LITERATURE ON HOVERFLIES

(1989) Hoverfly newsletter supplement.

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The references detailed below, have been chosen to represent the most important and/or interesting papers on various aspects of hoverfly biology. All can be obtained either directly from a local library, or by request via the British Lending Library (forms are held by most libraries); the format given here is suitable for librarians to find the paper. If great difficulty is experienced in finding a paper, FSG can help in getting a copy.

Several papers are not in English. Translations of most are available from FSG: these have been done by an unpaid translator, and a small charge of £5 per item will be levied to help to pay for her time and effort. The translations remain her copyright.

The most up to date review of the British fauna, with the best available keys to identification, superb colour plates, and a helpful bibliography (including much of the amateur literature, and many local/regional publications) is

Stubbs, A.E. & Falk, S.J. (1983). British Hoverflies: an illustrated identification guide. British Entomological & Natural History Society.

This is the standard work for all students of British hoverflies.

CONTENTS

REVIEWS

Schneider, F. (1969). The bionomics and physiology of aphidophagous Syrphidae. Ann. Rev. Ent. 14: 103-124.

A comprehensive review of many aspects of hoverfly biology, including seasonality and parasitism. Out of date in several areas, but still a very useful entry into the literature, including many obscure papers.

Parmenter, L. (1953). The hoverflies (Syrphidae). Ent. Rec. 65: 122-6, 154-9, 185-90, 234-8.

A review of hoverfly natural history; interesting reading, but out of date on several aspects of hoverfly biology. Good introduction to the amateur literature.

Gilbert, F.S. (1986). Hoverflies. Cambridge Naturalists Handbooks 5, CUP.

A review of hoverfly biology, written to sixth-formers and interested amateurs, this book tries to show areas where publishable knowledge can be gathered effectively by non-professionals interested in hoverfly natural history.

Rotheray, G.E. (1988). Aphid predators. Cambridge Naturalists Handbook 8, Richmond Publishing Co.

A review of the biology of aphid predators, this book has the aim of encouraging project work on predator biology with the view to collecting publishable data. It is the most up-to-date work on predatory hoverfly larvae.

Bastian, O. (1986). [Hoverflies] in German. Neue Brehm-Bucherei 576. A. Ziemsen Verlag, Wittenberg Lutherstadt.

A very comprehensive text of syrphid biology and natural history; includes keys to the central European species.

Torp, E. (1984) [Danish hoverflies] in Danish. Apollo Books, Copenhagen.

This book contains reviews of many aspects of hoverfly biology, and includes photographs and keys to Danish species.

van der Goot, V.S. (1981) [Hoverflies of NW Europe and European Russia, with special references to the Benelux countries] in Dutch. KNNV, Amsterdam.

The only modern key to all the species of this area of Europe. It is a translation of Stackelberg's key to European Russian species, published in 1970.

REPRODUCTION

Gasparini, F. (1939). Notes on the embryological development of Eristalis tenax. Wasmann Collector 3: 38-43.

This is the only paper that describes the developmental stages of hoverfly eggs.

Chandler, A.E. (1968a). Some host-plant factors affecting oviposition by aphidophagous Syrphidae. Ann. appl. Biol. 61: 415-423.

Chandler, A.E. (1968b). The relationship between aphid infestations and oviposition by aphidophagous Syrphidae. Ann. appl. Biol. 61: 425-434.

Chandler, A.E. (1968c). Some factors influencing the occurrence and site of oviposition by aphidophagous Syrphidae. Ann. appl. Biol. 61: 435-446.

Chandler, A.E. (1968d). Height preferences for oviposition by aphidophagous Syrphidae. Entomophaga 13: 187-195.

A very important set of papers, describing the difference between species that lay eggs on plants without aphids, and species that only lay when aphids are present. This difference is associated with a set of biological differences that are still being explored.

Chandler, A.E. (1968a). A preliminary key to the eggs of some of the commoner aphidophagous Syrphidae occurring in Britain. Trans. R. ent. Soc. Lond. 120: 199-218.
A workable key to the beautiful patterns of the outer layers of the egg. The key contains many more species than is suggested by the title.

Dixon, T.J. (1959). Studies on the oviposition behaviour of Syrphidae. Trans. R. ent. Soc. Lond. 111: 57-80.
A study of influences on oviposition in Metasyrphus luniger in the laboratory and Pipizella varipes on subterranean ant-tended aphids on wild parsnip.

Wilkening, K. (1961) [Experiments and observations on the laboratory rearing of Syrphus corollae Fabr.] in German. Z. angew. Zool. 48: 221-240.
Meticulous and very detailed study, which provided the basis for the long-term culturing of this species; hence the great deal of data on the biology of this species.

Sturken, K. (1964) [The significance of adult feeding for the reproductive capacity of syrphids] in German. Z. angew. Zool. 51: 385-417.
A superbly detailed study on the effect and necessity of pollen in the adult diet for egg production in Metasyrphus corollae.

