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Foraging ecology of hoverflies: morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species

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ABSTRACT. 1. Previous accounts of the feeding behaviour of hoverflies (Diptera: Syrphidae) are contradictory and in many cases do not correspond with field observations.

2. Patterns of feeding on nectar and pollen differ between species: these patterns are correlated with morphological differences.

3. The data indicate that there are two correlates of increasing tongue length: first, the proportion of pollen in the diet decreases; and second, the flies concentrate on visiting flowers with longer corollae, which contain more nectar sugar.

4. Reasons for these effects are discussed.

Introduction

Little is known of the feeding behaviour of adult syrphids. Some early authors thought that the adults attacked aphids (Lindner, 1919) or other flies (Curran, 1925), but these views have not since been confirmed. Müller, in 1883, meticulously noted whether the different species took nectar, pollen, or both nectar and pollen from a large variety of flowers; subsequent authors have in the main been content to record their presence on various flowers (Drabble & Drabble, 1917, 1927; Hamm, 1934; Emmett, 1971; El-Berry *et al.*, 1974a, b; Maier & Waldbauer, 1979). Although some workers have discounted any feeding by adults on protein (Oldroyd, 1964), breeding experiments with *Episyrphus balteatus* (DeGeer) and some other aphidophagous species have shown pollen to be necessary for ovarian development (Schneider, 1948). Pollen feeding would seem to be extensive in the family (Grinfeld, 1955; Schneider, 1958; Pino, 1962; Kugler, 1970), but no work appears to have been carried out to study the proportions of nectar, pollen and other foods in the diet.

In bumblebee studies much has been learnt from a consideration of the morphology of the mouthparts in relation to foraging behaviour (see Pekkarinen, 1979; Inouye, 1977, 1980), and a preliminary study indicated that a similar approach was instructive in the case of the Syrphidae (Gilbert, 1980). Comparative studies of the mouthparts of members of one family of Diptera are few (e.g. Lall & Davies, 1971, on three species of Tabanidae), although Pino (1962) provided sketches of the mouthparts of nine species of syrphid, and Maki (1935) depicted the sclerites of the mouthparts of a further eleven species. Lundbeck (1916) describes briefly the mouthparts of each genus of European Syrphidae, but these are difficult to follow without diagrams.

This paper considers the syrphid species common in two urban sites in Cambridge, England, and relates mouthpart morphology to the feeding mechanism; to the relative frequencies of nectar and pollen in the diet and the selection of flower species; and to the ecological correlates of these dietary choices.

Materials and Methods

Two main sites were chosen for study. The Fellows' Garden of St John's College, Cambridge (FG), is an area about 100 × 100 m

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delineated on three sides by water and on the fourth by a hedge and wide path. The vegetation consists of open woodland, mainly elm, with a large variety of naturalized spring flowers, giving way to grass in the summer and autumn. The main spring flowers are *Eranthis hyemalis* (L.), *Corylus avellana* L., *Cornus mas* L., *Anemone* (*blanda* and *nemorosa*) and *Endymion non-scripta* (L.) (nomenclature follows Clapham *et al.*, 1968): by early summer, grasses, such as *Arrhenatherum elatius* (L.) and *Dactylis glomerata* L., together with large numbers of *Lilium martagon* L., *Ranunculus* spp. and *Anthriscus sylvestris* (L.), form the dominant herb layer. In late summer one of the few flowers is *Heracleum sphondylium* (L.).

The second site was the Cambridge University Botanic Garden (BG), about 16 ha in area, with a very large diversity of flowers and types of habitat throughout the season (see Walters, 1979). The systematic beds, with a large range of flower types, include few trees, and the census walks described below therefore deliberately incorporated more wooded parts.

Supplementary visits were made to a third site, Hayley Wood, to observe the feeding behaviour of one species of hoverfly (*Rhingia campestris* Meigen) not present at the main sites. The vegetation of the wood has been extensively described (Rackham, 1975).

A standard census walk followed a route that covered most of each site, and was walked at as constant a speed as possible three times per day. Census days were chosen irrespective of weather conditions so that the two main sites were covered on adjacent days, once a week from April to early July 1979, and once per fortnight from July to the end of September 1979. Censuses usually began 30–60 min before sunrise, and ended between 16.00 and 16.30 hours B.S.T.; each round lasted 3–4 h, and there were gaps of 20 min between each round.

Each hoverfly seen was closely observed for a few seconds, identified, and its activity determined. Activities were variously classified as feeding on pollen, feeding on nectar, feeding on both nectar and pollen, feeding on aphid honeydew, imbibing water, resting, cleaning, hovering, mating (in cop.), mate-searching (males, where this was obvious) and ovipositing (females). A sample of the commoner species, and species that could not be identified on sight, were captured and anaesthetized with CO_2. Usually each specimen was put into a separate tube and transferred to a freezer, normally within 3 h. Flies were identified using Coe (1953), Verrall (1901), Speight (1978) and Speight *et al.* (1975). Nomenclature follows Kloet & Hincks (1976).

Handling time is defined as the time taken to insert the proboscis, suck up nectar, and withdraw the proboscis; it can be separated into the time spent ingesting the nectar (the 'sucking time') and the time spent moving the proboscis (the 'mechanical time'). The handling time was recorded using a small tape-recorder and transcribed with an event recorder designed and built by D. M. Unwin of the Department of Zoology, Cambridge University. Observations on handling time were limited to a short period (10–15 September 1979) to avoid major changes in environmental conditions, and all were made between 10.00 and 14.00 hours B.S.T., times when the quantity of nectar in the florets was immeasurably small. This had the effect of making the depth to nectar virtually equal to the corolla depth, and the sucking time negligible. Timings were taken only from closely related Compositae, to minimize the effects of the shape of the corolla. Handling times presented are mechanical times, and exclude time moving between florets. Only results from female *Eristalis tenax* L. are included here.

To look more closely at the mechanics of ingestion of nectar, video-recordings were made in the laboratory of flies sucking sucrose solutions from glass capillaries.

Mouthparts were measured using an eyepiece graticule after dissecting the sclerotized parts from the proboscis, which had been briefly immersed in alcohol. Measurements taken are shown in Fig. 1. The length of the proboscis was determined using a standard procedure: the head was secured with a pin and the labella grasped with fine forceps; in one movement the proboscis was pulled out to its furthest limit before the membranes split. The length was recorded as the distance from the lowest point of the face (a rounded projection of the lower mouth edge) to the tip of the labella, which pointed along the

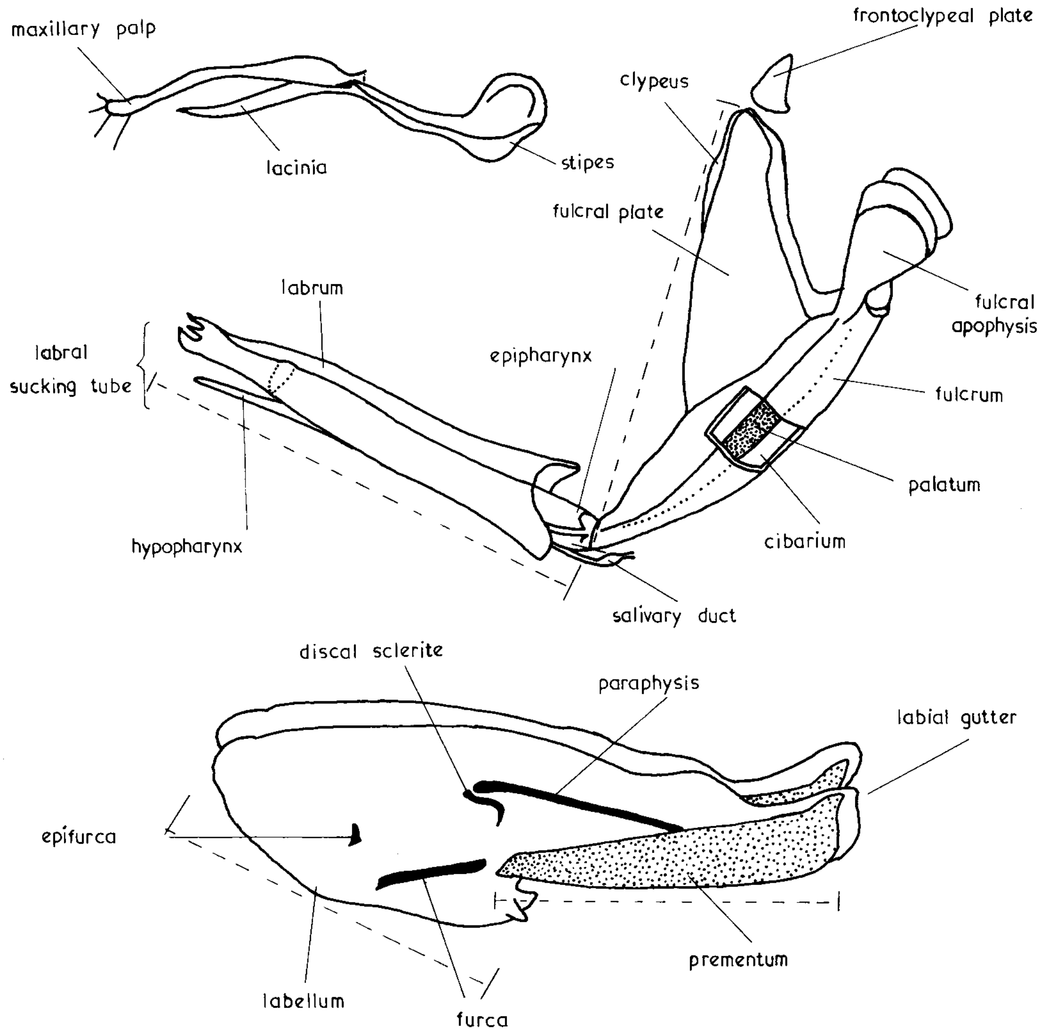

FIG. 1. The sclerites of the proboscis, taken from Schiemenz (1957); they are connected by more membranous cuticle. Measurements taken are indicated by the dashed lines, and shown in Table 3.

length of the proboscis. Drawings were made with the aid of a camera lucida from slides of representative specimens, the parts being mounted in Berlese fluid. Terminology follows Schiemenz (1957) (see Fig. 1).

