day); locality; vice county; ten KM grid ref; lat/long for marine records; numbers (approx) of each sex or of unsexed; direction of travel if moving; observers name and contact number. I shall file the records on 8 x 5 record cards so feel free to send me a card of this size with the data written legibly thereon; this will minimise the risk of transcription errors creeping into the data set.

I should particularly like to assess the 1991 immigration mentioned above. In this case I would also welcome negative reports from every county in the British Isles so I can establish how far the immigration reached and in which direction it came from. Did it affect Wales, Scotland or Ireland, and if not how far across Britain did the insects travel?

SPHAEROPHORIA RUEPPELLII: PLANT ASSOCIATIONS

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Sphaerophoria rueppellii, while not exactly a rarity, is a fairly elusive species. It does however have the distinction of being one of the few *Sphaerophoria* species that is easy to identify in both sexes.

Verrall reported that this species had a liking for asparagus plants, but I have no personal experience of an association with asparagus. Alan Stubbs has described *Polygonum persicaria* (Redshank) as a good lure for this species. Indeed my first ever sighting of *S. rueppellii* was on such a plant, though I have examined a great deal of redshank since without finding any more specimens.

On visits to Kew Gardens in September 1989 and September 1990, I came across several specimens of *S. rueppellii* in the area of the gardens set aside for the collections of herbaceous plants. They were on the flowers of *Chenopodium vulvaria* the larva of *S. rueppellii* has been found in aphid galls on this plant - see **Hoverfly Newsletter No. 7 p 9** and of two species of *Amaranthus*, (*A. albus*, and *A. retroflexus*). It is perhaps of interest that *Polygonum, Chenopodium,* and *Amaranthus* belong to families of plants that are considered to be closely related to one another in the accepted evolutionary order.

FEEDING IN ADULT HOVERFLIES

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Hoverfly collectors know well that the best place to find adults is on flowers. There are exceptions, of course, but overwhelmingly the adults feed from flowers of many different types. In the literature there are numerous papers that record the flowers on which adult hoverflies were caught: the series of papers by Parmenter in the 1950s is an obvious example. Surprisingly there are rather few studies of how syrphids choose which flowers to visit, what they actually feed on, and how they interact with other flower visitors. We know from rearing studies that females emerge with undeveloped ovaries, and need pollen in order to mature the eggs. Some species can mature a few eggs without taking pollen (e.g.

Merodon).

In this review I start by looking at the structure of the feeding apparatus, and how it is used and then look at selectivity in the diet. I then outline some of the techniques used in establishing the diets of hoverflies.

Feeding structures: the mouthparts

The structures used to take food have not been well described, with the exception of an amazingly detailed study of *Eristalis* by Schiemenz (1957), and another on several species by Schuhmacher & Hoffmann (1982). Unfortunately these papers are rather inaccessible to many syrphidologists since they are written in german, and very indigestible german at that! In spite of this, we are lucky that they exist, and are so detailed.

The mouthparts that Schiemenz describes are rather similar to those of the blowfly exhaustively described by Graham-Smith in 1930. However, it is easy to be misled into assuming that they are identical, and several writers have been caught out. For example, Percival in her book on floral biology states that the mouthparts of hoverflies have teeth, like blowflies: however, there are no signs of these teeth in syrphids. Instead, as might be expected, the mouthparts of hoverflies show a wonderful range of structures adapted to their feeding habits. We cannot interpret them fully yet, since we have no idea what are the function of some of the structures: for example, there is a set of mysterious projections on the end of the labrum.

In essence the mouthparts consist of two tubes at the end of which is a pair of flattened fleshy lobes (the labella) joined together. The labral sucking tubes are joined end to end, hinged at the joint. The labella have numerous narrow canals on their inner surfaces (the pseudotracheae) that guide food back to the entrance of the labral sucking tube. There are pumps operating in each tube, and coordinated pumping conveys fluid up the labral tube, into the cibarial tube, and thence out of the proboscis and into the gut.

