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# Selectivity in the exploitation of floral resources by hoverflies (Diptera: Syrphinae)

**Etienne Branquart and Jean-Louis Hemptinne**

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Adults of the Syrphinae subfamily display no strong flower preferences but exploit pollen and nectar produced by native plants having large inflorescences and flat corollae (e.g. Apiaceae, Asteraceae, Ranunculaceae and Rosaceae). Seven foraging guilds are defined according to the dietary patterns of hoverflies, reflecting mainly a sequential exploitation of flowers at different times of the year and in different habitats.

The majority of species live in forests where they form highly diversified communities. Few Syrphinae colonize successfully open and anthropogenic habitats, such as field margins and fallow areas. *Episyrphus balteatus*, *Melanostoma mellinum*, *Eupeodes corollae*, *Sphaerophoria scripta* and *Platycheirus* spp. are dominant in the communities of Syrphinae from open habitats, all over western Europe. These species are highly polyphagous and characterized by elongated mouthparts as well as a long and slender body. They have access to pollen and nectar in flowers with small and tubular corollae. It is suggested that their polyphagy is an important asset for colonizing open and ephemeral habitats.

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The potential importance of pollen and nectar in the population dynamic of numerous aphid predators and parasitoids has been recently emphasized in the literature; flower paucity in modern agricultural landscapes and in regions of intensive forestry is even put forward as a cause of the failure of natural enemies to control efficiently aphid populations on crops (Powell 1986, Hardwood et al. 1994, Jervis and Kidd 1996). Several attempts have been made to enhance the density, the diversity and the regulating action of predators of agricultural pests by providing additional flowering plants, but the results of these experiments were, however, quite lukewarm (e.g. Jervis et al. 1993, Hardwood et al. 1994, Wyss 1995, Hickman and Wratten 1996). A better understanding of flower-insect relationships is an essential prerequisite to develop efficient management practices: we need to know which flowers are mostly exploited, how the consumption of pollen coming from different plants affect female fecundity and if floral rewards consist in a limiting resource for aphidophagous insects.

This paper is devoted to the study of the exploitation of floral resources by Syrphinae (sensu Rotheray and Gilbert 1989), the larvae of which are very effective biocontrol agents of pest aphids in orchards and annual crops (Chambers and Adams 1986, Nawrocka 1988, Salveter 1996, Branquart 1999). Adults of Syrphinae are among the most common anthophilous insects and consume both pollen and nectar of flowers. The former is used as the main protein source to develop reproductive tissues; as in other synovigenic insects, the huge quantity of nitrogenous nutrients needed by females for yolk deposition is not gathered during the larval stage but depends exclusively on acquisition of food by adults (Schneider 1948, Stürken 1964, Haslett 1989b). On the other hand, nectar supplies fuel for the energy

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expensive hovering flight of these insects (Gilbert 1981, Kevan and Baker 1983).

Several studies have documented that hoverflies display floral preferences according to the colour and the depth of the corolla (Barendregt 1975, Gilbert 1981, Haslett 1989a). However, these results are based on limited observations made in one or two particular sites and, to our knowledge, no study has ever been undertaken to determine the use of floral resources by Syrphinae across a wide range of habitats. In these conditions, it is difficult to know if observed relationships correspond to fixed preferences or reflect the exploitation of resources that are locally and temporarily abundant, that is flower constancy or labile preference (Fox and Morrow 1981, Waser 1986).

In our study, we determine floral preferences of Syrphinae from a wide dataset covering the European Atlantic Region. We first define the plants most exploited by hoverflies. Afterwards, the degree of floral selectivity is measured for 67 species of Syrphinae. These are assigned to different trophic guilds, which are then interpreted according to the structure of syrphid communities from different habitats and to the relationships between plant and insect morphology.

## Material and methods

We extracted information on the exploitation of 123 plants by 67 Syrphinae species in Belgium, Germany, The Netherlands, United Kingdom and northern France from De Buck (1990), Ssymank and Gilbert (1993) and Barkemeyer (1994). A resource utilization matrix was constructed, whose cells contain the number of records for each species of hoverfly on each plant. Plants were all identified as far as the genus except grasses that were always referred to as Poaceae. Fly and plant nomenclature refers to Speight (1993 and 1994) and to De Langhe et al. (1983), respectively. Resource exploitation matrix is used together with plant and syrphid attributes to determine 1) global resource exploitation by hoverflies, 2) dietary patterns of individual species and foraging guilds and 3) relationship between syrphids and plant morphological traits.

## Resource exploitation by hoverflies

The preference of syrphids for flowers was deduced from the resource utilization matrix as the number of occurrences for all syrphid species on each plant. The preference expressed in such a way could be biased by the abundance of plants: anthophilous insects may be observed in larger numbers on common plants because these are more often encountered and are easily memorised as a search image or because they have been more intensively studied by biologists (Toft 1983, Ellis and Ellis-Adam 1993). In both cases, higher occurrences on these plants do not represent real preferences; to correct for this error, the linear regression of the logarithm of the number of occurrences on an index of plant abundance has been calculated and the residuals taken as an electivity index (Lawlor 1980) of syrphids for the different plants. The indication of plant abundance given by De Langhe et al. (1983) was used to calculate this relationship (Table 1).

The characteristics of the preferred flowers were determined by a principal component analysis of the relationships between the electivity index and the eco-morphological traits described in Table 1, except plant abundance that is already incorporated in the electivity index. This analysis was performed on the basis of correlation matrix because dimensions of variables are not homogeneous.