Volk, S. (1964) [Studies on oviposition in Metasyrphus corollae] in German. Z. angew. Ent. 54: 365-386.
The first to dissect the various influences on egg laying, studying the effect of the plant, aphid honeydew, aphid odour, and the aphids themselves as stimulants to oviposition.

LARVAL STRUCTURE AND APPEARANCE

Rotheray, G.E. (1986). Colour, shape and defence in aphidophagous syrphid larvae. Zool. J. Linn. Soc. 88: 201-216.
Describes the patterns of camouflage seen in predatory larvae, which range from simple cryptic patterns to bird-dropping mimics.

Bhatia, M.L. (1939). The biology, morphology and anatomy of aphidophagous Syrphid larvae. Parasitology 31: 78-112.
Very detailed account of anatomical details of the larvae of aphid-feeding species. Inaccurate in some details (see Rotheray & Gilbert, below), but remains the major description of larval anatomy.

Hartley, J.C. (1963). The cephalopharyngeal apparatus of syrphid larvae and its relationship with other Diptera. Proc. zool. Soc. Lond. 141: 261-280.
A very comprehensive account of the feeding structures of the larvae, and their possible evolution.

Hartley, J.C. (1961). A taxonomic account of the larvae of some British Syrphidae. Proc. zool. Soc. Lond. 136: 505-573.
Marvellously thorough account of the larvae of non-predatory hoverflies, with unrivalled illustrations, and including a key to the larvae for tribes, genera and species. Hartley discusses the evolution of the syrphid groups, as well as the external structure in detail.

Roberts, M.L. (1970). The structure of the mouthparts of syrphid larvae in relation to feeding habits. Acta zool. 51: 43-65.
An account of the mouthpart structure of phytophagous, saprophagous and aphidophagous species; should be read in conjunction with Hartley (1963).

Rotheray, G.E. & Gilbert, F.S. (1988). The phylogeny and systematics of European predacious Syrphidae (Diptera) using larval and puparial stages. Syst. Ent. submitted.
This paper considers the external structure of predatory syrphid larvae in some detail, since this has been misinterpreted in the past. It gives a key to and descriptions of the larvae of all available genera. An account is given of the probable way in which the genera have evolved, based on computer methods of phylogenetic reconstruction.

LARVAL FEEDING BEHAVIOUR

Rotheray, G.E. (1983). Feeding behaviour of Syrphus ribesii and Melanostoma scalare on Aphis fabae. Ent. exp. appl. 34: 148-154.
Describes the movements of aphid-feeding larvae, and uses them to test for differences between an advanced (S. ribesii) and a primitive species (M. scalare). Substantial difference were found.

Rotheray, G.E. & Martinat, P. (1984). Searching behaviour in relation to starvation in Syrphus ribesii Ent. exp. appl. 36: 17-21.
Describing how the feeding behaviour of the larva alters as the animal becomes more hungry, this study forms part of a long tradition of studying the effect of starvation in foraging animals.

Dowding, V.M. (1967). The function and ecological significance of the pharyngeal ridges occurring in the larvae of some cyclorrhaphous Diptera. Parasitology 57: 371-388.
A very interesting account of feeding behaviour in saprophagous Diptera including Eristalis.

Hagvar, E.B. (1970). Laboratory experiments on the biology of Syrphus corollae. Norsk ent. Tidsskr. 17: 77-85.

Hagvar, E.B. (1970). Food consumption at various temperature conditions in larvae of Syrphus corollae. Norsk ent. Tidsskr. 17: 87-91.

Hagvar, E.B. (1972). The effect of intra and interspecific larval competition for food (Myzus persicae) on the development at 20°C of Syrphus ribesii and Syrphus corollae. Entomophaga 17: 71-77.
A series of papers containing very interesting and detailed information on various aspects of biology of the two species.

Ruzicka, Z. (1975). The effect of various aphids as larval prey on the development of Metasyrphus corollae. Entomophaga 20: 353-402.

Ruzicka, Z. (1976). Prey selection by larvae of Metasyrphus corollae. Acta ent. bohemoslov. 73: 305-311.

Ruzicka, Z. & Cairo, V.G. (1976). The effect of larval starvation on the development of Metasyrphus corollae. Vestnik cesk. spol. Zool. 40: 206-213.
An excellent series of papers which demonstrate the potential of syrphids for testing ecological ideas. Pupal weight was used as a test of how suitable aphids are as prey; most were equally good, but some were poor food sources and at least one species in toxic. Larvae do not exert strong prey selection.

Brodsky, L.M. & Barlow, C.A. (1986). Escape responses of the pea aphids, Acyrthosiphum pisum : influence of predator type and temperature. Can. J. Zool. 64: 937-9.
The pea aphid has a characteristic 'drop' reaction: it does not seem to use it when confronted with a syrphid predator, but does when the attacker is a coccinellid.