It is easy to imagine what happens when flower nectar is sucked up the proboscis. The fly slides the proboscis down into the corolla of the flower until its labella touch the surface of the nectar. This brings the pseudotracheal canals into play since they usually extend over the edge of the labella. Nectar rushes into them by both capillary and a pumping action of the labella to the entrance of the labral sucking tube, and thence to the crop or the gut. The inner surfaces of the labella are hydrophillic, which also encourages nectar to move into the canals by capillary action.

The action of the mouthparts when feeding on pollen is not nearly so obvious, and many previous accounts are incorrect. What actually happens was worked out in 1982 by Schuhmacher and Hoffmann. They found that on the inner surfaces of the labella are soft inter-canal folds that form food-furrows over the top of the pseudotracheal canals. When the two labella are put together, these furrows form a new set of channels overlying the canals. It is these channels that are used when feeding on pollen.

If you have watched hoverflies taking pollen from the anthers of flowers, you will have seen that the operation involves a twisting motion, rubbing the labella together. What is actually happening is that, together with saliva, this twisting action disperses pollen from the anthers into the channels. The grains can then be sucked up in the saliva in the same way as nectar. These observations help to interpret data from other studies, which show that species specialising mainly on pollen have more pseudotracheal canals than species that take more nectar. This only makes sense if the canals are involved in collecting pollen. The width of the canals may be adapted to pollen grains of particular sizes, but this is not yet established.

What do they feed on?

It seems obvious that the adults feed on nectar and pollen. While this is clearly true, it is not the whole story, since some species are nearly always seen taking pollen from flowers, whereas others are more often seen taking nectar. In addition, particular flowers are visited, whereas others may be ignored. These sorts of patterns only become apparent after many observations on different hoverfly species. Female *Syrphus ribesii*, for example, are almost always feeding on pollen when you see them on the wide range of flowers that they visit: I have seen them taking nectar from only a few flowers, such as Hogweed. I have never seen *Pipiza austriaca* feeding on nectar, but always on pollen from *Ranunculus*. On the other hand, when I have seen male *Eristalis tenax* on flowers, more often than not they have been taking nectar, dipping their mouthparts deep into flower corollas.

There are some oddities in feeding behaviour, even among common species of hoverfly. The obvious examples of this are species of *Xylota*. These flies are rarely at flowers, but instead are frequently seen running erratically about over leaves. Looked at closely, you can see that they have their labella pressed down on the leaf surface, and they are clearly feeding. The contents of their guts reveal large amounts of pollen, and a close look at the leaves shows that they too have a great deal of pollen lying on them. *Xylota* specialize in picking pollen up from leaf surfaces. It is interesting that the old genus *Xylota* has recently been split into several different genera, including *Xylota* s.s. In both the USA and in Europe, species of *Xylota* always feed in this highly distinctive manner from leaves, whereas the related species of *Chalcosyrphus* (until recently placed in the genus *Xylota*) do not, but instead take pollen from flowers in the usual way. This indicates that the leaf feeding method evolved when the genus *Xylota* evolved; recent work shows that *Xylota* is one of the advanced of syrphid genera.

What are we to make of these differences? I interpret them as showing that the diets of hoverfly species are different: some species in general take more nectar than others. Looked at across species, there are other regular patterns too. The inferred dietary differences are related to body size and relative proboscis lengths of the different species. The larger the species, the more nectar it takes: this seems reasonable since larger species have a higher energy demand. Over and above the body size effect, the longer the proboscis, the more nectar is taken.

These patterns seem to make sense: the size and shape of hoverflies should be adapted to their ecology, and food is an important part of the ecology of a species. There is more nectar in flowers with deeper corollas, so it is appropriate to have a longer proboscis if more nectar is taken in the diet. The channels above the labellar canals are used for feeding on pollen, and so it makes sense to have more canals if pollen is the main food.

While my interpretation might seem reasonable, there are other ways of looking at it: John Haslett in particular feels that because he is able to find large amounts of pollen in the guts of species that I categorize from their behaviour as 'mostly nectar-feeders', then my interpretation must be incomplete. Only new data can resolve this basic difference. I suspect that the difference in interpretation is due to the different methods used to investigate hoverfly diets (see below).