Table 1. Ecological and morphological indices characterizing floral resources. Sources are as follows: [1] personal measures, [2] Blamey and Grey-Wilson (1991), [3] Coste (1937), [4] Cronquist (1981), [5] De Langhe et al. (1983), [6] Dennis (1992).

| Index | Values | Remarks | Sources |
|---|---|---|---|
| Plant abundance | 0–10 | from very rare (0) to very common (10) | [5] |
| Blooming time | 1–12 | correspond to the ordinal number of each month | [5] |
| Blooming duration | 1–12 | number of months during which plants are flowering | [5] |
| Perennity | 1–3 | correspond to the number of years (1, 2 or >2) a plant is able to produce flowers | [3], [5] |
| Habitat: woodlands | 0/1 | absence or presence (A/P) in woodland areas | [5] |
| wetlands | 0/1 | A/P in wetland and grassland areas | |
| farmlands | 0/1 | A/P in field margins and fallow areas | |
| Plant height | 1–6 | Height of flowers above ground: <15 cm (1), 15–30 cm (2), 30–60 cm (3), 60–120 cm (4), 120–200 cm (5), >200 cm (6) | [5] |
| Flower size | 1–6 | Corolla or inflorescence diameter: <1 cm (1), 1–2 cm (2), 2–3 cm (3), 3–5 cm (4), 5–15 cm (5), >15 cm (6) | [1], [2], [5] |
| Corolla depth | 0–4 | Flowers with fully accessible and unconcealed nectar (0), with open corolla and concealed nectar (1), with corolla tube length of 1–3 mm (2), 4–6 mm (3), ≥7 mm (4) | [1], [2], [4], [6] |

Table 2. Ecological and morphological indices used to describe hoverfly species. Sources are as follows: [1] Personal measures, [2] Gilbert (1981, 1985a), [3] Speight et al. (1998), [4] Ssymank (1991b), [5] Stubbs and Falk (1983), [6] Verlinden and Decleer (1987). A/P is absence or presence of species in a habitat.

| Index | Values | Remarks | Sources |
|---|---|---|---|
| Season | 1–12 | correspond to the median value of the flight period | [6] |
| Habitat: woodlands | 0/1 | A/P in woodland areas | [3], [5], [6] |
| wetlands | 0/1 | A/P in wetland and grassland areas | |
| farmlands | 0/1 | A/P in field margins and fallow areas | |
| Head width (HW) | mm | index of body size | [1], [2] |
| Tongue length (TL) | mm | length of proboscis in extended position, from head to labellum tip | [1], [2], [4] |
| Relative size of proboscis (TL/HW) | – | index of proboscis elongation and narrowness | [1], [2], [4] |

## Foraging guilds, dietary patterns and hoverfly communities

*Foraging niche width and foraging guilds*

The foraging niche width was calculated from the relative frequencies of hoverfly visits to different flower species. We used to this purpose the Shannon-Wiener index of diversity, H′, for each syrphid species (Hanski 1978). Overlap between foraging niches of each pair of species was calculated by the proportional similarity measure (Schoener 1970). We chose this method because of its convenience and its lack of assumption about the nature of underlying competitive processes (Abrams 1980, Slobodchikoff and Schulz 1980). Ward's method of hierarchical clustering was performed on these overlap values; as a result, foraging guilds of species sharing the same resources and having therefore high values of overlap were determined (Simberloff and Dayan 1991). Each guild is characterized by 1) the major resources consumed by hoverflies (accounting at least for 10% of the total guild diet), 2) time in the season when most individual syrphids are flying and 3) their habitat preferences (Table 2).

*Organization of hoverfly communities*

We analysed eleven syrphid communities corresponding to different habitats in the light of the guilds previously formed: seven communities refer to woodlands and four communities to farmland habitats. Information concerning community structure and composition was extracted from the literature for eight sites (see references in Table 6). Three more communities were described using data collected during a field survey we performed from April 1996 to October 1997 on Belgian territory. Study sites are a two-year-old fallow area in a region of intensive agriculture at Gembloux, an alluvial deciduous wood of 50 ha in the same region and a mature beech-spruce forest at Paliseul in Ardenne. At each location, we counted hoverflies monthly on sunny days, between 0900 and 1300 following a standard census walk, viz. a route edged with flowers that covered most of each site and was walked at constant speed two times a day (Gilbert 1981). Specimens that could not be identified visually in the field were caught in a sweepnet for later identification in the laboratory. We described each community by the total number of species of Syrphinae found in each habitat and by a list of dominant species, accounting at least for 3% of the total number of Syrphinae found at one site. The dominant species that are present in > 50% of sites from the same habitats are called core-species according to Hanski (1982).

## Relationships between syrphid morphology and resource exploitation

As syrphids belonging to a particular foraging guild visit a well-defined set of plants, they are likely to exhibit morphological adaptations for foraging efficiently for nectar and pollen on these plants (Kearns and Inouye 1993, Jervis and Kidd 1996). In order to test this hypothesis, two morphological variables frequently associated with the partitioning of floral resources, body size and tongue length, were subjected to interguild comparisons. Between guild comparisons of body size and proboscis length were analysed by Kruskall-Wallis tests. We also calculated correlations between these morphological traits and the average size of inflorescence as well as the average corolla depth of resources exploited by each hoverfly species, weighted by species occurrence on each flower.

Body size was estimated by measuring the head width of hoverflies (Kikuchi 1965, Gilbert 1985a). Data for 14 species were available in Gilbert (1985a) and we measured the head width of the remaining 53 species on specimens in the entomological collections of Lucien Verlinden and of the "Faculté Universitaire des Sciences agronomiques de Gembloux". We took the proboscis length of 27 species from Gilbert (1985a) and Ssymank (1991b) and made measurements on fresh specimens of 29 additional species, using the technique described by Gilbert (1981). As recommended by Gilbert (1981, 1985a, b), we used the ratio of proboscis length to head width as an index of tongue length, to describe the ability of hoverflies to exploit nectar from deep and narrow corollae.

## Results

### Resource exploitation by hoverflies

The projection of plant attributes in the equilibrium circle of descriptors for axes I and II of the principal component analysis is illustrated in Fig. 1. Except for the variable "wetlands" not represented on the graph, all the attributes contribute strongly to the formation of the reduced space. The first axis of the principal component analysis accounts for 25% of the total variance in the dataset and corresponds to a gradient of habitats. It opposes forest plants to farmland flowers. The former are mostly perennial plants of short blooming duration and early flowering time. The latter display exactly the opposite characteristics, and wetland flowers are at an intermediate position.

Floral preferences displayed by the 67 species of hoverflies are independent of this ecological gradient as the electivity index has a very low contribution to the formation of axis I. It is however closely linked to the second component of the analysis which explains 17% of the total variance. The most visited plants are therefore projected towards the positive end of the second axis and are listed in Table 3. Most of them have large inflorescences and produce unconcealed nectar as it is indicated by the high correlation between the electivity index and, on one side the size of inflorescence ($r = 0.44$; $p < 0.001$), and on the other side the corolla depth ($r = -0.33$; $p < 0.001$). The best examples in this respect are plants with corymb and umbel inflorescences like *Filipendula*, many Apiaceae (*Aegopodium*, *Angelica*, *Anthriscus*, *Chaerophyllum*, *Foeniculum*, *Heracleum*, *Pastinaca*) and some trees (*Crataegus*, *Prunus*, *Sambucus*). Even if they individually produce small amounts or even no nectar, plants forming large patches and having numerous stamens like *Allium*, *Caltha*, *Potentilla*, *Ranunculus*, *Rubus* and *Salix*, are also very attractive to hoverflies. Note that most of the plants with a high attraction for hoverflies are perennial.