Samples of florets visited in the experiments on handling time were taken and the corolla depth measured. The floret of a composite consists of a narrow basal section, inaccessible to the majority of hoverflies due to the breadth of the proboscis, and a wider apical section. All estimates refer to the distance from the base of the wider section to the splits in the corolla tube.

Results

Eight species (Table 1) constituted 80% of the sightings in the Botanic Garden and 87.5% of those in the Fellows' Garden. The results focus almost entirely upon these eight, with occasional remarks about *Rhingia* in Hayley Wood. Foods other than nectar and pollen were rarely taken by these species and are not considered further here.

Close-up filming, mainly of *Eristalis tenax*, demonstrated the method of ingesting nectar from a wide glass tube. The proboscis is extended until the tips of the labella touch

TABLE 1. A list of the most common species of this study.

Species	Per cent of all observations
Syrphus ribesii L., 1758	15.2
Metasyrphus corollae Fabr., 1794	10.5
Episyrphus balteatus De Geer, 1776	29.9
Melanostoma (*scalare* Fabr., 1794 and *mellinum* L., 1758)	12.9
Platycheirus albimanus Fabr., 1781	5.5
Syritta pipiens L., 1758	5.6
Eristalis (*Eoseristalis*) *arbustorum* L., 1758	2.3
Eristalis tenax L., 1758	3.9

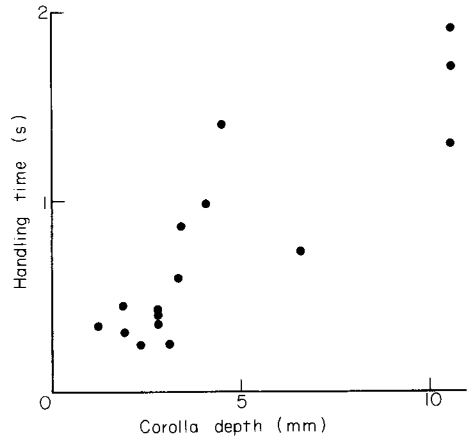

FIG. 2. The relationship between handling time (predominantly mechanical time, see text) and the depth of the corolla of florets of Compositae ($r=0.86$, $n=17$ each a mean of from five to seventy-four observations, $P<0.001$).

the surface of the nectar, where the labella separate so that they come to lie flat upon the meniscus. Pumping movements of the cibarium commence, and nectar is sucked up the proboscis. As the level of the fluid goes down the proboscis is not extended further to keep pace, but the labella are gradually closed until no more nectar can be obtained: the fluid level is then 1–2 mm lower than the tip of the labella. Only then is the proboscis extended so that the process may be repeated, and more fluid extracted. In tubes too narrow for the labella to be separated, sucking is still possible; the pseudotracheae are probably used to draw the fluid into the proboscis, and in some circumstances they extend over the edge of the labella.

In the field, nectar feeding occurs from a wide variety of flowers. The nectar can be present solid on the surface of the nectary or sequestered in tissue in some open flowers, especially Umbelliferae, and it is sometimes possible to see the flies spitting fluid (presumably saliva or regurgitated crop contents; see Hansen Bay, 1978) on to the nectary, producing a medium in which the nectar sugar can dissolve. Corbet *et al.* (1979a) have reported that sequestered sugar is rapidly released into water deposited in a flower of *Crataegus*.

Handling times are shown in Fig. 2: there is a highly significant relationship between mechanical time and the corolla depth ($P<0.001$).

During pollen feeding of all species, typically an anther is held between the labella which are then rubbed together. The proboscis is in continual motion, and it would appear that the labial gutter moves up and down relative to the labral sucking tube. The movement is extremely rapid, however, making the sequence of events difficult to determine. When the anther is relatively large and elongated, it is passed by the fly between the labella removing pollen from the entire surface (e.g. *Melanostoma* on *Arrhenatherum*).

When feeding, hoverflies frequently stop to clean the face and proboscis, ingesting the cleaned material. Between feeding bouts they usually fly to a leaf in the sun and clean the whole body, paying particular attention to the wings and face; only material from the face and proboscis, wiped clean by the forelegs, is normally eaten, the rest apparently being discarded (but see Holloway, 1976, and Discussion). Overall in both sites, hoverflies spent 20% of their time cleaning.

The numbers and proportions of female hoverflies feeding on nectar and pollen are shown in Table 2: data for the males are similar in their patterns, but the males of all species but one took pollen less frequently (*S.ribesii* ♀98.1% pollen, ♂95.6%; *Metasyrphus corollae* ♀52% pollen, ♂36%; *E.tenax* ♀20% pollen, ♂11.8%). Assuming that these proportions are equivalent to the proportions of each food in the diet of individuals, it is clear that there is wide variation in the diet between species. *Melanostoma*, *Episyrphus* and *Syrphus* almost always take pollen; *Metasyrphus* and *Platycheirus* appeared to feed on a more or less equal mixture of nectar and

TABLE 2. Numbers of females seen feeding.

Species	Nectar		Pollen		Both		Totals (%)	
	FG	BG	FG	BG	FG	BG	Nectar	Pollen
Syrphus ribesii	0	2	51	201	2	1	5 (1.9)	255 (98.1)
Metasyrphus corollae	1	100	55	57	0	31	132 (48)	143 (52)
Episyrphus balteatus	1	17	240	333	1	35	54 (8.1)	609 (91.9)
Melanostoma scalare	1	11	117	85	1	1	14 (6.4)	204 (93.6)
Platycheirus albimanus	2	75	11	63	1	34	112 (50.7)	109 (49.3)
Syritta pipiens (♂ also)	4	63	20	25	4	10	81 (57.9)	59 (42.1)
Eristalis arbustorum	0	34	0	10	1	28	63 (62)	39 (38)
Eristalis tenax	7	95	2	6	0	10	112 (80)	28 (20)

pollen; *Syritta* and the *Eristalis* species more often take nectar. *Rhingia campestris* was always seen taking nectar in Hayley Wood, although it is known to take pollen (Müller, 1883).

The morphology of the mouthparts varies with species (Fig. 3): some have a short thick proboscis with broad fleshy labella (e.g. *Episyrphus balteatus*) whereas others have relatively long and slim mouthparts (e.g. *Eristalis tenax*). *Rhingia* has the longest proboscis of all the British species, and its labellum is contrasted with those of *Eristalis* and *Episyrphus* in Fig. 4. Both *Rhingia* and *Eristalis* have short labellar hairs, whereas these hairs are relatively much longer in pollen-feeding species (Figs. 3 and 4). Morphometric data are shown in Table 3. Only values for females are given: those for males are similar in mean values but are less variable (e.g. *Syrphus ribesii*, coefficient of variation of head width: ♀6.27%, ♂3.93%). Weights are quite variable between species: this may be attributable to crop contents, and also because some individuals were obtained from a Malaise trap and had lost weight before collection. Interspecific wet weights have a 60-fold range between the smallest *Melanostoma* and the largest *Eristalis tenax*. In addition to size differences between species, the shapes of the sclerotized parts change according to the diet (Fig. 5). A greater proportion of nectar in the diet is associated with a longer and thinner proboscis and sclerites. Correlations between measurements are shown in Table 4: all sizes are highly intercorrelated, as expected. When shape is expressed as ratios of sizes, significant correlations exist only with the proportion of pollen in the diet. This emphasizes my hypothesis that natural selection has operated on the relative sizes of parts of the proboscis.

The length of the proboscis is important in nectar feeding, and there is a significant correlation between the percentage of pollen in the diet and proboscis length (Table 4). A quadratic function can be fitted to this relationship (Fig. 6). The initial decline reflects the disproportionate size of the labellum among pollen specialists. The morphology of the sclerites also demonstrates this correlation (Fig. 5).