In addition to the overall differences between species that I have described, there are sex and individual differences too. While female *Syrphus ribesii* are nearly always seen taking pollen from flowers, males are most often to be seen hovering in swarms, or resting on leaves while they are waiting for mates. When males are seen feeding, they are usually taking aphid honeydew that coats the leaves of trees such as sycamores. Again, this is reasonable. Males have a high energy demand, and thus need the sugars in nectar. However, they only have a very short proboscis suitable for only the most open of flowers. We don't know exactly how much sugar there is on honeydew-encrusted leaves, but it is probably considerable.

Individuals also feed on different foods during various phases of their lives. John Haslett has documented such a pattern in *Rhingia campestris*. In my experience, this species is predominantly a nectar-feeder, since it is most often seen taking nectar from deep flowers such as Ground Ivy. However, when maturing eggs, females need the protein they can only get from pollen. It comes as no surprise, therefore, to find that you can find substantial amounts of pollen in the gut and crop only during those times when eggs are developing in the ovaries.

Choosing a flower to visit

How do hoverflies choose between flowers? An analysis of the pollens in their guts, and behavioural data, show that some species are rather choosy in the face of the range of pollens available to them in the habitat. Other species are not very selective. How do they make this choice?

In the case of nectar feeding, species tend to select flowers on the basis of corolla depth, although they probably manage this choice by selecting on the basis of colour or some odour cue. From census data we can show that species with long mouthparts tend to go for flowers with deep corollas, whereas those with short mouthparts are restricted to more open flowers. Thus the rather long proboscis of *Eristalis* species allows them to make nectar from the deeper yellow or white flowers of plants such as the larger types of Compositae. The amazingly long proboscis of *Rhingia* is useful for getting the deeply hidden nectar from flowers such a Bugle; this species tends to visit blue or purple flowers.

When feeding on pollen, again some species are highly selective, whilst others are generalists. At least part of this selectivity comes again from selecting flowers of a particular colour. For example, *Cheilosia albitarsis* feeds exclusively on buttercup pollen, and adults prefer the particular yellow of this flower. Incidentally, the larvae are also restricted to feeding in the roots of buttercup, and thus the species is completely specialized to this plant. Similarly, *Volucella pellucens* prefers white flowers, explaining in part its pollen selectivity.

Pollen specialization in some species cannot be due to responses to flower colour, since these syrphids take mainly pollen from wind-pollinated flowers. The fact that *Melanostoma* and some *Platycheirus* (e.g. *clypeatus*) species feed mainly on grass, sedge and plantain pollens is well known. Axel Ssymank in Germany has recently looked at the feeding behaviour and gut pollen of various early-season hoverfly species, with some interesting results. In particular he finds that several of these early-season syrphids specialize in taking the pollen of wind-pollinated trees and shrubs. *Melangyna* species are a case in point. Most of the *M. barbata* individuals dissected had empty guts, but others had guts packed with alder pollen; one individual has only hazel pollen. *M. lasiophthalma* had a wide range of pollen types from trees and shrubs, from elder and honeysuckle to alder and anemone. *M. quadrimaculata* had a mixture of pollen types from shrubs and herbs.

Why do hoverflies visit different flowers?

I have described some of the basic differences between the feeding behaviour of various hoverfly species. Why should they differ? 'Why' questions are the hardest to answer, since so many factors might be involved. Thus it might be that hoverflies compete for nectar and pollen, and so natural selection has resulted in different diets in order to minimise the effects of competition. Alternatively, preferences may have evolved randomly. Finally, diets may be optimal for each species, and since species probably differ in their physiology, then optimal diets will also differ.

The simplest explanation is that preferences evolve randomly. It is only when this explanation is untenable that some other explanation must be devised. However, in order to test this we need to know the evolutionary tree of syrphids. Thus, experiments to test whether preferences evolve randomly have yet to be done!

Methods of discovering adult feeding patterns

Basically there are two main methods for studying diet in hoverflies. Neither is wholly satisfactory; rather, each illuminates a different aspect of feeding ecology. This bias in each method means that care is always needed in interpreting the results, as I have already described. The best studies also estimate the availability of flowers in the habitat independently (e.g. by regular counting of flowers of each species that are open on the sampling dates).