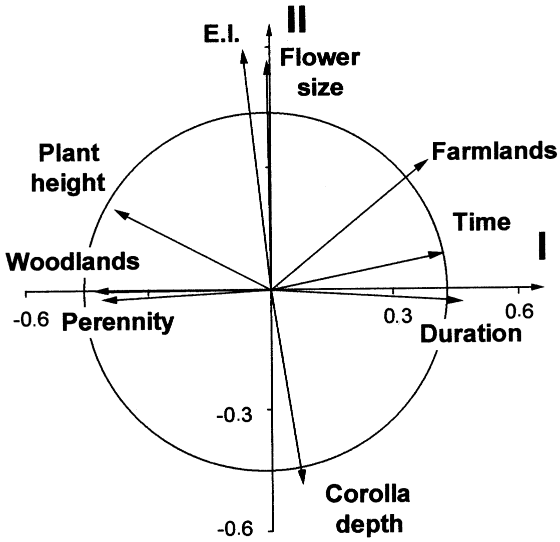

Fig. 1. Principal component analysis: projection of plant attributes in the equilibrium circle for the space defined by axes I and II. The attractiveness of flowers for the assemblage of 67 species of Syrphinae as a whole is expressed by the electivity index (E.I.).

### Foraging guilds, dietary patterns and hoverfly communities

*Foraging niche width and foraging guilds*

Foraging niche width values form a continuum from the highly specialized flies to the generalist ones (Fig. 2A; see also individual values of foraging niche width in Appendix). Most species are situated between these two extremes and seem to be moderately selective in their floral choices. Patterns of resource utilization are, however, diversified as pair-wise overlap values are often very low. Hence, seven foraging guilds have been separated by the clustering procedure (Fig. 2B); they were sorted into three categories according to the degree of polyphagy of their species. Each guild is characterized hereafter according to the major resources exploited by hoverflies (Table 4) and their ecological preferences (Table 5).

The most specialized species (foraging niche width $< 2.5$) are in guilds A, B and D. Syrphids in guild A are forest dwellers that are mainly encountered in summertime on Apiaceae growing in alluvial deciduous woodlands (*Aegopodium*, *Angelica* and *Heracleum*). Guild B is again an assemblage of species living in forest. In this case, they are active early in spring and exploit anemophilous pollen produced by trees, mainly *Salix* and *Prunus*. In guild D, syrphids are specialized to exploit so-called "anemophilous" pollen of herbaceous plants (Poaceae, Cyperaceae, Plantaginaceae). They fly from June to August in marshes and damp meadows.

Species from guilds E, F and G have niche width values ranging from 2.5 to 3.5 and are less specialized on a particular resource. These three guilds group syrphids of forests. Species in guild E visit mainly flowers of *Prunus*, *Crataegus* and *Anthriscus* along wood margins during May and June. Syrphids in guild F were encountered during the same season in conifer plantations, where they visit different species of Ranunculaceae, *Taraxacum* and *Salix* along forest tracks. Guild G includes hoverflies with two annual generations, feeding mostly on Ranunculaceae during springtime and on Apiaceae during summertime; in contrast

Table 3. Presentation of the most important floral resources for the 67 species of Syrphinae under study. Plant genera are sorted out by decreasing values of attractiveness: electivity index (EI) and occurrence number (OCN). Three morphological traits related to plant attractiveness are also specified: flower size, corolla depth and plant perennity.

| Resources | | Attractiveness | | Flower traits | | |
|---|---|---|---|---|---|---|
| Plant genus | Plant family | EI | OCN | size | depth | perennity |
| *Ranunculus* | Ranunculaceae | 0.94 | 254 | 3 | 1 | 3 |
| *Pastinaca* | Apiaceae | 0.77 | 70 | 5 | 0 | 2 |
| *Sambucus* | Caprifoliaceae | 0.71 | 49 | 6 | 0 | 3 |
| *Salix* | Salicaceae | 0.67 | 87 | 2 | 1 | 3 |
| *Heracleum* | Apiaceae | 0.62 | 120 | 6 | 0 | 3 |
| *Aster* | Asteraceae | 0.62 | 39 | 3 | 3 | 3 |
| *Potentilla* | Rosaceae | 0.61 | 76 | 2 | 0 | 3 |
| *Foeniculum* | Apiaceae | 0.61 | 25 | 6 | 0 | 3 |
| *Allium* | Alliaceae | 0.60 | 38 | 4 | 1 | 3 |
| *Prunus* | Rosaceae | 0.57 | 69 | 4 | 0 | 3 |
| *Solidago* | Asteraceae | 0.57 | 44 | 5 | 2 | 3 |
| *Aegopodium* | Apiaceae | 0.56 | 68 | 5 | 0 | 3 |
| *Calluna* | Ericaceae | 0.54 | 51 | 2 | 3 | 3 |
| *Crataegus* | Rosaceae | 0.51 | 60 | 3 | 0 | 3 |
| *Caltha* | Ranunculaceae | 0.49 | 57 | 4 | 1 | 3 |
| *Angelica* | Apiaceae | 0.43 | 63 | 5 | 0 | 3 |
| *Senecio* | Asteraceae | 0.41 | 60 | 5 | 3 | 3 |
| *Chaerophyllum* | Apiaceae | 0.41 | 38 | 4 | 0 | 2 |
| *Rubus* | Rosaceae | 0.40 | 72 | 2 | 0 | 3 |
| *Filipendula* | Rosaceae | 0.40 | 46 | 5 | 0 | 2 |
| *Cirsium* | Asteraceae | 0.39 | 57 | 4 | 4 | 3 |
| *Euphorbia* | Euphorbiaceae | 0.39 | 57 | 4 | 0 | 3 |
| *Leontodon* | Asteraceae | 0.39 | 45 | 3 | 2 | 3 |
| *Anthriscus* | Apiaceae | 0.34 | 63 | 5 | 0 | 3 |
| *Pulicaria* | Asteraceae | 0.32 | 31 | 3 | 3 | 3 |
| *Daucus* | Apiaceae | 0.31 | 30 | 5 | 0 | 2 |
| – | Poaceae | 0.30 | 58 | 2 | - | 3 |
| *Convolvulus* | Convolvulaceae | 0.30 | 37 | 3 | 3 | 3 |
| *Matricaria* | Asteraceae | 0.29 | 45 | 3 | 2 | 1 |
| *Rosa* | Rosaceae | 0.29 | 36 | 3 | - | 3 |
| *Taraxacum* | Asteraceae | 0.28 | 69 | 4 | 4 | 3 |

to species in guild F, they favour large gaps in the canopy and some of them may also colonize grassy habitats outside forests.