Banks, C. (1962). Effects of the ant, Lasius niger (L.) on insects preying on small populations of Aphis fabae Scop. on bean plants. Ann. appl. Biol. 50: 619-679.
An elegant experimental study of the protective effect of ants on aphids against various predators including syrphids.

Barlow, C.A. (1979). On the biology and reproductive capacity of Syrphus corollae in the laboratory. Ent. exp. appl. 4: 91-100.
Like the previous papers on the species, this provides detailed information on aspects of syrphid biology.

Cornelius, M. & Barlow, C.A. (1980). Effect of aphid consumption by larvae on development and reproductive efficiency of a flower fly, Syrphus corollae. Can. Ent. 112: 989-992.

Leir, V. & Barlow, C.A. (1982). Effects of starvation and age on foraging efficiency and speed of consumption by larvae of a flower fly, Metasyrphus corollae. Can. Ent. 114: 897-900.

Scott, S.M. & Barlow, C.A. (1984). Effect of prey availability during development on the reproductive output of Metasyrphus corollae. Environ. Ent. 13: 669-674.
A set of papers looking at the effect of larval feeding on larval and adult characteristics; especially valuable since it looks at adult reproductive output as a function of larval feeding.

Richardson, C.H. (1915). A contribution to the life-history of the corn-feeding Syrphus fly (Mesogramma polita Say). J. econ. Ent. 8: 338-342.
The life-cycle and feeding habits of this unusual species, the only syrphine with a non-carnivorous larva: the larva eats pollen and sucks out the contents of surface cells of maize.

PREDATION AND PARASITISM

Rotheray, G.E. (1979). The biology and host-searching behaviour of a cynipoid parasite of aphidophagous syrphid larvae. Ecol. Ent. 4: 75-82.

Rotheray, G.E. (1981). Host searching and oviposition behaviour of some parasitoids of aphidophagous Syrphidae. Ecol. Ent. 6: 79-87.

Rotheray, G.E. (1984). Host relations, life cycles and multiparasitism in some parasitoids of aphidophagous Syrphidae. Ecol. Ent. 9: 303-310.
A series of very elegant experiments outlining the superb behaviour of several syrphid parasites. There is much to be learnt about the biology of these species.

Schneider, F. (1950) [The development of the syrphid parasite, Diplazon fissorius in uni-, pauci- and multivoltine hosts, and its behaviour in parasitic activation of diapause larvae by Diplazon pectoratorius] in German. Mitt. schweiz. ent. Ges. 23: 155-162.

Schneider, F. (1951) [Some physiological relationships between syrphid larvae and their parasites] in German. Z. angew. Ent. 33: 151-162.
Extraordinary experiments that have never been repeated, concerned with the delicate hormonal balance that is the battle between host and parasite.

Pickard, R.S. (1975). Relative abundance of syrphid species in a nest of the wasp Ectemnius cavifrons compared with that in the surrounding habitat. Entomophaga 20: 143-151.
The only study that compares the prey spectrum of a specialised syrphid predator with prey availability.

ECONOMIC USE OF PREDATORY LARVAE

Guppy, P.L. (1914). Breeding and colonising the syrphid. Circular Dep. Agric., Trinidad & Tobago 10: 217-226.
Early use of syrphids in biological control. Salpingogaster nigra was bred and circulated to planters of sugar for the biological control of froghopper nymphs.

Chambers, R.L. (1986). Preliminary experiments on the potential of hoverflies for the control of aphids under glass. Entomophaga 31: 197-204.
Control of cucumber aphids was achieved using syrphids as predators.

Chambers, R.L. et al (1986). Control of cereal aphids in winter wheat by natural enemies: aphid specific predators, parasitoids and pathogenic fungi. Ann. appl. Biol. 108: 219-231.

Chambers, R.L. & Adams, T.H.L. (1986). Quantification of the impact of hoverflies on cereal aphids in winter wheat: an analysis of field populations. J. app. Ecol. 23: 895-904.
A study demonstrating the potential of syrphids in controlling cereal aphids.

Way, M.J. et al (1969). Experiments on integration of chemical and biological control of aphids on brussels sprouts. Ann. appl. Biol. 63: 459-475.
Control of aphids on brussels by natural enemies such as syrphids was ineffective, requiring chemicals to achieve complete control.

Hassan, S.A. et al (1983). Results of the second joint pesticide testing programme by the IOBC/WPRS-working group 'Pesticides and beneficial arthropods'. Z. angew. Ent. 95: 151-8.
The dangers of pesticide use are obvious from this report, which collates work done on the lethal action of pesticides on beneficial insects including syrphids.