This functional continuum is further illustrated by an analysis of the depths of corolla visited; frequencies of nectar visits to different corolla depths are given in Table 5. Species with short proboscides visit open flowers to a greater extent than those with longer mouthparts, which are more often found feeding from deeper corollae. *Rhingia*, with a proboscis of about 12 mm long, was most commonly found taking nectar from *Glechoma hederacea* L. (corolla depth about 12 mm). The relationship between the range of corolla depths visited, weighted by the frequencies of visitation (see legend to Fig. 7), is highly significant ($n=8$, $r=0.80$, $P<0.01$), and is shown in Fig. 7 together with similar values from a previous study (Gilbert, 1980). In the latter study nectar and pollen visits were not differentiated; the coincidence for species in common is remarkable, particularly for those which take mainly nectar in their diet. The weighted averages for *Eristalis* and also for some other species not considered in detail here (e.g. *Sphaerophoria scripta* (L.)), are almost identical, and other pairs are similar. When all values of Fig. 7 are used in the regression, a higher correlation is obtained ($n=17, r=0.82, P<0.001$).

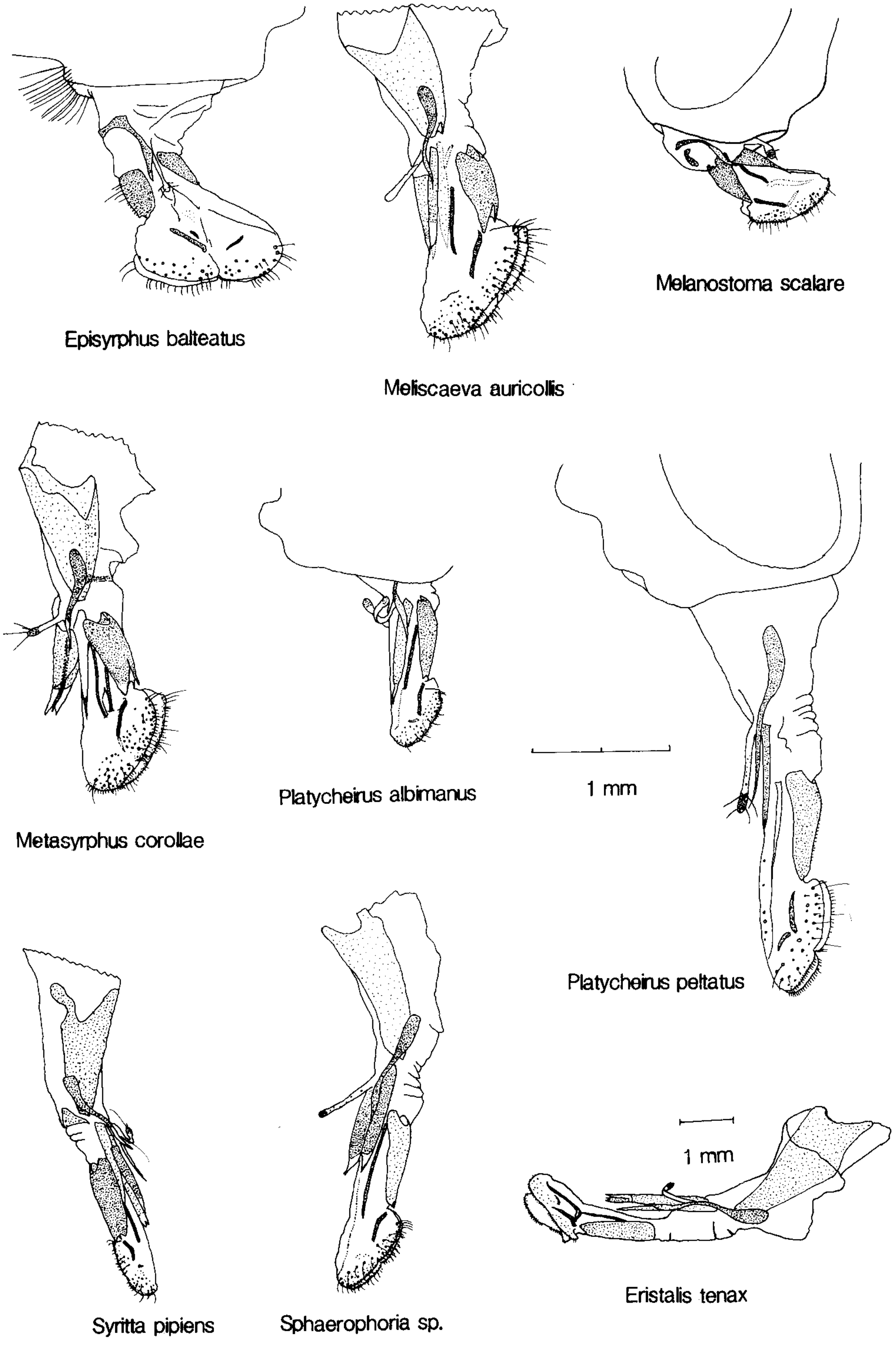

FIG. 3. The proboscides of various species of hoverfly. Note the change of scale for *Eristalis tenax*. *Sphaerophoria* and *Platycheirus peltatus* (Meigen) take more nectar than pollen, and *Meliscaeva auricollis* (Meigen) belongs to the pollen-feeding group; the numbers of these species seen during the year were not sufficient to warrant inclusion in the main analysis of this report. Scale marks are in mm.

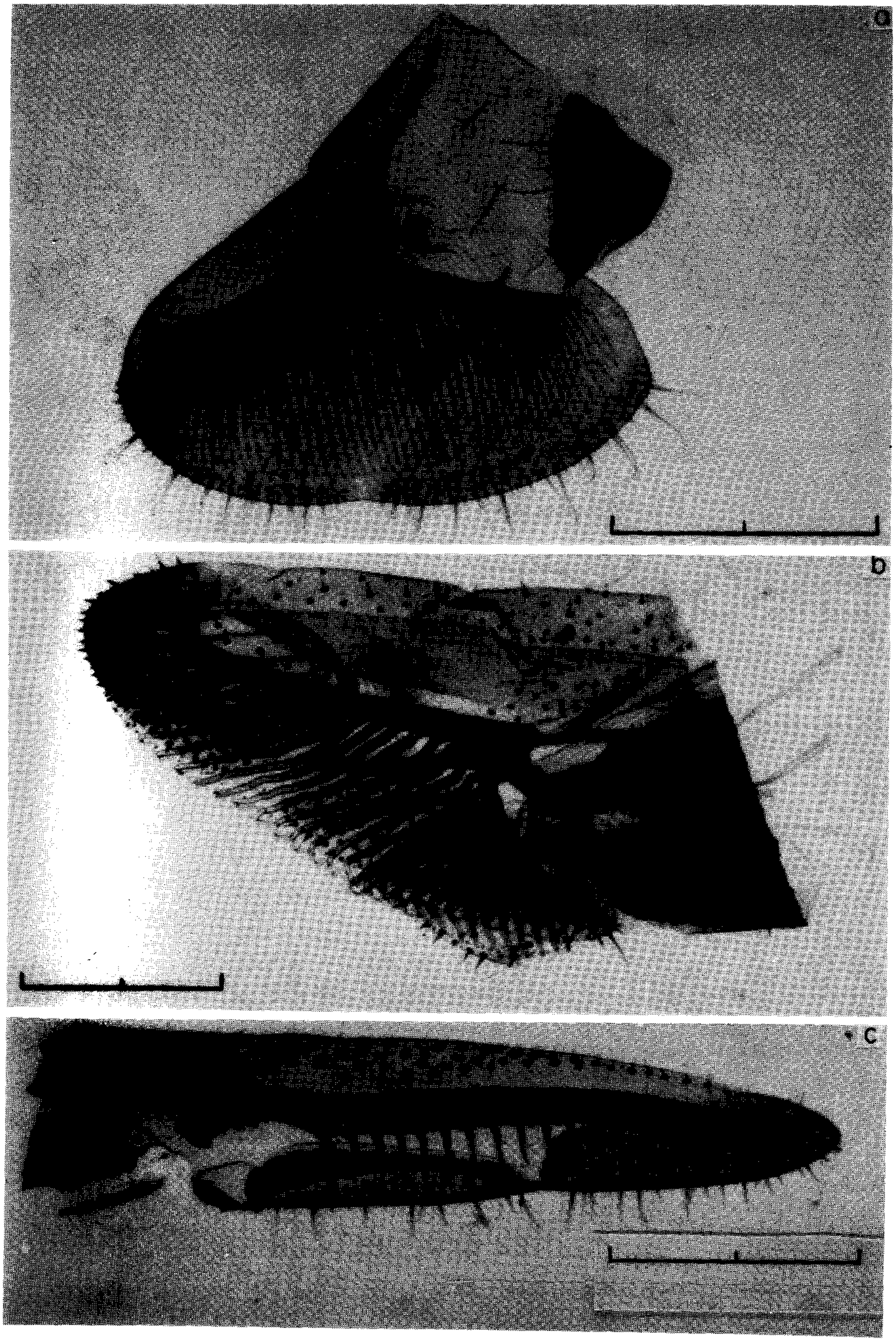

FIG. 4. The labella of three species of hoverfly: (a) *Episyrphus balteatus* takes 92% pollen in its diet; (b) *Eristalis tenax* takes 20% pollen; (c) *Rhingia campestris* takes more than 95% nectar in the diet. 0.5 mm scale marks are indicated.