Species in guild C do not display any clear floral preference and have the widest foraging niche. Few individuals are already flying in May but they become very numerous during summertime, especially along field margins, in fallow areas and in large forest clearings.

*Organization of hoverfly communities*

The eleven communities of Syrphinae from woodland and farmland habitats described in Table 6 present some striking features. They all include a group of five to ten co-dominant syrphids and some satellite species present in low densities. Most of the species that are numerous at one site are also present in high numbers at other sites of the same habitat all over western Europe. As a result, they are called core-species for this

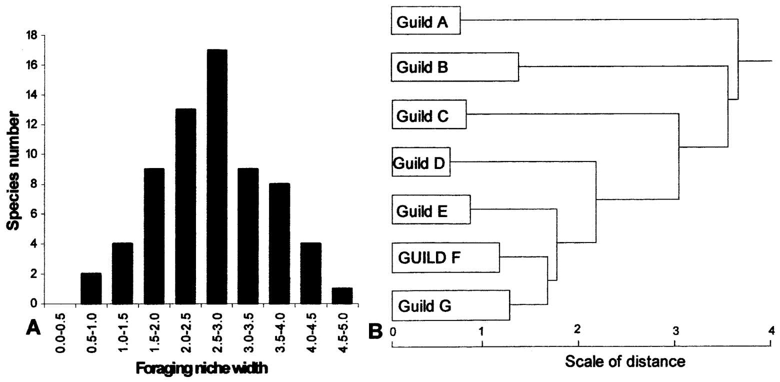

Fig. 2. (A) Frequency distribution of foraging niche width for the 67 species of Syrphinae in analysis. (B) Overlap dendrogram constructed using Ward's method of hierarchical clustering performed on pair-wise overlap values: seven foraging guilds are defined.

habitat. In woodlands habitats, some additional species may also achieve high densities at one or two particular sites: they are referred to as “other species” in Table 6. *Episyrphus balteatus* is clearly the most ubiquitous core-species because it is dominant at all the sites, irrespective of the type of habitat.

All the core-species are generalist feeders in guild C; satellite species are usually more specialized and belong to other guilds. Most of them are found in woodland communities that are much more diversified than those found in farmlands. It is noticeable that hoverflies with predacious larvae are primarily forest dwellers.

### Relationships between syrphid morphology and resource exploitation

Foraging guilds can hardly be characterized using morphological traits of hoverflies as these are quite variable within each guild. Nevertheless, some trends may be depicted. The syrphids in guilds B and D are the smallest, those in guilds A, E and G the largest (Table 7). The former exploit mainly pollen from tree flowering early in spring (B) or from anemophilous grasses (D). The largest syrphids are found on large inflorescences of trees and Apiaceae. Across the guilds, there is a significant relationship between the head width and the mean size of the inflorescences exploited by each hoverfly species ($r = 0.32$; $p < 0.01$).

Most Syrphinae have a short proboscis related to their size ($TL/HW < 1.10$) except some small species living in open habitats and belonging to guilds C and G (Table 7): *Eupeodes corollae*, *E. luniger*, *Platycheirus albimanus*, *P. manicatus*, *P. peltatus*, *P. tarsalis*, *P. scutatus*, *Sphaerophoria scripta* and *S. interrupta*. Therefore, a marked proboscis elongation seems restricted to three genera and concerns only 16% of the 56 species for which tongue measurements are available. The relative size of the proboscis is correlated with the depth of corolla tubes of flowers visited by hoverflies ($r = 0.56$; $p < 0.001$) (Fig. 3) and with their foraging niche width ($r = 0.35$; $p < 0.01$). With their long and narrow proboscis (dimensions: 3–5 mm × 0.25–0.35 mm), the nine species mentioned above are able to exploit nectar in a wider diversity of corolla shapes and especially in deep and narrow flowers, as those of many Asteraceae whose nectar is out of reach for other Syrphinae.

## Discussion

### Food specialization

As many Diptera, Coleoptera and Hymenoptera, Syrphinae mainly visit wide actinomorphic native plants belonging to Ranunculaceae, Rosaceae, Apiaceae and Asteraceae. Most of them produce large quantities of pollen and nectar, which can be easily collected by insects with short proboscis (Proctor and Yeo 1973, Ellis and Ellis-Adam 1993). Hoverflies rarely display strong preferences for a particular plant species; in this study, the only syrphids that can be considered as oligolectic (sensu Pekkarinen 1998) are those feeding selectively on Apiaceae (guild A), on tree inflorescences (guild B) and on grass or sedge spikes (guild D). They represent only 24 (36%) of the 67 species studied.

Table 4. Structure of foraging guilds: number of hoverfly species (N), mean foraging niche width (FNW) with standard deviation (SD) and major resources with their relative importance in the total diet. Major resources: Ranunculaceae (Ran), trees (Tre), Apiaceae (Api), anemophilous herbs (Her) and Asteraceae (Ast).

| Guild | N | FNW | | Major resources | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Mean | SD | Ran | Tre | Api | Her | Ast | Main taxa |
| A | 7 | 1.89 | 0.42 | – | – | 80% | – | – | *Heracleum*, *Aegopodium*, *Angelica* |
| B | 9 | 1.54 | 0.65 | – | 67% | – | – | – | *Salix*, *Prunus* |
| C | 13 | 3.98 | 0.22 | – | – | – | – | 24% | – |
| D | 4 | 1.90 | 0.48 | 12% | – | – | 42% | – | *Ranunculus*, *Molinia*, *Plantago* |
| E | 9 | 2.75 | 0.32 | – | 28% | 21% | – | – | *Crataegus*, *Prunus*, *Anthriscus* |
| F | 10 | 2.74 | 0.32 | 26% | – | – | – | – | *Ranunculus*, *Salix*, *Taraxacum* |
| G | 15 | 2.63 | 0.43 | 13% | – | 23% | – | 17% | *Ranunculus*, *Heracleum*, *Pastinaca* |