ADULT ANATOMY

Nayar, J.L. (1964a) (nervous system) J. anim. Morph. Physiol. 11: 257-266.
(1964b) (respiratory system) Ibid 12: 17-31
(1965a) (reproductive system) Indian J. Ent. 27: 31-45
(1965b) (musculature) Agra Univ. J. Res. 14: 29-45
(1965c) (digestive system) Ibid 14: 111-125
A series of papers on the anatomy of Episyrphus balteatus, these constitute the only really detailed study of the adult anatomy of syrphids.

ADULT FEEDING BEHAVIOUR

Haslett, J.R. (1983). A photographic account of pollen digestion by adult hoverflies. Physiol. Ent. 8: 167-171.
Shows by photographs that material is extracted from pollen grains without breaking the tough coat, leaving intact grains to be excreted.

Kugler, H. (1970) [The flower visits of the Drone-Fly, Eristalis tenax] in German. Z. vergl. Physiol. 32: 328-347.
Almost a classic study of flower-visiting behaviour.

Gilbert, F.S. (1981). The foraging ecology of hoverflies: morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. Ecol. Ent. 6: 245-262.
Provides an account of the mouthparts of syrphids and how they might be used in feeding, together with data on the diets of various species.

Schneider, F. (1958) [Artificial flowers in the determination of overwintering, food plants, and the daily movements of Lasiopticus pyrastri and other hoverflies] in German. Mitt. schweiz. ent. Ges. 31: 1-24.
Using pollen analysis of gut contents, he showed that Scaeva pyrastri made very long foraging flights in the search for food, and that they overwintered as adults.

Stelleman, P. (1978). The possible role of insect visits in pollination of reputedly anemophilous plants, exemplified by Plantago lanceolata and syrphid flies. In A J Richards (ed) 'The pollination of flowers by insects'. Linnean Soc. Symposium 6.
A very careful study of the role of Melanostoma and Platycheirus species in the pollination of plantains, with some lovely experiments on pollent transfer.

Kay, Q.O.N. (1976). Preferential pollination of yellow-flowered morphs of Rapahanus raphanistrum by Pieris and Eristalis. Nature 261: 230-232.
Eristalis species prefer to visit yellow flowers, and thereby affect the pollination of different colour varieties of oil-seed rape.

Jones, A.W. (1954). Notes on the Dronefiles of Wimbledon Common. London Naturalist 33: 83-88.

Jones, A.W. (1955). The Dronefly visitors to flowers of the city bombed sites. London Naturalist 34: 154-7.
Two papers which provide quantitative data on visiting patterns by these species.

Morse, D. (1981). Interactions among syrphid flies and and bumblebees on flowers. Ecology 62: 81-8
Toxomerus and Melanostoma are brutally treated by the foraging behaviour of bumblebees and lose out in competition.

Parmenter, L. (1956). Flies and their selection of the flowers they visit. Ent. Rec. 68: 242-3.
An interesting compilation of data and ideas on the visiting patterns of syrphids.

Schuhmacher, H. & Hoffmann, H. (1982) [Functional analysis of the mouthparts of hoverflies when feeding] in German. Entomologia generalis 7: 327-342.
A beautiful study, clearly describing for the first time how pollen is taken from anthers, separated into individual grains, and sucked into the crop in saliva. The way in which mouthpart structure is adapated to this is described and figured.

Holloway, B.A. (1976). Pollen feeding in hoverflies. New Zealand J. Zool. 3: 339-350.
A study of Eristalis tenax and Melanostoma; describes how Eristalis combs pollen from its body hairs and eats it while in flight.

COLOUR AND MIMCRY

Dusek, J. & Laska, P. (1974). Influence of temperature during pupal development on the colour of syrphid adults. Folia prirod. Fak. Univ. Purkyne 15: 77-81.
Outlines the darker colours resulting from low temperatures during rearing.

Heal, J. (1979). Colour patterns of Syrphidae. I. Genetic variation in the drone fly Eristalis tenax. Heredity 42: 223-236.

Heal, J. (1979). Colour patterns of Syrphidae. II. Eristalis intricarius. Heredity 43: 229-238.

Heal, J. (1981). Colour patterns of Syrphidae. III. Sexual dimorphism in Eristalis arbustorum. Ecol. Ent. 6: 119-127.

Heal, J. (1982). Colour patterns of Syrphidae. IV. Mimicry and variation in natural populations of Eristalis tenax. Heredity 49: 95-110.
A careful and detailed study exploring the genetic control of colour patterns in Eristalis species, the effects of colour on behaviour, and temperature and age on colour.

Conn, D.L.T. (1972). The genetics of the mimetic colour polymorphism in the large narcissus bulb fly, Merodon equestris. Phil. Trans. Roy. Soc. B 264: 353-402.
A large and technical study on genetic control of the polymorphism in colour patterns of Merodon.

Evans, D.L. & Waldbauer, G.P. (1982). Behaviour of adult and naive birds when presented with a bumblebee and its mimic. Z. Tierpsychol. 59: 247-259.
One of the few experimental studies of mimicry in syrphids, finding a substantial mimetic effect in a non-British species of Mallota.