TABLE 3. Morphological measurements of female hoverflies. Measurements taken are shown in Fig. 1. All figures are ± one standard deviation.

Species	n	1	2	3	4	5	6	7	8	9	10	11
Syrphus ribesii	10	31.7 ± 17.9	3.67 ± 0.23	3.43 ± 0.26	1.24 ± 0.11	0.96 ± 0.08	0.80 ± 0.05	1.18 ± 0.09	1.49 ± 0.15	1.05	47.5	98.1
Metasyrphus corollae	10	22.1 ± 8.6	3.13 ± 0.19	3.25 ± 0.33	1.11 ± 0.06	0.92 ± 0.05	0.70 ± 0.05	0.84 ± 0.11	1.21 ± 0.16	1.32	39.3	52.0
Episyrphus balteatus	10	17.1 ± 7.0	3.07 ± 0.07	2.90 ± 0.23	1.05 ± 0.04	0.78 ± 0.04	0.63 ± 0.05	0.96 ± 0.05	1.55 ± 0.07	1.09	44.8	91.9
Melanostoma scalare	10	8.1 ± 4.4	2.11 ± 0.12	2.13 ± 0.19	0.72 ± 0.06	0.62 ± 0.04	0.50 ± 0.03	0.71 ± 0.06	1.40 ± 0.06	1.01	36.6	93.6
Platycheirus albimanus	10	8.5 ± 4.3	2.36 ± 0.07	3.31 ± 0.26	1.10 ± 0.04	0.96 ± 0.06	0.64 ± 0.02	0.62 ± 0.04	0.97 ± 0.06	1.77	40.3	49.3
Syritta pipiens (3 ♂, 6 ♀)	9	13.4 ± 5.6	2.12 ± 0.17	3.43 ± 0.21	1.09 ± 0.09	0.97 ± 0.05	0.74 ± 0.05	0.59 ± 0.06	0.80 ± 0.04	1.85	37.3	42.1
Eristalis arbustorum	10	40.1 ± 17.6	3.94 ± 0.38	5.36 ± 0.50	1.70 ± 0.16	1.62 ± 0.16	1.12 ± 0.11	1.04 ± 0.10	0.93 ± 0.05	1.63	33.6	38.0
Eristalis tenax	10	125.8 ± 21.4	5.43 ± 0.22	7.85 ± 0.22	2.39 ± 0.11	2.37 ± 0.07	1.57 ± 0.06	1.44 ± 0.06	0.92 ± 0.04	1.66	26.4	20.0

n = number of individuals measured; 1 = wet weight (mg); 2 = head width (mm); 3 = tongue length (mm); 4 = fulcrum length (mm); 5 = length of labrum–epipharynx (mm); 6 = prementum length (mm); 7 = labellum length (mm); 8 = labellum/prementum ratio; 9 = fulcrum/labellum ratio; 10 = number of pseudotracheae per mm length of labellum; 11 = percentage of individuals seen taking pollen.

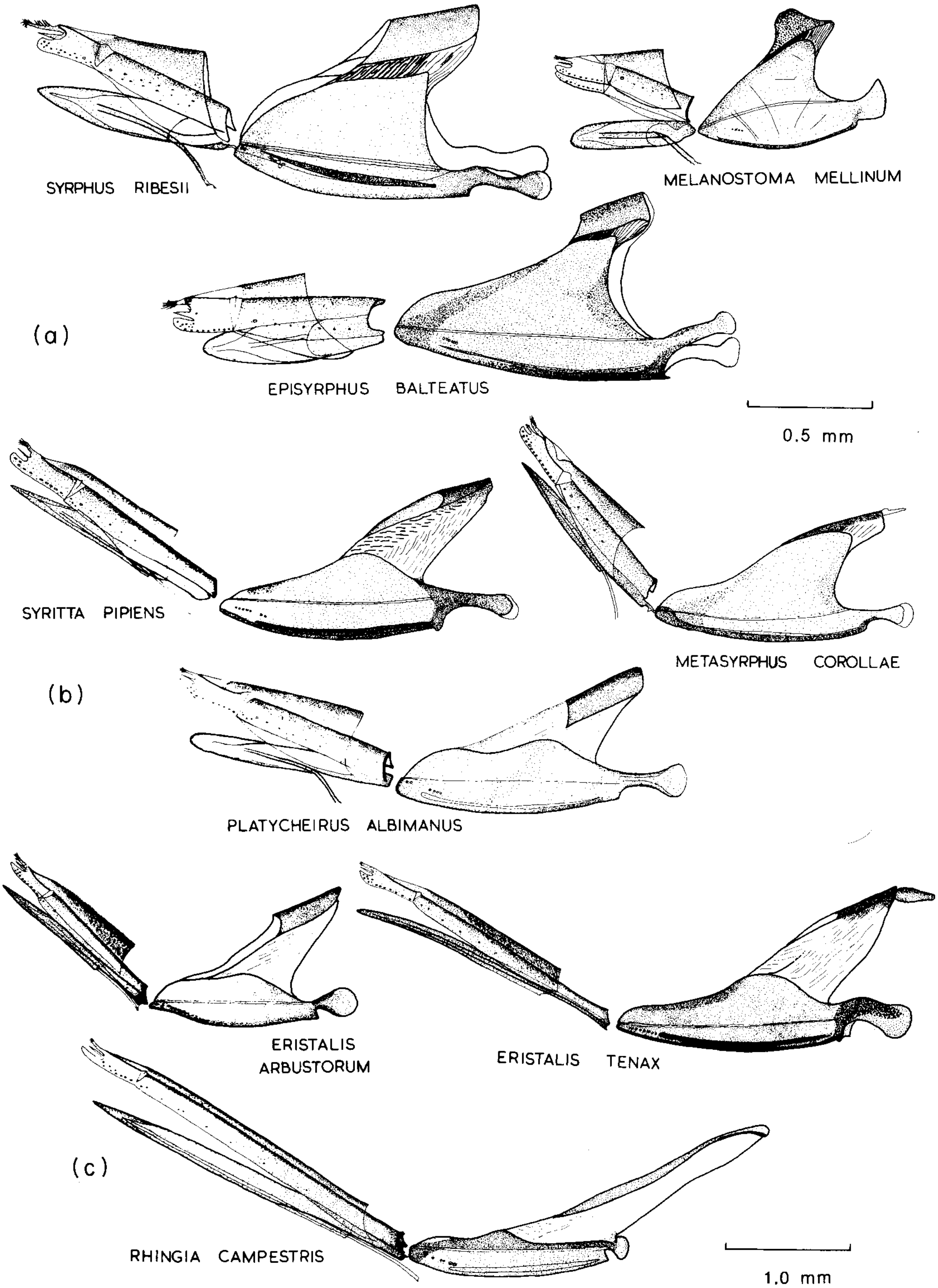

FIG. 5. The fulcra and mediproboscides of the species included in this study. Orientation of the parts with respect to one another has no significance. (a) Pollen feeders; (b) mixed; (c) mainly nectar feeders. Note the change of scale between the first two and (c).

TABLE 4. Matrix of correlations between the measurements of Table 3.

	Weight	Head width	Tongue length	Fulcrum length	Labrum – epipharynx length	Prementum length	Labellum length	Labellum/ prementum ratio	No. of pseudo-trachae per mm labellum length	Fulcrum/ labellum ratio
Head width	0.92									
Tongue length	0.94	0.89								
Fulcrum length	0.94	0.92	0.99							
Labrum–ephipharynx	0.94	0.88	0.99	0.99						
Prementum length	0.95	0.91	0.99	0.99	0.99					
Labellum length	0.84	0.95	0.75	0.80	0.74	0.79				
Labellum/prementum	0.31	0.13	0.53	0.47	0.55	0.49	0.11			
No. of pseudotrachae	0.70	0.49	0.75	0.69	0.78	0.73	0.30	0.68		
Fulcrum/labellum	0.25	0.09	0.48	0.46	0.49	0.42	0.15	0.96	0.53	
Pollen in diet (%)	0.56	0.42	0.74	0.69	0.74	0.69	0.15	0.91	0.78	0.88

$n = 8$ when $r > 0.62, P < 0.05$; $r > 0.79, P < 0.01$; $r > 0.90, P < 0.001$.