Table 5. Ecological characterization of the foraging guilds: environment, seasonality (flight period) and short description of habitats of flowers exploited by each guild.

| Environment | Season | Guild | Description of resource patches |
|---|---|---|---|
| Woodlands | April–May | B | Clumps of flowering trees and shrub areas |
| | May–June | E | Flowering trees and Apiaceae along forest margins |
| | May–June | F | Plants growing along tracksides in conifer forest |
| | June–August | G | Grassy felling areas and large clearings in woodland habitats |
| | July–August | A | Patches of Apiaceae found in alluvial deciduous forests |
| Wetlands | June–August | D | Anemophilous herbs in marshes and damp meadows |
| Varia | May–Sept. | C | Field margins, fallow areas and forest clearings |

Table 6. Communities of Syrphinae in Western Europe: comparison of woodland and farmland habitats. Indication of species richness (N) and of core species, accounting at least for 3% of the total number of Syrphinae found at one site. References are as follows: [1] personal data, [2] Cowgill et al. (1993b), [3] Decleer (1990), [4] Kula (1997), [5] Pollard (1971), [6] Salveter (1996), [7] Ssymank (1991a). Species are identified by a number corresponding to the code given in Appendix.

| Vegetation | Ref. | Locality and country | N | Core-species<br>20 | 21 | 22 | 27 | 28 | 29 | 17 | 18 | 19 | 26 | Other species |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Woodlands | | | | | | |
| *Picea* | [4] | Sneznik (CZ) | 47 | ● | ● | ● | ● | ● | | ● | | | | 10, 44, 48 |
| *Fagus-Fraxinus* | [7] | Freiburg (D) | 66 | ● | ● | ● | ● | ● | ● | ● | | | ● | 9, 14, 46 |
| – | [6] | Bern (CH) | 40 | ● | ● | ● | ● | | ● | ● | ● | ● | | 14, 34, 46 |
| *Fagus-Picea* | [1] | Paliseul (B) | 46 | ● | ● | ● | ● | ● | ● | ● | ● | | ● | 14, 43, 48, 49 |
| *Quercus-Fraxinus* | [1] | Gembloux (B) | 38 | ● | ● | ● | ● | ● | ● | ● | | | | 2, 34, 44 |
| *Quercus-Alnus* | [3] | Wingene (B) | 34 | ● | | | ● | | | ● | | ● | | 44 |
| *Quercus-Fraxinus* | [5] | Cambridge (GB) | 35 | ● | | ● | ● | | ● | ● | | | | 34 |
| | | | | | | | | Farmlands | | | | | | |
| Cereal, Sugar beat | [6] | Bern (CH) | 15 | | | | | | | ● | ● | ● | ● | 23 |
| Fallow | [1] | Gembloux (B) | 14 | | | | | | ● | ● | ● | ● | ● | 31 |
| Cereal | [2] | Southampton (GB) | 11 | | | | | | ● | ● | ● | ● | ● | |
| Cereal, Sugar beat | [5] | Cambridge (GB) | 13 | | | | | | | ● | ● | ● | ● | 23, 31, 63 |

Flower preferences depicted by guild typology result mainly from a sequential exploitation of flowers at different times and in different habitats: hoverflies usually visit the most abundant and rewarding flowers they can find as predicted by simple optimal-foraging theory (Waser 1986, Haslett 1989a, Cowgill et al. 1993a). For example, several species of *Melanostoma* and *Platycheirus*, found in very high numbers in grass- and wetlands, mainly feed on the huge quantities of pollen produced by patches of grasses and sedges (Van der Goot and Grabandt 1970, Leereveld 1982, Ssymank and Gilbert 1993). A majority of species are closely linked to forests and most of them are typical univoltine (guilds A, B, E and F). Their foraging niche width is narrow because their flight period is short. They display a precise timing in adult emergence regulated by an obligatory diapause and synchronized with seasonal availability of prey for their progeny (Goeldlin 1974, Dusek and Laska 1986, Branquart 1999). They follow each other in three waves across floral and prey succession: species foraging on *Salix* and *Prunus* in March–April (guild B), on *Taraxacum*, *Rancunculus*, *Crataegus* and *Anthriscus* in May–June (guilds E and F), on Apiaceae and *Filipendula* in summertime (guild A).

Our results demonstrate that polylectism is widely adopted among Syrphinae and do not reveal the existence of a "pollination syndrome" between plants and insects. Polylectism is expected when the profitability of flower rewards is similar across plant species and when travel is costly for insects (Courtney 1982, Waser et al. 1996). The need to reduce both time and energetic costs when searching for floral resources is very important for hoverflies as they already have huge travel costs in search for suitable, often scattered, oviposition sites: aphid colonies for Syrphinae; dead wood, sap runs, ponds or cow dung for other hoverflies.

## Habitat preferences

Woodlands shelter the major part of the syrphid fauna in Atlantic Europe; this habitat is not only very favourable for aphidophagous species, but also for syrphids whose larvae feed on plants, sap exudations from trees and wet rotting wood (Rotheray 1993, Speight 1996). Note that the dominance of woodland syrphids in this fauna is not surprising as deciduous forests have been the dominant natural vegetation in this region (Ozenda et al. 1979).