Osten Sacken, Baron (1894). On the Bugonia, or the Oxen-born bees of the ancients. Heidelberg.

Atkins, E.L. (1948). Mimicry between the drone fly Eristalis tenax, and the honeybee, Apis mellifera: its significance in ancient mythology and present-day thought. Ann. ent. Soc. Amer. 41: 387-392.
Describes the interesting history of the confusion between the honeybee and the dronefly.

Waldbauer, G.P. & Sheldon, J.K. (1971). Phenological relationships of some aculeate Hymenoptera, their Dipteran mimics and insectivorous birds. Evolution 25: 371-382.
The idea put forward here is that hoverflies have evolved their seasonal patterns of emergence so as to avoid the period when naive fledgling birds are present. It may explain the 'hole' in the seasonality of hoverflies at the beginning of July.

COMMUNITIES AND INTERACTIONS

Seifert, R.P. & Seifert, F.H. (1979). A Heliconia insect community in a Venezuelan cloud forest. Ecology 60: 462-7.
A fascinating account of community interactions in the water-filled bracts of Heliconia. The community is dominated by two syrphids (Quichuana, a xylotine, and Copestylum, related to Volucella) and two beetles.

Disney, R.H.L. et al (1982). Collecting methods and the inadequacy of attempted faunal surveys, with reference to Diptera. Field Studies 5: 607-621.
An excellent study that tries to establish sound methods for determining the species richness of a site, and therefore a quantitative assessment of how 'good' the site is.

Robertson, I. (1953). The hypopus of Hericia hericia. Proc. zool. Soc. Lond. 123: 267-271.
A very interesting report on dispersal by a mite from sap flows by hitch-hiking on ovipositing female Brachyopa, know also for treehole mites and Mallota.

Owen, J. (1981). Trophic variety and abundance of hoverflies in an English suburban garden. Holarctic Ecology 4: 221-8.
An interim report on Owen's mammoth recording programme, with fascinating data on long-term patterns of abundance in syrphids.

POLLINATION

Proctor, M. & Yeo, P.F. (1973). The pollination of flowers. Collins New Naturalist.
The classic review, superbly detailed and thorough.

Stelleman, P. (1978). (see above).

Atwood, J.T. (1985). Pollination in Paphiopedilum rothschildianum: brood-site deception. National Geogr. Res. 1: 247-254.
Beautiful story of adaptation in an orchid to pollination by a syrphid, Dideopsis: female flies are attracted to the flowers because the flowers mimic an aphid colony where she normally lays her eggs.

MATING BEHAVIOUR

Collett, T.S. & Land, M.F. (1975). Visual spatial memory in a hoverfly. J. comp. Physiol. 100: 59-84.

Collett, T.S. & Land, M.F. (1975). Visual control of flight behaviour in the hoverfly Syritta pipiens. J. comp. Physiol. 99: 1-66.

Collett, T.S. & Land, M.F. (1978). How Hoverflies compute interception courses. J. comp. Physiol. 125: 191-204.
Fascinating work on how hoverflies use their eyes to best effect in searching for and capturing mates.

Gilbert, F.S. (1984). Thermoregulation and the structure of swarms in Syrphus ribesii (Syrphidae). Oikos 42: 249-255.
This species regulates its thoracic temperature, and therefore is able to swarm early in the morning under trees; large males are at a distinct advantage because of their thermoregulation abilities.

Heinrich, B. & Pantle, C. (1975). Thermoregulation in small flies (Syrphus sp.): basking and shivering. J. exp. Biol. 62: 599-610.
Also detailing the ability of these syrphids to thermoregulate, quite remarkable in so small an insect.

Maier, C.T. & Waldbauer, G.P. (1979). Dual mate-seeking strategies in male syrphid flies. Ann. ent. Soc. Amer. 72: 54-61.
Males switch at midday from searching for females near flowers to waiting by tree-holes where the females come in for oviposition.

Fitzpatrick, S.M. & Wellington, W.G. (1983). Contrasts in the territorial behaviour of three species of hoverflies. Can. Ent. 115: 559-566.

Fitzpatrick, S.M. & Wellington, W.G. (1983). Insect territoriality. Can. J. Zool. 61: 471-486.
Fascinating account of territorial behaviour in Eristalis, Merodon and Eumerus; males fight, occasionally killing one another. Territoriality has a dramatic effect on flowers in the territory.

DAILY ACTIVITY PATTERNS

Campan, M. (1973) [Preliminary observations of the influence of meteorological factors on the rhythm of activity of female Eristalis tenax at the oviposition site] in French. Revue Comport. anim. 3: 69-76.

Kato, M. (1943). Ecological notes on the activities of some insects coming to the flowers of 'Yatude' (Fatsia japonica) with special reference to the ecological importance of the solar radiant energy. Sci. Rep. Tohoku Univ. IV (Biol.) 17: 255-262.

