-species play a considerable role in the pollination of grasses and in wind-protected sites of internal edge communities within forests. In *Plantago lanceolata* STELLEMAN (1983) has shown that the predominance of either wind- or syrphid-pollination depends on local wind exposure of the plant population.

This behaviour is not taxonomically restricted, since we report here various species of *Melangyna* (Syrphinae: Syrphini) and *Xylota* (Eristalinae: Xylotini) and there are other syrphids from different habitats that have similarly been recorded as feeding predominantly on anemophilous flowers: *Lejops vittata* and *Anasimyia transfuga* (Eristalinae: Eristalini) on *Typha* pollen (IMHOF 1979); *Taxomerus* (Syrphinae: Taxomerini) on *Plantago* (MESLER 1977) and the grass *Olyra* (SÖDERSTROM & CALDERON 1971); *Copestylum* spp. (Eristalinae: Volucellini) on palms (e.g. SCHMID 1970). Many of these papers interpret such visits in the context of pollination, but few have experimentally verified such speculations. However, a comprehensive study of the role of *Melanostoma*- and *Platycheirus*-species as pollinators has revealed a complex situation in *Plantago*: in plant populations where the role of the wind in moving pollen is restricted, the pollen is stickier and syrphid pollination plays a greater role (STELLEMAN 1984). As in the dioecious gymnosperm species of *Ephedra* (BINO et al. 1984), syrphids may well play a previously undetected but important role in the pollination of other "anemophilous" flowers. Even "rare" species may be much more important than is realized: part of the reason why species such as many *Melangyna* spp. are regarded as rare is precisely because they feed in early spring high up in the canopy.

It is well-known that *Salix*-species and *Corylus avellana* attract syrphid flies in spring; for example, KORMANN (1977) lists 21 species of syrphid flies visiting *Salix caprea*. However, the relative importance of pollen from trees and shrubs in the diet of syrphids has not been analysed before. We have shown that in early flying species such as *Melangyna*, pollen of different trees and shrubs, including anemophilous species, may constitute a major part of their diet. Specializations on flower-visiting in the canopy are likely to occur also in other genera with early flying syrphids.

All that we know about species of *Xylota* (s. s.) indicates clearly that they specialize in taking pollen and other nutrients from leaf surfaces (GILBERT & PERRY 1982; GILBERT 1985; DE BUCK 1985; LÖHR 1990) and have a proboscis morphology adapted to this end (GILBERT 1985). DE BUCK (1985) made a coprological analysis, and found that the faeces contained mainly pollen, spores of fungi and bits of epidermal plant structures. He concluded that faeces of other flower-visiting insects and pollen are taken up by *Xylota* from leaf surfaces. The only gut analysis of a *Xylota*-species other than DE BUCK's (1985) in the literature is a qualitative study of *Xylota meigeniana* STACKELBERG. LÖHR (1990) reports finding the pollen of grasses, *Pinus*, and *Epilobium* in the guts of this species. As deformed

pollen and fungus-spores were rare in the guts of our material we conclude that *Xylota* do not feed on faeces of other insects, but take up mainly fresh pollen from leaf surfaces. This is supported by the occurrence of bits of leaf epidermis and mites in the crop and gut. Because all species of *Xylota* but no other syrphids appear to have this manner of feeding, and because *Xylota* is probably a relatively apomorphic genus of Syrphidae (ROTHERAY & GILBERT, unpubl. data), we suggest that the switch from flower to leaf feeding occurred close to or at the speciation event that gave rise to the genus.

Occasionally other syrphid species that are flower visitors use the leaf-feeding method, e.g. *Melanostoma mellinum* on the leaves of *Mercurialis annua* in vineyards. During our observations in forests *Dasysyrphus tricinctus* and *Cheilosia maculata* occasionally feed on leaves of *Allium ursinum*. The greatest user of the "leaf-feeding method" apart from *Xylota* appears to be *Syrphus ribesii* (field data from England) with 6.3% of the feeding-observations (GILBERT 1985), but this was a quite different phenomenon because they were feeding on honeydew, not on pollen. Honeydew and leachates from leaves may also constitute an important source of nutrients for *Xylota*, as those individuals without pollen often contain a clear liquid in the crop. Testing this liquid with a refractometer gave a reading of 43–64% sucrose equivalents.

### Acknowledgements

We are grateful to Dr. W. VÖLKL, Bonn, for critical discussion. Dr. RÖSCH, Hemmenhofen (FRG) gave advice for pollen identification and Prof. P. GOELDIN DE TIEFENAU, Lausanne (CH) helped with the syrphid determinations.

### Zusammenfassung

Anemophiler Pollen kann bei bestimmten Syrphidenarten einen bedeutenden Teil der Nahrung der Imagines ausmachen. Pollenanalysen des Mageninhalts und Beobachtungen bei Syrphiden, die beim Farbschalfang häufig waren, aber bei Standardbegehungen wenig oder keine Blüten besuchten, lassen drei Gruppen erkennen: 1. Blütenbesuch von Gräsern und Seggen bei der Gattung *Melanostoma*, 2. Blütenbesuch von meist anemophilen Sträuchern und Bäumen bei den frühliegenden Arten der Gattung *Melangyna* und 3. Aufnahme von Pollenniederschlag von Blattoberflächen bei den Xylotini.

Allein aus Beobachtungen des Blütenbesuchs lassen sich bei diesen Schwebfliegengruppen nur bedingt Rückschlüsse auf die für die Eireifung notwendige Hauptpollennahrung der Imagines ziehen.

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