Foraging guild C includes mainly ubiquitous, plurivoltine and polyphagous species that are dominant in most habitats while more specialized species, in other guilds, are usually less abundant and restricted to forest or wetland habitats. A subset of species from the guild C (Table 6) colonize fallow and field areas. As their larvae are still developing in large numbers on herba-

Table 7. Mean values of head width (HW) and relative size of proboscis (TL/HW) of hoverflies from different guilds. Interguild comparisons are made using Kruskall-Wallis tests. P-value of this test is given in the last column.

| Trait | Guild A | Guild B | Guild C | Guild D | Guild E | Guild F | Guild G | p |
|---|---|---|---|---|---|---|---|---|
| HW | 2.88 | 2.41 | 2.76 | 2.08 | 3.31 | 2.83 | 2.99 | 0.047* |
| TL/HW | 0.92 | 0.91 | 1.16 | 0.94 | 0.95 | 0.84 | 1.08 | 0.009** |

ceous plants growing in clearings and along woodland tracks, these species are assumed to be originally forest dwellers. The link with the arboreal habitat is particularly evident for species like *Episyrphus balteatus* and *Syrphus* spp. that congregate in swarms under trees before mating (Downes 1969, Gilbert 1984), while females are frequently wandering outside woods and lay eggs in open fields. As predicted by theory (Pianka 1981, Southwood 1988, Futuyma and Moreno 1988), polyphagy, ecological plasticity and mobility characterize these species that are able to develop important populations in unstable, disturbed or ephemeral environments like farmland habitats and those in the early stages of ecological successions. Thanks to their great dispersal power, and their ability to migrate (Aubert et al. 1976, Gatter and Schmid 1990), these species are widespread all over western Europe and constitute the core of most Syrphinae communities from this region (Owen and Gilbert 1989).

## Morphometry

Proboscis size suggests that most Syrphinae are generalist consumers of pollen and do not display any evidence of diet specialization corresponding to our guild typology. Oligolectic species have a short tongue like most other Syrphinae; as for bees (Pekkarinen 1998), specialization is essentially an ethological character that does not necessarily require any visible morphological qualification.

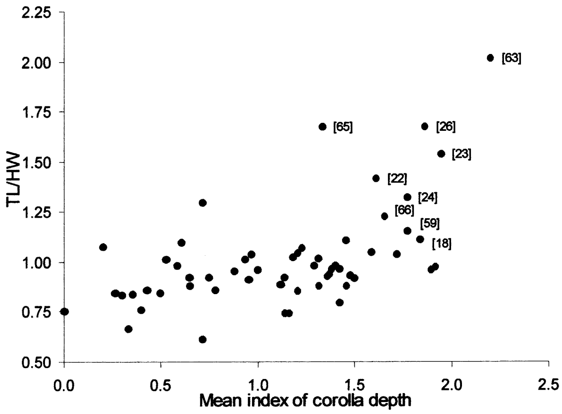

Fig. 3. Relationship between mouthpart elongation (TL/HW) and mean corolla depth of flowers exploited by each hoverfly species. Scale of corolla depth is explained in Table 1 and codes for species are given in Appendix.

However, some morphometric traits seem to be linked with polyphagy and the ability of hoverflies to colonize open habitats. The most ubiquitous species of guilds C, D and G are small to medium sized with a proboscis that is narrower and longer than those of typical forest dwellers. Small size allows syrphids to collect pollen and nectar in more flowers, especially those with small corollae or inflorescences. These species are able to feed while still flying, landing on narrow inflorescences or going deep into corollae. They can exploit nectar in deep corollae of Asteraceae that, together with Poaceae, constitute the dominant flowers in open habitats and ruderal sites (Rotenberry 1990, Cowgill et al. 1993a). In contrast, large Syrphinae are mostly forest dwellers having short mouthparts with a broad labellum. Owing to their great size, they concentrate on large inflorescences producing unconcealed nectar, like those of trees and Apiaceae. They are superior competitors and frequently displace small flies when landing on a flower (Kikuchi 1965).

Gilbert (1981, 1985b) found a positive relationship between the size of hoverflies, the time spent feeding on nectar and mouthpart elongation. Since flowers with deeper corollae often produce more nectar with a higher sugar content (Prys-Jones 1982, Kevan and Baker 1983), he suggested that the elongation of proboscis was adaptive to fulfil the greater energy requirements of the largest species of hoverflies. His hypothesis is not confirmed by our results because Syrphinae with long proboscis are, on the contrary, small species. As an alternative hypothesis, we suggest that elongation of the mouthparts might have favoured the expansion of the foraging niche and the exploitation of more energy resources, allowing the colonization of open and unpredictable habitats and the achievement of long migrations. This assumption should, however, require a detailed comparative analysis in focussing on those genera including species with a long proboscis (*Eupeodes*, *Platycheirus* and *Sphaerophoria*), to test if tongue elongation has co-evolved with the development of long-scale migration, a shift of habitat preferences and, possibly, a modification of larval feeding habits.

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Appendix. List of the 67 species of Syrphinae with their attributes, sorted out by foraging guild.

| Code | Name | Guild | FNW | Wood (P/A) | Wet (P/A) | Farm (P/A) | Season (month) | HW (mm) | TL/HW | Average flower traits | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | height | size | depth |
| 1 | *Epistrophe grossulariae* (Meigen, 1822) | A | 2.29 | 1 | 1 | 0 | 7.2 | 4.3 | 0.91 | 4.1 | 4.6 | 0.9 |
| 2 | *Leucozona glaucia* (L., 1758) | A | 1.63 | 1 | 0 | 0 | 7.5 | 3.8 | 1.07 | 4.1 | 5.0 | 0.2 |
| 3 | *Leucozona laternaria* (Muller, 1776) | A | 1.86 | 1 | 0 | 0 | 6.9 | 2.9 | 1.01 | 3.8 | 5.0 | 0.5 |
| 4 | *Melangyna compositarum* (Verrall, 1873) | A | 1.15 | 1 | 0 | 0 | 6.9 | 2.6 | * | 3.9 | 5.4 | 0.0 |
| 5 | *Melangyna umbellatarum* (F., 1794) | A | 2.34 | 1 | 0 | 0 | 7.9 | 2.5 | 0.84 | 4.0 | 4.6 | 0.3 |
| 6 | *Meligramma guttata* (Fallen, 1817) | A | 1.77 | 1 | 0 | 0 | 7.3 | 2.0 | 0.75 | 4.2 | 5.1 | 0.0 |
| 7 | *Pipizella virens* (F., 1805) | A | 2.10 | 1 | 0 | 0 | 6.3 | 2.0 | * | 3.9 | 4.5 | 0.0 |
| 8 | *Epistrophella euchroma* (Kowarz, 1885) | B | 1.10 | 1 | 0 | 0 | 4.8 | 2.8 | * | 5.5 | 3.7 | 0.2 |
| 9 | *Melangyna barbifrons* (Fallen, 1817) | B | 1.10 | 1 | 0 | 0 | 4.0 | 2.0 | 0.95 | 5.6 | 2.1 | 1.0 |
| 10 | *Melangyna quadrimaculata* (Verrall, 1873) | B | 1.86 | 1 | 0 | 0 | 3.3 | 2.5 | 0.74 | 4.7 | 2.7 | 1.2 |
| 11 | *Fagisyrphus cinctus* (Fallen, 1817) | B | 1.77 | 1 | 0 | 0 | 5.7 | 2.5 | * | 5.7 | 4.3 | 0.1 |
| 12 | *Parasyrphus macularis* (Zetterstedt, 1843) | B | 1.86 | 1 | 0 | 0 | 5.5 | 2.8 | 0.98 | 4.7 | 3.3 | 0.6 |
| 13 | *Parasyrphus malinellus* (Collin, 1952) | B | 2.34 | 1 | 0 | 0 | 5.3 | 2.7 | * | 4.1 | 3.2 | 0.7 |
| 14 | *Parasyrphus punctulatus* (Verrall, 1873) | B | 2.29 | 1 | 0 | 0 | 5.2 | 2.3 | 0.95 | 4.2 | 3.3 | 0.9 |
| 15 | *Platycheirus ambiguus* (Fallen, 1817) | B | 0.86 | 1 | 0 | 0 | 4.3 | 2.2 | * | 4.8 | 3.7 | 0.3 |
| 16 | *Platycheirus discimanus* (Loew, 1871) | B | 0.57 | 1 | 0 | 0 | 4.0 | 2.0 | 0.92 | 6.0 | 2.5 | 0.7 |
| 17 | *Episyrphus balteatus* (De Geer, 1776) | C | 4.49 | 1 | 1 | 1 | 7.8 | 3.0 | 0.97 | 3.4 | 3.3 | 1.9 |
| 18 | *Eupeodes corollae* (F., 1794) | C | 3.92 | 0 | 1 | 1 | 7.7 | 3.0 | 1.11 | 3.2 | 3.5 | 1.8 |
| 19 | *Melanostoma mellinum* (L., 1758) | C | 3.87 | 0 | 1 | 1 | 7.5 | 1.8 | 1.10 | 3.0 | 3.2 | 1.5 |
| 20 | *Melanostoma scalare* (F., 1794) | C | 3.63 | 1 | 1 | 0 | 6.7 | 2.0 | 1.07 | 3.2 | 3.2 | 1.2 |