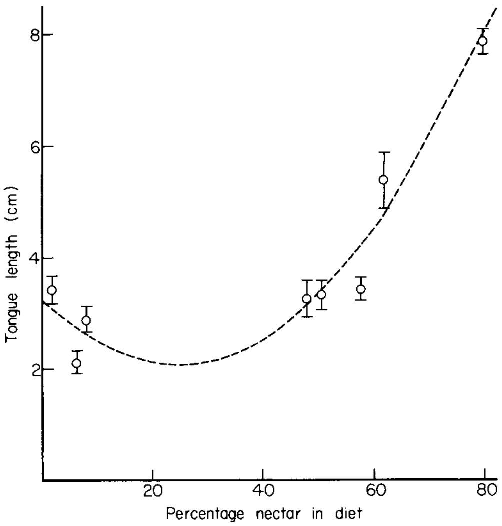

FIG. 6. The relationship between tongue length (mean and standard deviation) and diet. A curve has been fitted by computer using the GENSTAT package. The initial decline in tongue length with increasing %nectar in the diet is reflecting the disproportionate size of the labella in the species which take mainly pollen. The equation: $\%\text{nectar} = 3.3 - 0.1(\text{TL}) + 0.02(\text{TL})^2$, where TL = tongue length, accounts for 90.7% of the variance, and the addition of the squared term significantly improves the fit ($P < 0.005$).

Discussion

It is now possible to supplement existing accounts of the feeding behaviour of hoverflies using both behavioural observations, direct and from the filming sessions, and interspecific correlations between morphology and diet. Hypotheses can also be formulated about the ecological correlates of diet selection and the associated morphology of the mouthparts.

The available literature dealing with mouthparts of hoverflies is summarized in Table 6; most authors are concerned only with the external morphology and few deal with more than the basic details.

Feeding on pollen

Some authors (Nayar, 1964; Zimina, 1957; Percival, 1965) thought that pollen was taken directly into the labral sucking tube with no involvement of the labella. Others (Künckel d'Herculais, 1875; Müller, 1883; Buckton, 1895; Lindner, 1919; McAlpine, 1965) recognized that the anthers of the flower are grasped by the labella and relieved of their pollen by a rubbing motion. Buckton (1895) and Schiemenz (1957) believed that the laciniae played a part in this process, and Vine (1895) stated that the pollen is brushed off the anthers by hairs on one of several divisions at the end of the labrum. These peculiar and in many cases diagnostic (Lundbeck, 1916) divisions are very highly developed in syrphids compared with other groups (Dimmock, 1881); Zimina (1957) also thought that they served to break apart lumps of pollen. Percival reported that pollen was rasped off the anthers with prestomal teeth; no such teeth have been observed in the species of this study. Dimmock (1881) and Müller (1883) considered that the pseudotracheae were chitinous ridges to help convert lumps of pollen into strings suitable for ingestion, but

TABLE 5. Frequencies of visits for nectar to the various depths of corolla (males and females combined). 'Others' are corollae more than 10 mm in length, or undetermined; *n* is the number of observations.

Species	Corolla depth (mm)											*n*	Weighted average
	0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	Others		
Syrphus ribesii	50.0		35.7	7.1								13	9.27
Episyrphus balteatus	26.1	43.5	18.6	1.9	6.8	0.6	1.9				1.2	162	12.80
Metasyrphus corollae	10.9	37.5	39.5	6.5	1.5	0.9	0.6			0.3	2.4	339	15.28
Melanostoma	66.7	3.0	21.2	6.0	3.0						3.0	34	7.54
Platycheirus albimanus	3.7	8.0	29.8	23.9	26.1	5.3		1.1			2.2	188	27.79
Syritta pipiens	16.9	11.1	43.4	9.6	9.6	1.2		1.2		2.4	10.8	83	18.49
Eristalis arbustorum	7.2	10.4	44.8	10.4	25.6	0.8				0.8		125	24.48
Eristalis tenax	5.8	7.1	27.4	9.7	15.9	6.2	9.3	11.5	0.4	0.9	6.2	227	33.32

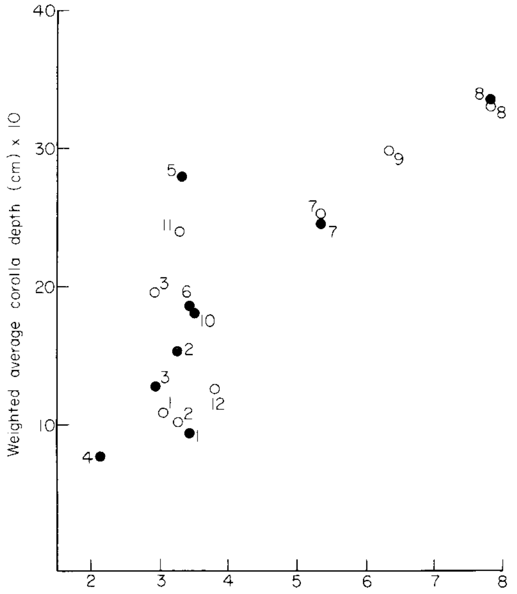

FIG. 7. The relationship between the proboscis length and the average corolla depth (CD), weighted by the frequencies of visitation (weighted average = sum of (% X CD/10). Only nectar visits are considered. Values for this study are plotted as filled circles; results from a previous study (Gilbert, 1980) are shown as open circles. Species are: 1, *Syrphus ribesii*; 2, *Metasyrphus corollae*; 3, *Episyrphus balteatus*; 4, *Melanostoma*; 5, *Platycheirus albimanus*; 6, *Syritta pipiens*; 7, *Eristalis arbustorum*; 8, *Eristalis tenax*; 9, *Eristalis nemorum*; 10, *Sphaerophoria* (this study); 11, *Sphaerophoria* (males); 12, *Sphaerophoria* (females).

the role of these channels is still unclear. They undoubtedly strain the food of houseflies and blowflies (Graham-Smith, 1930; Deithier, 1976), but there is little need to strain nectar. That the pseudotracheae are not of primary importance in nectar feeding is supported by the fact that *Bombylius*, which feeds almost entirely on nectar, has very few pseudotracheae (Proctor & Yeo, 1973); *Empis livida* L., a predator that also takes nectar from flowers, has none at all (Bletchly, 1954). Many dissected specimens in this study had pollen grains present inside the pseudotracheal canals, and there is a highly significant positive correlation between the density of canals on the labellum and the percentage of pollen taken in the diet (Table 4). However, there were also individuals with a few pollen grains in the crop that were too large ever to have entered the pseudotracheal canals. It is likely that the pseudotracheae have an important though not exclusive role in pollen feeding.

There is no evidence that the pollen is ground to a pulp, as suggested by Lindner (1919), Percival (1965), Elton (1966) and Faegri & van der Pijl (1979); on the contrary, many studies including the present one report the occurrence of undamaged grains in the gut (Müller, 1883; Vine, 1895; Schiemenz, 1957; Schneider, 1958; van der Goot & Grabandt, 1970), and these can be identified (e.g. Stelleman & Meeuse, 1976). Zimina (1957) reported the presence of groups of bristle-like outgrowths at the entrance to the crop which penetrate the grains; he found that the pollen appeared to become clear in the crop, lose part of the extine, and pass out of the hindgut in a damaged condition. According to Parmenter (1953), some species of syrphids squeeze the pollen grains between the labella, secrete digestive juices on to the crushed mass, and ingest the resulting liquid. There seems to be little evidence for this view: nutrients can escape from pollen even without enzymatic action (Linskens & Schrauwen, 1969; Gilbert, 1972). Enzymes are probably present in the crop (Zimina, 1957) and the gut (Schiemenz, 1957; Kevan, 1970) of syrphids.

Table 4 demonstrates that the relative size of the labellum is highly correlated with the observed pattern of pollen feeding; the larger the relative size of the labella of a particular species (compare Fig. 4 with weights in Table 3), the greater is the proportion of pollen in its diet. A broad and fleshy labellum may be advantageous in pollen feeding by reducing the time required to crop the pollen from an anther, and thus increasing its rate of ingestion.

One may assume that the percentage of individuals seen feeding on a particular food item reflects its importance in the diet; this seems reasonable here in view of the extensive period of data collection: the standard walks lasted all day and were done throughout the season. However, it may be argued that such an assumption is misleading because of the large amounts of time devoted to cleaning, and therefore that those species described here as mainly nectar feeders (*Eristalis* and *Rhingia*) were not seen eating pollen from anthers, and do not have labella adapted for such a method, because they obtain their

TABLE 6. Literature dealing with the mouthparts of hoverflies. Nomenclature follows Kloet & Hincks (1976), Thompson *et al.* 1976 and Knutson *et al.* (1975).