Nielsen, T.R. (1966). Species of the genus Helophilus (Dipt., Syrphidae) found on Jaeren, Rogaland. Norsk. ent. Tidsskr. 13: 427-439.
Interesting account of the behaviour of these flies, including a short description of territoriality.

Gilbert, F.S. (1985). Diurnal activity patterns of hoverflies (Diptera, Syrphidae). Ecol. Ent. 10: 385-92.
Documents the daily activity patterns of common British species, and compares them: Melanostoma is shade tolerant and Metasyrphus corollae is particularly sun-loving. Daily activity is dependent upon the thermal balance of the body.

Wellington, W.G. (1976). Applying behavioural studies in entomological problems. pp. 87-97 in Anderson, DF & Kaya, HK (eds) 'Perspectives in forest entomology'. Academic Press.
A unique study that includes the influence of the plane of polarisation on the activity of Eristalis.

Maier, C.T. & Waldbauer, G.P. (1979). Diurnal activity patterns of flower flies in an Illinois sand area. Ann. ent. Soc. Amer. 72: 237-245.
The influence of temperature causes changes in diurnal activity; feeding (am) and then in the woods (pm).

MIGRATION

Aubert, J. et al (1976) [12 years of systematic captures of syrphids (Diptera) at the Bretolet Pass in the Valais Alps] in French. Mitt. schweiz. ent. Ges. 49: 115-142.
The numbers of syrphids passing through the alpine passes in autumn is staggering, running into hundreds of thousands at the one pass where a type of Malaise trap catches them.

Svensson, B.G. & Janzon, L.A. (1984). Why does the hoverfly Metasyrphus corollae migrate? Ecol. Ent. 9: 329-335.
An ecological study of the migration from SE Sweden in the autumn. Females are reproductively immature; the authors suggest that patterns in aphid population density trigger the migrations.

SEASONALITY AND POPULATION DYNAMICS

Pollard, E. (1971). Hedges. VI. Habitat diversity and crop pests: a study of Brevicoryne brassicae and its syrphid predators. J. appl. Ecol. 8: 751-780.
A very comprehensive and detailed study of syrphids in the crop, including a great deal of information on seasonality.

Schneider, F. (1948) [A contribution on the phenological strategies and diapause in predatory hoverflies] in German. Mitt. schweiz. ent. Ges. 21: 249-285.
The classic work on seasonality in various species of hoverfly, including experimental work on diapause and overwintering.

Kula, E. (1980) [Hoverflies overwintering in the spruce forest floor of Moravia] in Czech. Casopis Slez. Muzea, Vedy Prirod A 29: 269-281.

Kula, E. (1982). The syrphid flies of spruce forest. Folia Fac. Sci. Nat. Univ. Purkyn. Brun. Biol. 23: 61-4.
The tables of data show an incredible variety of species caught using emergence traps, and include several species that have invaded Britain with the advent of conifer plantations.

Smith, K.G.V. (1974). Changes in the British Dipterous fauna. pp. 371-391 in Hawksworth, DL (ed) 'The changing flora and fauna of Britain'. Academic Press, London.
Interesting for its account of the abundance of wasps over many years, and the corresponding changes in the abundance of Volucella.

REARING

Frazer, B.D. (1972). A simple and efficient method of rearing aphidophagous hoverflies. J. ent. Soc. Br. Columbia 69: 23-24.
Details a straightforward (and time-consuming) method.

Maier, C.T. (1978). The immature stages and biology of Mallota posticata Fabr. Proc. ent. Soc. Wash. 80: 424-440.
A very careful account of the biology of this species, which includes an artificial diet that could be adapted for other saprophagous species.

Adashkevich, B.P. (1983) [Biological control of Brassicaceae vegetable pests] in Russian. FAN, Tashkent, 200 pp.
A very detailed description of the rearing methods used in Russia for aphidophagous species.

Bombosch, S. (1957) [Studies on laboratory rearing of aphid-feeding hoverflies] in German. Wanderversamml. deutsch. Ent. 8: 160-2.
The initial breakthrough in rearing syrphids was made in Germany, leading to the successful long-term rearing of Metasyrphus, and now Episyrphus.

Tokmakoglu, O. (1965) [Studies on laboratory rearing of Syrphus luniger] in German. Anz. Schadlingsk. 38: 23-5.
Methods of rearing species other than M. corollae could follow these techniques.

Heal, J. (1979) (see above).

Conn, D.L.T. (1971). Rearing the narcissus bulb fly in captivity. Bull. Amat. ent. Soc. 35: 20-21.

SAMPLING METHODS

Disney, R.H.L. et al (1982). (Water traps: see above).

Banks, C.J. (1959). Experiments with suction traps to assess the abundance of Syrphidae, with special reference to aphidophagous species. Ent. exp. appl. 2: 110-124.