Appendix. List of the 67 species of Syrphinae with their attributes, sorted out by foraging guild.

| Code | Name | Guild | FNW | Wood (P/A) | Wet (P/A) | Farm (P/A) | Season (month) | HW (mm) | TL/HW | Average flower traits | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | height | size | depth |
| 21 | *Meliscaeva cinctella* (Zetterstedt, 1843) | C | 3.68 | 1 | 0 | 0 | 7.5 | 2.7 | 1.04 | 3.8 | 3.7 | 1.2 |
| 22 | *Platycheirus albimanus* (F., 1781) | C | 4.11 | 1 | 1 | 1 | 6.8 | 2.4 | 1.41 | 3.3 | 3.1 | 1.6 |
| 23 | *Platycheirus peltatus* (Meigen, 1822) | C | 3.87 | 0 | 1 | 0 | 7.0 | 2.7 | 1.53 | 3.2 | 3.3 | 1.9 |
| 24 | *Platycheirus scutatus* (Meigen, 1822) | C | 3.78 | 1 | 0 | 0 | 6.7 | 2.2 | 1.32 | 3.2 | 3.1 | 1.8 |
| 25 | *Scaeva pyrastri* (L., 1758) | C | 3.97 | 1 | 1 | 1 | 7.5 | 3.6 | 1.04 | 3.5 | 3.6 | 1.7 |
| 26 | *Sphaerophoria scripta* (L., 1758) | C | 4.16 | 0 | 1 | 1 | 7.7 | 2.3 | 1.67 | 3.1 | 3.5 | 1.9 |
| 27 | *Syrphus ribesii* (L., 1758) | C | 4.06 | 1 | 1 | 1 | 6.0 | 3.7 | 0.93 | 3.5 | 3.7 | 1.5 |
| 28 | *Syrphus torvus* Osten-Stacken, 1875 | C | 3.82 | 1 | 0 | 0 | 6.0 | 3.6 | 0.96 | 3.5 | 3.4 | 1.4 |
| 29 | *Syrphus vitripennis* Meigen, 1822 | C | 3.92 | 1 | 1 | 1 | 7.0 | 3.1 | 0.96 | 3.6 | 3.6 | 1.4 |
| 30 | *Platycheirus angustatus* (Zetterst., 1843) | D | 1.77 | 0 | 1 | 0 | 7.0 | 1.7 | 1.02 | 2.9 | 2.3 | 1.3 |
| 31 | *Platycheirus clypeatus* (Meigen, 1822) | D | 2.58 | 0 | 1 | 1 | 7.0 | 2.0 | 1.03 | 3.0 | 3.0 | 1.0 |
| 32 | *Platycheirus fulviventris* (Macquart, 1829) | D | 1.48 | 0 | 1 | 0 | 6.3 | 2.2 | 0.76 | 2.8 | 2.2 | 0.4 |
| 33 | *Platycheirus scambus* (Staeger, 1843) | D | 1.72 | 0 | 1 | 0 | 6.7 | 2.3 | 0.98 | 2.8 | 2.6 | 1.4 |
| 34 | *Baccha elongata* (F., 1775) | E | 3.01 | 1 | 0 | 0 | 6.7 | 1.7 | 0.98 | 3.7 | 3.0 | 1.3 |
| 35 | *Chrysotoxum cautum* (Harris, 1776) | E | 2.77 | 1 | 1 | 0 | 5.4 | 4.1 | 1.09 | 3.7 | 3.3 | 0.6 |
| 36 | *Dasysyrphus albostriatus* (Fallen, 1817) | E | 3.25 | 1 | 0 | 0 | 6.3 | 2.8 | 0.88 | 3.6 | 3.9 | 1.3 |
| 37 | *Didea fasciata* Macquart, 1834 | E | 2.58 | 1 | 0 | 0 | 7.7 | 3.7 | 0.85 | 4.4 | 4.2 | 0.4 |
| 38 | *Epistrophe eligans* (Harris, 1780) | E | 2.20 | 1 | 0 | 0 | 5.0 | 3.8 | 0.83 | 5.1 | 3.0 | 0.3 |
| 39 | *Epistrophe nitidicollis* (Meigen, 1822) | E | 2.58 | 1 | 0 | 0 | 5.3 | 3.8 | 0.88 | 4.2 | 3.9 | 0.7 |
| 40 | *Megasyrphus annulipes* (L., 1758) | E | 2.63 | 1 | 0 | 0 | 6.4 | 3.7 | 0.80 | 4.1 | 3.6 | 1.4 |
| 41 | *Leucozona lucorum* (L., 1758) | E | 2.72 | 1 | 1 | 0 | 5.2 | 3.8 | 1.29 | 3.7 | 3.6 | 0.7 |
| 42 | *Pipiza noctulica* (L., 1758) | E | 2.82 | 1 | 0 | 0 | 5.7 | 2.4 | * | 3.3 | 3.7 | 0.9 |
| 43 | *Dasysyrphus pinastri* (Meigen, 1822) | F | 2.34 | 1 | 0 | 0 | 5.8 | 2.9 | 0.88 | 3.0 | 3.0 | 1.5 |
| 44 | *Dasysyrphus venustus* (Meigen, 1822) | F | 2.44 | 1 | 0 | 0 | 5.3 | 3.3 | 0.88 | 3.2 | 3.4 | 1.1 |