Species described	References
General description	Gerstfeld (1853), Lundbeck (1916), Wesché (1904)
Most European genera	Lundbeck (1916)
Asarkina porcina (Coq.)	Maki (1935)
Baccha (Allobaccha) amphithoe Walker	Maki (1935)
Carposcalis chalconota (Philippi)	Pino (1962)
Copestylum scutellatum (Rondani)	Pino (1962)
Dideopsis aegrota (Fabr.)	Maki (1935)
Dolichogyna chilensis (Guérin-Men.)	Pino (1962)
Episyrphus balteatus (DeGeer)	Müller (1883), Nayar (1964)
Episyrphus nectarinus (Wied.)	Maki (1935)
Eristalinus obscuritarsis (= *laetus* (Wied.))	Maki (1935)
Eristalinus quinquestriatus (Fabr.)	Maki (1935)
Eristalis arbustorum (L.)	Müller (1883), Schiemenz (1957)
Eristalis horticola (DeGeer)	Dimmock (1881)
Eristalis tenax (L.)	Meinert (1881), Müller (1883), Buckton (1895), Vine (1895), Wesché (1904), Peterson (1916), Gouin (1946, 1949), Pino (1962), Percival (1965), Holloway (1976)
Eumerus figurans Walker	Maki (1935)
Ischiodon scutellaris (Fabr.)	Maki (1935)
Helophilus pendulus (L.)	Wesché (1904)
Melanostoma fasciatum (Macq.)	Holloway (1976)
Metasyrphus luniger (Meigen)	Vine (1895)
Microdon violaceus (Macq.)	Pino (1962)
Paragus (Pandasyophthalmus) politus Wied.	Maki (1935)
Phytomia zonata (Fabr.)	Maki (1935)
Pipiza aurantipes (Bigot)	Pino (1962)
Rhingia sp.	Meinert (1881), Müller (1883), Dorsman (1920)
Scaeva melanostoma (Macq.)	Pino (1962)
Sterphus coeruleus (Rondani)	Pino (1962)
Sphaerophoria taeniata (Meigen)	Menzbier (1880)
Syritta orientalis Macq.	Maki (1935)
Syritta pipiens (L.)	Wesché (1900, 1902)
Syrphus sens.lat.	Lindner (1919), Zimina (1957)
Syrphus octomaculatus Walker	Pino (1962)
Syrphus ribesii (L.)	Meinert (1881)
Volucella spp.	Künckel d'Herculais (1875)
Volucella elegans Loew	Arnal (1955)

pollen in a manner similar to that of bees. This is by exploiting the adherence of pollen to specialized body hairs, the pollen then being removed and ingested during cleaning or in flight. The method was described by Holloway (1976) in *Eristalis tenax*; I would disagree as to its importance relative to direct feeding. Holloway's claim that in some species this method has replaced direct feeding altogether is particularly open to question. Of the samples collected and from observation, only some *Cheilosia* species, especially *Cheilosia paganus* Meigen, and *Eristalis arbustorum* were regularly carrying appreciable amounts of external pollen, and their frequency was low. *Cheilosia paganus* was more often seen taking pollen direct from the anthers than feeding on nectar (twenty-four of thirty-seven observations). Cleaning occurs whether or not the flies are dusted with pollen, or have hairy bodies: many species seem to reject this source of food. It seems more likely that heavy pollen loads result from visiting certain flowers, and *Ranunculus* in particular (used by Holloway in her experiments) seems able to cover its visitors (J. Haslett, personal communication; personal observation). Holloway thought that the extraordinary hairs on the front femora of *Platycheirus* species were palynophilic: gut analyses of hoverflies have shown that in general females have more pollen in the alimentary canal than the males (J. Haslett, personal communication), yet only the male *Platycheirus* have these hairs, and in *P.albimanus* at least the males were frequently seen (52.0% of feeding observations) feeding directly from anthers.

Feeding on nectar

The pseudotracheal role in nectar feeding has never been precisely determined. Buckton (1895) and Schiemenz (1957) envisaged nectar travelling by capillary action to the common duct and thence directly into the labral sucking tube and pharynx by means of the double pump (see Schiemenz, 1957; Rice, 1970; Dethier, 1976). Nayar's claim that the labella are spread flat when sucking fluid (Nayar, 1964) applies only on flat nectaries: usually a narrow corolla tube precludes the opening of the labella. Lindner (1919) described the ingestion of nectar directly from the end of the labral sucking tube; observations have failed to support this view.

From filming it is clear that hoverflies are not only capable of sucking fluid from a glass capillary at the fullest extension of the proboscis, but can also obtain nectar from a few millimetres deeper than this by drawing it up the sides of the capillary. This implies first that nectar can travel along the labial gutter between the labella and the proximal end of the prementum without the need to be contained within the labral sucking tube; and secondly that the inner surfaces of the labella are hydrophilic. A hydrophilic labellar surface could be a valuable adaptation to nectar feeding. Adaptive pressure to obtain nectar from deep corollae can be seen in the shape of the labellum in *Rhingia*: the labellum is narrow and pointed (Fig. 4c), apparently functioning as an extension to the length of the proboscis.

The relationship between the average corolla depth and proboscis length (Fig. 7) has previously been found for bumblebees (Brian, 1957; Heinrich, 1976; Inouye, 1978) and for hoverflies (Gilbert, 1980). Lall & Davies (1971) interpreted Hocking's (1953) data for tabanids in a similar manner. The remarkable correspondence between results shown in Fig. 7 lends strong support to the idea that each species has a more or less fixed pattern of visiting frequencies to flowers of different corolla depths, because the two studies were carried out in different counties, over different periods of time, and on very different ranges of flowers. The patterns moreover cannot be coevolved since most of the flowers in the Botanic Garden are not native to Britain.

Why should proboscis length and floral morphology be correlated in this way? It is likely that these patterns are common to many flower-feeding insects since many show similar differences in proboscis length; for example, the Tabanidae (Lall & Davies, 1971; Faegri & van der Pijl, 1979) and Nemestrinidae (Vogel, 1954). It is obvious why nectar in longer corollae is unavailable to short-tongued species, but what discourages the longer-tongued species from visiting short corollae? Optimal foraging theory (for review see Pyke *et al.,* 1977) usually uses energy as the currency to be 'optimized', and hypothesizes that foraging behaviour maximizes the rate of acquisition of energy. In nectar feeding there may be a 'trade-off' between the amount of nectar expected from a flower and the time required to extract it. Both parameters may be affected by the length of the proboscis (Inouye, 1980). More nectar sugar (i.e. more energy) has been found in flowers with longer corollae both interspecifically (O. E. Prŷs-Jones, personal communication, $r = 0.58$, $n = 91$ species, each a mean of 10 samples, $P < 0.001$) and intraspecifically (Brink & deWet, 1980). In association with handling time considerations (Holm, 1966; Inouye, 1977, 1980) this may be partly responsible for the lack of visits by long-tongued bees to short corollae. For *Eristalis tenax* there is a relationship between mechanical handling time and corolla depth (Fig. 2); the relationships already established for bumblebees therefore also hold good for hoverflies. Differences in mechanical handling time are fairly small, however, and each point is a mean with a coefficient of variation of between 25% and 50%; since there is more nectar in longer corollae, these handling time differences will be exaggerated when sucking time is included. The relationship between sucking time and nectar concentration is complex even if only one type of sugar is present (Kingsolver & Daniel, 1979). Quantitative work is being carried out to assess mechanical and sucking time for several species; these results may partly explain the relationship seen in Fig. 7.

Ecological correlates of the diet

Overall hoverfly numbers were higher in the Botanic Garden (4478 individuals seen, 3314 in the Fellows' Garden); the site is larger and has a greater density of flowers. Nectar feeders were rarely seen in the Fellows' Garden, and *Metasyrphus* and *Platycheirus* took mostly pollen there (Table 2); this was due to the lack of sources of nectar for most of the season in this site. Females were more often seen taking pollen than males, and in general their crops contained more pollen. Pollen has been shown to be required for egg maturation in *Episyrphus balteatus* (Schneider, 1948). Stürken (1964) has investigated further the nutritional requirements for egg production in *Metasyrphus corollae*, and found that none of the pollen substitutes tried could replace pollen in the diet, the number of eggs being substantially reduced under any artificial regime. I have shown that in part flower choice depends upon the corolla depth, but this may also depend upon species-specific differences between the nutritive value of pollens, which can be considerable (Stanley & Linskens, 1974). The two species of *Melanostoma* were specialists on the pollen of anemophilous grasses, principally *Arrhenatherum* and *Dactylis* (31% of feeding observations of *M.scalare*), also visiting *Ranunculus* in the spring. These results agree with previous authors (Müller, 1883; Drabble & Drabble, 1927; van der Goot & Grabandt, 1970; Stelleman & Meeuse, 1976; Leereveld *et al.*, 1976; Stelleman, 1978). The other two pollen feeders, *Episyrphus* and *Syrphus*, were seen in the main taking the pollen of Umbelliferae and Compositae; possibly these pollens are more nutritious. It is assumed that the nutritive value of pollen lies in its protein and amino acids: Stürken (1964) found a dramatic reduction in the number of eggs laid by *Metasyrphus corollae* when any single amino acid except cystine was omitted from an artificial diet.