The first method uses behavioural observation. Regular recording of what hoverflies are feeding on gradually builds up into a picture of their diet. This can be done in several different ways. One method is to walk along standard census paths for a set period of time (say, two hours), recording what flowers are being visited at the instance you first seen each hoverfly. The best type of data here includes the sex and species of every hoverfly seen, together with the flower species, and whether it was taking nectar or pollen. Obviously this means that each hoverfly must be looked at pretty closely. With practice, most hoverflies can be identified without capture.

Alternatively one could watch individual hoverflies for set periods of time, noting how long they spend feeding on nectar/pollen from each flower visited. Given enough data, either type of data leads to an estimate of the length of time each sex of each species spends feeding on nectar and pollen from each type of flower available in the habitat. This is a good method for species that visit herb-layer flowers, but is not very good for those visiting the flowers of trees or tall shrubs (since they are very difficult or impossible to see). In addition, a major weakness is that, in order to estimate what the average diet is for a hoverfly species, one must assume that the proportion of time spent feeding on one food represents the proportion of that food in the diet. This may not be a good assumption in some cases.

The second method is to study the pollen types in the gut. Pollen is almost indestructible, and many flower species have distinctive pollens that can be identified using a high-power microscope. Counting the pollen grains of each type in the gut will give a quantitative estimate of the relative importance of different pollen types in the diet. Given enough data, this will give an estimate of the diet in terms of different flowers used, and can be used on museum specimens too (although only destructively!). It is a very time consuming method, however, and needs a good deal of equipment and experience to get accurate data. Identifying pollen types can be difficult, too. A major drawback is that nectar feeding is ignored. In addition, the spectrum of pollen types in the guts can be misleading. For example, *Xylota* guts are full of pollen, sometimes only of a few types (e.g. Wild Garlic pollen), but this does not imply any specialization to this flower, as we have seen. Some eristaline species have special body hairs that pick up pollen, and then these grains are cleaned off and eaten, either at rest or in flight. Thus here again pollen in the gut may not imply feeding from the relevant flower.

Conclusion

Hoverflies have varied diets, from specialized to generalized. We know too little about these differences, and need much more information to make valid statements about them. Once we have this information, then discovering the way in which dietary evolution has happened will be fascinating!

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REVIEW

Flower visiting and pollination ecology of hoverflies (Diptera, Syrphidae) in particular for Belgium by N De Buck Studiedocumenten K.B.I.N./Documents de Travails de l'I.R.Sc.N.B. Price 450 Belgian Francs, postage not included. Orders: K.B.I.N., Vautierstraat 29, B-1040 Brussels, Belgium

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The author of this work compiled more than 8,000 records of flower visiting hoverflies, including 3,500 by the author himself. He also carried out research on mouthpart structure and subjected gut contents and faeces of flies to microscopic examination. Almost 5,000 records were obtained from the literature and from other dipterists.

Following the introduction the first part of the work gives a compilation of all these records. This results in an extensive list of flowers visited per hoverfly species and a list of flower visiting hoverflies per plant species. In the second part, these data are shown in a table only covering Belgian species with some additional information for each species.

The introduction gives a general impression of flower visiting behaviour and mentions the main reference works. Fortunately, the Dutch introduction is also presented in English. Unfortunately some information is not translated into English.

The whole work is concluded with a table presenting data on the (Belgian) species (size, distribution class, type of flower visited and flower visiting frequency and a chapter on pollination ecology. The latter is, unfortunately, not translated into English.

The list of references gives most literature on identification of Western European Syrphidae and, of course, many titles on flower visiting behaviour and pollination.

It is generally thought that flower colour is of the utmost importance for the flower visiting behaviour of hoverflies. De Buck gives for every flowering plant included in the list whether it is a white-yellow-green flower or a red-blue flower. Nevertheless he gives us in the introduction a warning (only in the Dutch version!) that the shape of the flower may be of more importance than its colour. In the corresponding English paragraph he elaborates on the possibilities of UV spectral diagrams in which UV-pictures of flowers display an even more striking "HERE I AM" star shape than the colours visible to us.

De Buck presents a valuable review which will be most helpful in further studies. Particularly, because hoverflies seem to be gaining ground as indicator species. This work is important for anyone interested in the relationship between flowers and hoverflies.