| 45 | *Eupeodes lapponicus* (Zetterstedt, 1838) | F | 2.68 | 1 | 0 | 0 | 6.3 | 3.0 | 0.92 | 3.3 | 3.0 | 1.4 |
| 46 | *Melangyna lasiophthalma* (Zetterst., 1843) | F | 2.29 | 1 | 0 | 0 | 4.0 | 2.5 | 0.91 | 4.4 | 3.1 | 1.5 |
| 47 | *Meliscaeva auricollis* (Meigen, 1822) | F | 3.15 | 1 | 0 | 0 | 7.0 | 2.8 | 0.85 | 3.9 | 3.2 | 1.2 |
| 48 | *Parasyrphus annulatus* (Zetterstedt, 1838) | F | 2.63 | 1 | 0 | 0 | 5.9 | 2.3 | 0.92 | 3.3 | 3.7 | 0.6 |
| 49 | *Parasyrphus lineolus* (Zetterstedt, 1843) | F | 3.01 | 1 | 0 | 0 | 7.3 | 2.8 | 0.74 | 3.4 | 3.4 | 1.1 |
| 50 | *Parasyrphus vittiger* (Zetterstedt, 1843) | F | 2.58 | 1 | 0 | 0 | 7.2 | 2.5 | * | 3.2 | 3.2 | 1.4 |
| 51 | *Pipiza quadrimaculata* (Panzer, 1804) | F | 2.53 | 1 | 0 | 0 | 5.5 | 2.3 | 0.61 | 3.0 | 3.3 | 0.7 |
| 52 | *Scaeva selenitica* (Meigen, 1822) | F | 3.15 | 1 | 0 | 0 | 6.2 | 3.9 | * | 3.8 | 3.6 | 1.5 |
| 53 | *Chrysotoxum arcuatum* (L.) | G | 2.63 | 1 | 1 | 0 | 6.9 | 4.1 | 1.01 | 4.0 | 4.4 | 0.9 |
| 54 | *Chrysotoxum bicinctum* (L.) | G | 2.63 | 1 | 1 | 0 | 7.1 | 3.4 | 0.86 | 3.2 | 3.7 | 0.8 |
| 55 | *Chrysotoxum fasciatum* (Muller, 1764) | G | 2.39 | 1 | 1 | 0 | 6.7 | 3.5 | * | 2.6 | 3.3 | 1.6 |
| 56 | *Dasysyrphus tricinctus* (Fallen, 1817) | G | 3.11 | 1 | 0 | 0 | 7.7 | 3.3 | 0.96 | 2.9 | 3.2 | 1.9 |
| 57 | *Eriozona syrphoides* (Fallen, 1817) | G | 2.39 | 1 | 0 | 0 | 7.6 | 5.4 | 0.94 | 4.4 | 4.2 | 1.4 |
| 58 | *Eupeodes latifasciatus* (Macquart, 1829) | G | 2.87 | 0 | 1 | 0 | 7.6 | 2.9 | * | 2.8 | 3.4 | 1.3 |
| 59 | *Eupeodes luniger* (Meigen, 1822) | G | 3.25 | 0 | 1 | 1 | 7.0 | 2.9 | 1.15 | 3.1 | 3.5 | 1.8 |
| 60 | *Pipiza austriaca* Meigen, 1822 | G | 2.34 | 1 | 0 | 0 | 7.5 | 2.4 | 0.83 | 3.1 | 4.0 | 0.4 |
| 61 | *Pipizella viduata* (L., 1758) | G | 2.63 | 1 | 1 | 0 | 6.6 | 1.8 | 0.66 | 3.2 | 3.9 | 0.3 |
| 62 | *Pyrophaena granditarsa* (Forster, 1771) | G | 2.77 | 0 | 1 | 0 | 6.9 | 2.4 | 1.02 | 3.2 | 3.3 | 1.2 |
| 63 | *Platycheirus manicatus* (Meigen, 1822) | G | 3.06 | 0 | 1 | 0 | 5.8 | 2.4 | 2.01 | 2.8 | 3.2 | 2.2 |
| 64 | *Pyrophaena rosarum* (F., 1787) | G | 1.63 | 0 | 1 | 0 | 6.9 | 2.4 | 0.92 | 2.4 | 2.8 | 1.1 |
| 65 | *Platycheirus tarsalis* (Schummel, 1837) | G | 2.10 | 1 | 1 | 0 | 5.0 | 2.5 | 1.67 | 2.8 | 2.8 | 1.3 |
| 66 | *Sphaerophoria interrupta* (F., 1805) | G | 3.01 | 0 | 1 | 0 | 6.3 | 2.2 | 1.23 | 2.9 | 3.5 | 1.7 |
| 67 | *Xanthogramma pedissequum* Harris, 1776 | G | 2.58 | 1 | 1 | 0 | 6.7 | 3.1 | 0.84 | 3.8 | 4.1 | 0.5 |

Abbreviations of attributes. Foraging niche width (FNW). Habitats: presence or absence in woodlands (Wood), in wet- and grasslands (Wet) and in farmland areas (Farm). Morphometry: head width (HW) and tongue length (TL). Flower traits: height of plants (height), size of inflorescences (size) and depth of corolla tubes visited by hoverflies (see scales and references in Tables 1 and 2).