There may be two groups of smaller hoverflies, namely the pollen specialists and those taking nectar also (Fig. 6). Larger species mainly take nectar, possibly because they require more energy, or because larger organisms in general devote proportionately fewer resources to reproduction than do smaller ones (Reiss, 1981). Appreciable quantities of amino acids and other substances can also be found in nectar (Baker & Baker, 1973a,b, 1975, 1976, 1977; Corbet *et al.*, 1979b), although quantitatively most of these are probably contaminants (Willmer, 1980). Sugars are also present in pollen, and the two groups of smaller hoverflies may represent alternative strategies for obtaining nutritional needs; pollen specialists rely on cropping large amounts of pollen from which they obtain both energy and other substances needed for reproduction and maintenance. The other group adopts a mixed strategy, taking nectar to satisfy their energetic needs and pollen to obtain particular nutrients.

Male *Syrphus ribesii* and *Episyrphus balteatus* have particularly high energetic requirements because they hover in 'leks' (Heinrich & Pantle, 1975) for most of the day; their crops were devoid of pollen grains, containing only a clear syrupy fluid. The few grains in the crops of males caught during May were all probably *Crataegus*. It is likely that newly emerged males require some pollen to mature the testes and initiate sperm production, as suggested for *Carposcalis carinata* Curran in the high Arctic (Kevan, 1970), but the maintenance of spermatogenesis probably requires comparatively few resources. Therefore males may switch from pollen to nectar or honeydew feeding once they are ready to mate. If they feed from trees they are unlikely to have been included in the standard censuses.

It seems clear that the diets of syrphids are more complex than previously realized, and that patterns of feeding on nectar and pollen differ widely between species. The data presented above describe these patterns and suggest possible interpretations. Evolution has clearly affected the morphology of the mouthparts, despite the views of Pino (1962), who suggested that they were not well adapted to feeding from flowers. The evidence indicates that relevant parsimonious explanations are available to interpret morphological differences between syrphid species in terms of adaptation to ecological factors, and these explanations are supported by evidence of these ecological factors. In this way it is hoped that a panglossian interpretation of adaptation (Gould & Lewontin, 1979) can be avoided.

In summary, it seems that body size may be an important factor influencing the diets of hoverflies, and that dietary differences are matched by differences in the morphology of the mouthparts. A more complete explanation awaits the results of ecological and physiological experimentation.

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References

Arnal, A. (1955) El aparato digestivo de *Volucella elegans* (Dipt.). *Trabajos del Instituto de Ciencias Naturales 'José de Acosta', Madrid (Ser. Biol.)*, **4**, 91–112.

Baker, H.G. & Baker, I. (1973a) Amino acids in nectar and their evolutionary significance. *Nature*, **241**, 543–545.

Baker, H.G. & Baker, I. (1973b) Some anthecological aspects of the evolution of nectar-producing flowers, particularly amino-acid production in nectar. *Taxonomy and Ecology* (ed. by V. H. Heywood), pp. 243–264. Academic Press, London.

Baker, H.G. & Baker, I. (1975) Studies of nectar constitution and pollinator plant coevolution. *Coevolution of Animals and Plants* (ed. by L. E. Gilbert and P.H. Raven), pp. 100–140. University of Texas Press, Austin.

Baker, H.G. & Baker, I. (1977) Intraspecific constancy of floral nectar amino acid complements. *Botanical Gazette*, **138**, 183–191.

Baker, I. & Baker, H.G. (1976) Analysis of amino acids in flower nectars of hybrids and their parents, with phylogenetic implications. *New Phytologist*, **76**, 87–98.

El-Berry, A.R., Abdel-Gawaad, A.A., Moustafa, M.A. & El-Gayar, F.H. (1974a) Pollinators other than honeybees visiting certain medicinal plants in Egypt. *Zeitschrift für Angewandte Entomologie*, **76**, 113–119.

El-Berry, A.R., Moustafa, M.A., Abdel-Gawaad, A.A. & El-Bialey, S. (1974b) Pollinators other than honeybees visiting certain vegetable plants in Egypt. *Zeitschrift für Angewandte Entomologie*, **77**, 106–110.

Bletchly, J.D. (1954) The mouthparts of the Dance Fly, *Empis livida* L. (Diptera, Empididae). *Proceedings of the Zoological Society of London*, **124**, 317–334.

Brian, A.D. (1957) Differences in the flowers visited by four species of bumblebees and their causes. *Journal of Animal Ecology*, **26**, 71–98.

Brink, D. & deWet, J.M.J. (1980) Interpopulation variation in nectar production in *Aconitum columbianum* (Ranunculaceae). *Oecologia (Berlin)*, **47**, 160–163.

Buckton, G.B. (1895) *The Natural History of Eristalis tenax or the Drone-Fly*. Macmillan & Co., London.

Clapham, A.R., Tutin, T.G. & Warburg, E.F. (1968) *Excursion Flora of the British Isles*, 2nd edn. Cambridge University Press.

Coe, R.L. (1953) Diptera: Family Syrphidae. *Royal Entomological Society Handbooks for the Identification of British Insects*, **10**, 1–98.

Corbet, S.A., Unwin, D.M. & Prŷs-Jones, O.E. (1979a) Humidity, nectar and insect visits to flowers, with special reference to *Crataegus*, *Tilia*, and *Echium*. *Ecological Entomology*, **4**, 9–22.

Corbet, S.A., Willmer, P.G., Beament, J.W.L., Unwin, D.M. & Prŷs-Jones, O.E. (1979b) Post-secretory determinants of sugar concentration in nectar. *Plant, Cell and Environment*, **2**, 293–308.

Curran, C.H. (1925) Contribution to a monograph of the American Syrphidae from North of Mexico. *Kansas University Scientific Bulletin*, **15**, 1–216.

Dethier, V.G. (1976) *The Hungry Fly*. Belknap Press, Harvard.

Dimmock, G. (1881) The anatomy of the mouthparts and of the sucking apparatus of some Diptera. Inaugural Dissertation, Boston.

Dorsman, L. (1920) De gesnavelde zweefvlieg (*Rhingia rostrata* L.). *De Levende Natuur*, **24**, 336–339.

Drabble, E. & Drabble, H. (1917) The syrphid visitors to certain flowers. *New Phytologist*, **16**, 105–109.

Drabble, E. & Drabble, H. (1927) Some flowers and their dipteran visitors. *New Phytologist*, **26**, 115–123.

Elton, G.S. (1966) *The Pattern of Animal Communities*. Methuen & Co., London.

Emmett, B.J. (1971) Insect visitors to pear blossom. *Plant Pathology,* **20,** 36–40.

Faegri, K. & van der Pijl, L. (1979) *The Principles of Pollination Ecology.* Pergamon Press, Oxford.

Gerstfeld, G. (1853) *Uber die Mundtheile der Saugenden Insekten.* Dorpat.

Gilbert, F.S. (1980) Flower visiting by hoverflies (Syrphidae). *Journal of Biological Education,* **14,** 70–74.

Gilbert, L.E. (1972) Pollen feeding and reproductive biology of *Heliconius* butterflies. *Proceedings of the National Academy of Sciences of the United States of America,* **69,** 1403–1407.

van der Goot, V.S. & Grabandt, R.A.J. (1970) Some species of the genera *Melanostoma, Platycheirus,* and *Pyrophaena* (Diptera, Syrphidae) and their relation to flowers. *Entomologische Berichten, Amsterdam,* **30,** 135–143.

Gouin, F. (1946) Morphologie de l'appareil buccal d'un Diptère Syrphide (*Eristalomyia* sp.). *Comptes Rendus des Séances de l'Academie des Sciences,* **223,** 867–869.

Gouin, F. (1949) Recherches sur la morphologie de l'appareil buccal des Diptères. *Mémoires du Museum National d'Histoire Naturelle,* N.S. **28,** 167–269.

Gould, S.J. & Lewontin, R.C. (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptionist programme. *Proceedings of the Royal Society of London,* B, **205,** 581–598.

Graham-Smith, G.S. (1930) Further observations on the anatomy and function of the proboscis of the blowfly *Calliphora erythrocephala* L. *Parasitology,* **22,** 47–113.

Grinfeld, E.K. (1955) [The feeding of hoverflies (Diptera, Syrphidae) and their role in the pollination of plants]. *Entomologicheskoe Obozrenie,* **34,** 164–166.

Hamm, A.H. (1934) Syrphidae (Dipt.) associated with flowers. *Journal of the Society for British Entomology,* **1,** 8–9.

Hansen Bay, C.M. (1978) Control of salivation in the blowfly *Calliphora. Journal of Experimental Biology,* **75,** 189–201.

Heinrich, B. (1976) Resource partitioning among some eusocial insects: bumblebees. *Ecology,* **57,** 874–889.

Heinrich, B. & Pantle, C. (1975) Thermoregulation in small flies (*Syrphus* sp.): basking and shivering. *Journal of Experimental Biology,* **62,** 599–610.

Hocking, B. (1953) The intrinsic range and speed of flight in insects. *Transactions of the Royal Entomological Society of London,* **104,** 233–345.

Holloway, B.A. (1976) Pollen-feeding in hoverflies (Diptera: Syrphidae). *New Zealand Journal of Zoology,* **3,** 339–350.