Kula, E. (1980). (Photoeclectors: see above).

INTERESTING ODDITIES

Riek, E.F. (1954). The Australian syrphid flies of the subfamily Cerioidinae: systematics and wing folding. Australian J. Zool. 2: 100-130.
The extraordinary wing-folding mimicry of these Australian species is described.

Thompson, F.C.T. (1972). A new Platycheirus from New Zealand: first records of a melanostomine syrphid fly associated with ants. N.Z.J. Sci. 15: 77-84.
A Platycheirus larva looking more like a wierd Microdon!

Röder, G. (1980) [A new species of Chelosia from Baltic amber, with SEM studies of recent species] in German. Stuttgarter Beitr. Naturk. 64 B: 1-18.
Pictures of a very modern-looking Chelosia preserved in amber.

Wheeler, W.M. (1924). Two extraordinary larval myrmecophiles from Panama. Proc. Nat. Acad. Sci. Wash. 10: 237-244.
Surely the only genus to be described from only larval material; the adult has never been found, and the larvae are truly incredible!

Aoki, S. (1978). Two pemphigids with first-instar larvae attacking predatory intruders (Homoptera, Aphidoidea). New Entomologist, Ueda 27(3): 67-72.

Ohara, K. (1985). Observations on the prey-predator relationship between Pseudoregma bambucicola (Homoptera, Pemphigidae) and Metasyrphus confrater (Diptera, Syrphidae) with special reference to the behaviour of the aphid soldiers. Esakia 23: 107-110.
There first-instar 'soldiers' and the very exciting discovery of real aphid soldiers in Pseudoregma show that predatory syrphids do not always have it their own way.

Hartley, J.C. (1958). The root-piercing spiracles of the larva of Chrysogaster hirtella Loew (Diptera, Syrphidae). Proc. R. ent. Soc. Lond. (A) 33: 81-87.
Describes the extraordinary way in which this larva obtains air, by piercing the root air-spaces of the aquatic plant Glyceria.

CLASSIFICATION AND EVOLUTION

Syrphidae

Hull, F.M. (1949). The morphology and inter-relationship of the genera of syrphid flies, recent and fossil. Trans. zool. Soc. Lond. 26: 257-408.
Contains wonderful drawings of examples of many of the world's genera, including some real oddities. The classification and discussion of syrphid evolution is not very useful since it is badly out of date.

Goffe, E.R. (1952). An outline of a revised classification of the Syrphidae (Diptera) on Phylogenetical lines. Trans. Soc. Brit. Ent. 11: 97-124.
Of historical interest only, as the sole British attempt at a classification and phylogeny of the family. The result is not useful at all, except in the division of the family into two subfamilies.

Syrphinae

Dusek, J. & Laska, P. (1967) [A study of the structure of a natural classifiction of middle-European species of the subfamily Syrphinae (Diptera)] in German. Acta sci. nat. Brno 1: 349-390.
Restricted to European genera, but a classic study, the conclusions of which have withstood the test of time.

Vockeroth, J.R. (1969). A revision of the genera of the Syrphini (Diptera, Syrphidae). Mem. ent. Soc. Canada 62: 1-176.
A detailed world-wide survey of the genera of the Syrphini, with keys and distribution maps as well as generic diagnoses of adult morphology. Done independently of Dusek & Laska, but comes to almost identical conclusions about the way to split up the old genus Syrphus sens. lat.

Rotheray, G.E. & Gilbert, F.S. (1988) (see above).

Eristalinae

Thompson, F.C. (1972). A contribution to the generic revision of the Neotropical Milesiinae (Diptera, Syrphidae). Archiv. Zool. Sao Paulo 23: 73-213.
Although dealing with the Neotropical fauna, Thompson's study was based on the world fauna, and much of his discussion is general and relevant to European species.

Hippa, H. (1978). Classification of Xylotini (Diptera, Syrphidae). Acta zool. Fenn. 156: 1-153.
Based on the world fauna, this is a meticulous work.

GENERA

Microdon

Syms, E. (1935). Notes on the biology of Microdon eggeri. Trans. Soc. Br. ent. 2: 163-5.
Describes the biology and life history from several years observation of larvae and puparia from a nest of Lasius niger.

Duffield, R.M. (1981). Biology of Microdon fuscipennis, with interpretations of the reproductive strategies of Microdon species found north of Mexico. Proc. ent. Soc. Wash. 83: 716-724.
Detailed observations of M. fuscipennis, together with a review of the biology of the many North American species.