Holm, S.N. (1966) The utilization and management of bumblebees for red clover and alfalfa seed production. *Annual Review of Entomology,* **11,** 55–182.

Inouye, D.W. (1977) Resource partitioning in bumblebees. *Journal of the New York Entomological Society,* **85,** 253–254.

Inouye, D.W. (1978) Resource partitioning in bumblebees: experimental studies of foraging behaviour. *Ecology,* **59,** 672–678.

Inouye, D.W. (1980) The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumblebees. *Oecologia (Berlin),* **45,** 197–201.

Kevan, P.G. (1970) High arctic insect–flower relations: the interrelationships of arthropods and flowers at Lake Hazen, Ellesmere Island, N.W.T., Canada. Ph.D. thesis, University of Alberta, Canada.

Kingsolver, J.G. & Daniel, T.L. (1979) The mechanics and energetics of nectar feeding in butterflies. *Journal of Theoretical Biology,* **76,** 167–179.

Kloet, G.S. & Hincks, W.D. (1976) *A Checklist of British Insects,* 5. Diptera and Siphonaptera, 2nd edn.

Knutson, L.V., Thompson, F.C. & Vockeroth, J.R. (1975) Family Syrphidae. In: *A Catalog of the Diptera of the Oriental Region* (ed. by M. D. Delfinado and D. E. Hardy), Vol. 2. University Press of Hawaii, Honolulu.

Kugler, H. (1970) *Blütenökologie.* Fischer, Stuttgart.

Künckel d'Herculais, J. (1875) *L'organisation et le Développement des Volucelles, Insectes Diptères de la Famille Syrphides.* G. Masson, Paris.

Lall, S.B. & Davies, D.M. (1971) An intergeneric comparison of cephalic structure in tabanids (Diptera) in relation to feeding habits. *Journal of Medical Entomology,* **8,** 700–706.

Leereveld, H., Meeuse, A.D.J. & Stelleman, P. (1976) Anthecological relations between reputedly anemophilous flowers and syrphid flies. II. *Plantago media. Acta Botanica Neerlandica,* **25,** 205–211.

Lindner, H. (1919) Uber die Mundwerkzeuge einige Dipteran und ihre Beziehungen zur Ernährungsweise. *Zoologischer Anzeiger,* **50,** 19–27.

Linskens, H.F. & Schrauwen, J. (1969) The release of free amino acids from germinating pollen. *Acta Botanica Neerlandica,* **18,** 605–614.

Lundbeck, W. (1916) *Diptera Danica: genera and species of flies hitherto found in Denmark.* Part V. Lonchopteridae, Syrphidae. Copenhagen.

McAlpine, J.F. (1965) Observations on anthophilous Diptera at Lake Hazen, Ellesmere Island. *Canadian Field Naturalist,* **79,** 247–256.

Maier, C.T. & Waldbauer, G.P. (1979) Diurnal activity patterns of flower flies (Diptera, Syrphidae) in an Illinois sand area. *Annals of the Entomological Society of America,* **72,** 237–245.

Maki, T. (1935) Anatomical studies of alimentary canals and their appendages in syrphid flies. *Transactions of the Natural History Society of Formosa,* **25,** 379–391.

Meinhert, Fr. (1881) *Fluernes Munddele. Trophi Dipterorum.* Copenhagen.

Menzbier, M.A. (1880) Uber das Kopfskelett und die Mundwerkzeuge der Zweiflugler. *Bulletin de la Société de Naturalistes de Moscou,* **55,** 8–71.

Müller, H. (1883) *The Fertilisation of Flowers.* Transl. D'Arcy Thompson. Macmillan & Co., London.

Nayar, J.L. (1964) External morphology of head capsule of *Syrphus balteatus* de Geer (Syrphidae, Diptera). *Indian Journal of Entomology,* **26,** 135–151.

Oldroyd, H. (1964) *The Natural History of Flies.* Weidenfeld & Nicholson, London.

Parmenter, L. (1953) The hoverflies (Syrphidae). *Entomologist's Record and Journal of Variation,* **65,** 185–190.

Pekkarinen, A. (1979) Morphometrics, colour and enzyme variation in bumblebees (Hymenoptera, Apidae, *Bombus*) in Fennoscandia and Denmark. *Acta Zoologica Fennica,* **158,** 1–60.

Percival, M.S. (1965) *Floral Biology.* Pergamon Press, Oxford.

Peterson, A. (1916) The head capsule and mouthparts of Diptera. *Illinois Biological Monographs,* **3,** 177–280.

Pino, G. (1962) Estudio de algunos caracteres morfologicos de nueve especies de Syrphidae chilenos de differentes generos (Diptera). *Publicaciones del Centro de Estudios Entomologicos,* **4,** 45–58.

Proctor, M. & Yeo, P.F. (1973) *The Pollination of Flowers.* Collins, London.

Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977) Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology,* **52,** 137–154.

Rackham, O. (1975) *Hayley Wood: its History and Ecology.* Cambridge.

Reiss, M.J. (1981) The allometry of reproduction: why larger species invest relatively less in their offspring. *Journal of Theoretical Biology* (submitted).

Rice, M.J. (1970) Cibarial stretch receptors in the tsetse fly (*Glossina austeni*) and the blowfly (*Calliphora erythrocephala*). *Journal of Insect Physiology,* **16,** 277–289.

Schiemenz, H. (1957) Vergleichende funktionell-anatomische Untersuchungen der Kopfmuskulatur von *Theobaldia* und *Eristalis* (Dipt. Culicid. und Syrphid.). *Deutsche Entomologische Zeitschrift* (N.F.), **4,** 268–331.

Schneider, F. (1948) Beitrag zur Kenntnis der Generationsverhältnisse und Diapause räuberischer Schwebfliegen (Syrphidae, Dipt.). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft,* **21,** 249–285.

Schneider, F. (1958) Künstliche Blumen zum Nachweis von Winterquartiern, Futterpflanzen und Tageswanderungen von *Lasiopticus pyrastri* (L.) und andern Schwebfliegen. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft,* **31,** 1–24.

Speight, M.C.D. (1978) *Melanostoma dubium* (Dipt., Syrphidae) in Britain and a key to the British Isles *Melanostoma* species. *Entomologist's Record and Journal of Variation,* **90,** 226–230.

Speight, M.C.D., Chandler, P.J. & Nash, R. (1975) Irish Syrphidae (Diptera): notes on the species and an account of their known distribution. *Proceedings of the Royal Irish Academy,* B, **75,** 1–80.

Stanley, R.G. & Linskens, H.F. (1974) *Pollen: Biology, Biochemistry, Management.* Springer, New York.

Stelleman, P. (1978) The possible role of insects in the pollination of reputedly anemophilous plants, exemplified by *Plantago lanceolata* and syrphid flies. *Pollination of Flowers by Insects* (ed. by A.J. Richards), *Linnean Society Symposium,* **6,** 41–46.

Stelleman, P. & Meeuse, A.D.J. (1976) Anthecological relations between reputedly anemophilous flowers and syrphid flies. I. The possible role of syrphid flies as pollinators of *Plantago. Tijdschrift voor Entomologie,* **119,** 15–31.

Stürken, K. (1964) Die Bedeutung der Imaginalernährung für das Reproduktionsvermögen der Syrphiden. *Zeitschrift für Angewandte Zoologie,* **25,** 385–417.

Thompson, F.C., Vockeroth, J.R. & Sedman, Y.S. (1976) Family Syrphidae. Chapter 46 of *A Catalogue of the Diptera of the Americas South of the United States.* University of São Paulo, Brazil.

Verrall, G.H. (1901) *British Flies,* Vol. 8; Platypezidae, Pipunculidae and Syrphidae. Reprinted 1969. E. W. Classey, Hampton, England.

Vine, H.C.A. (1895) Predacious and parasitic enemies of aphides, including a study of hyperparasites. Part II continued. *Journal of Microscopy and Natural Science* (3rd Ser.), **5,** 33–43.

Vogel, S. (1954) Blütenbiologische Typen als Elemente der Sippengliederung. *Botanische Studien,* **1,** 1–338. G. Fischer, Jena.

Walters, S.M. (1979) *A Guide to Cambridge University Botanic Garden.* University Botanic Garden, Cambridge.

Wesché, W. (1980) The fly, *Syritta pipiens. Knowledge,* **1900,** 33–35.

Wesché, W. (1902) Undescribed palpi on the proboscis of some dipterous flies, with some remarks on the mouthparts in several families. *Journal of the Royal Microscopical Society,* **1902,** 412–416.

Wesché, W. (1904) The labial and maxillary palpi in Diptera. *Transactions of the Linnean Society,* **9,** 219–230.

Willmer, P.G. (1980) The effects of insect visitors on nectar constituents. *Oecologia (Berlin),* **47,** 270–277.

Zimina, L.V. (1957) [Structure and function of the intestine of *Syrphus* (Diptera, Syrphidae)]. *Zoologicheskii Zhurnal,* **36,** 1039–1043.

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