Garnett, W.B. et al (1985). Cocoon mimicry and predation by myrmecophilous Diptera. Florida Ent. 68: 615-621.
From observations of ant nests in glass-sided boxes, the larvae of three species of Microdon were seen to feed on ant cocoons. They also mimic ant cocoons and are transported by the ants along

Akre, R.D., Sehlke, G. & Zack, R.S. (1985). Chemical mimicry by Microdon larvae (Diptera, Syrphidae). Proc. Wash. State ent. Soc. 47: 754-5.
It was inevitable that, as in other myrmecophilous insects, Microdon should use chemicals to aid in its parasitization of ant's nests. The mimicry of cocoons is aided by chemicals, stimulating ants to transport larvae as if they were their own cocoons.

Merodon & Eumerus

Doucette, F.G. et al (1942). Biology of the Narcissus Bulb Fly in the Pacific North West. Tech. Bull. USDA 809: 1-67.
Superbly detailed review of experiments on the biology of Merodon, which was accidently introduced into America and caused a great deal of damage to the bulb industry.

Hodson, W.E.H. (1932). The large Narcissus Fly, Merodon equestris Bull. ent. Res. 23: 429-449.
British work on the biology of this species, with many interesting details.

Broadbent, B. (1925). Notes on the life history of the lesser bulb-fly, Eumerus strigatus Fallen. J. econ. Ent. 18: 141-3.

Eristalis

Kendall, D.A. & Stradling, D.J. (1972). Some observations on the overwintering of the drone-fly, Eristalis tenax. Entomol. 105: 229-230.
Short but very interesting account of some experiments on overwintering Eristalis.

Chelosia

Rotheray, G.E. (1987). Larval morphology and feeding patterns of four Chelosia species associated with Cirsium palustre in Scotland. J. nat. Hist.**
The first really detailed ecological and behavioural study of species of this genus, with some startling results on larval feeding behaviour.

Smith, K.G.V. (1979). The larva and puparium of Chelosia bergenstammi, with a summary of the known biology of the genus in Europe. Ent. Rec. J. Var. 91: 190-194.
The paper includes a table summarising information about the feeding habits of European species.

Burke, H.E. (1905). Black check in western hemlock. USDA Bureau of Entomology Circular 61.
Extraordinary life-history of several Chelosia species living just beneath the bark of different conifer species; we have at least one European species in the same situation, C. morio, about which very little is known.

Volucella

Smith, K.G.V. (1955). Notes on the egg and first instar larva of Volucella bombylans. Ent. mon. Mag. 91: 52-4.

Nixon, G.E.J. (1934). Two notes on the behaviour of Volucella pellucens in its association with the wasps Vespa vulgaris L. and Vespa germanica Fab. Ent. mon. Mag. 70: 17-18.
Observations done under glass, with some very interesting results. This work needs to be extended.

Rhingia

Coe, R.L. (1942). Rhingia campestris Meigen: an account of its life-history and descriptions of the early stages. Ent. mon. Mag. 87: 121-130.
Superbly detailed work.

Mallota

Maier, C.T. (1978) (see above).

Pocota

Shillito, J.F. (1947). Pocota personata (Harris) (Dipt., Syrphidae) from Epping Forest. Ent. mon. Mag. 83: 180-181.
This rare species was bred in large numbers from one tree, allowing unique data to be collected.

Temnostoma

Stammer, H.-J. (1933) [The metamorphosis of the syrphid Temnostoma vespiforme (L.) and the characteristic adaptation of the larva of this creature for boring into wood]. Z. Morph. Okol. Tiere 26: 437-443.
The modifications to external structure associated with wood boring are quite extaordinary, including a protective plate against parasitoids.

Pipizini

Kurir, A. (1963) [On the biology of two aphidophagous syrphids (Diptera, Syrphidae), Heringia heringi Zett. and Pipiza festiva Meigen in the galls of the late leaf-petiole-gall poplar aphid (Pemphigus spirothecae Passerini) on the black poplar] in German. Z. angew. Ent. 52: 61-83.

Dusek, J. & Kristek, J. (1967) [A study of the hoverfly larvae (Diptera, Syrphidae) in the galls of the poplar aphid (Homoptera, Pemphigidae)] in German. Z. angew. Ent. 60: 124-136.
Two very detailed and painstaking studies on two of the gall-specialist pipizines, with some fascinating adaptations for preying on gall aphids.

Sedlag, U. (1966) [Triglyphus primus, a much overlooked hoverfly] in German. Ent. Ber., Berlin 1966: 88-90.
[redacted] Contains virtually the only biological information on this rare syrphid.

Xanthandrus

Lyon, J.P. (1968) [Contribution to the biology of Xanthandrus comtus Harris] in French. Ann. Epiphyties 19: 683-693.
Thorough account of the biology of this species, whose larva is a specialist feeder on some lepidopteran larvae.

Paragus

Kaufmann, T. (1973). Biology of Paragus borbonicus (Diptera, Syrphidae) as a predator of Toxoptera aurantii (Homoptera, Aphididae) attacking cocoa in Ghana. Amer. Midl. Nat. 90: 252-6.
Material on the biology of Paragus is very scattered and obscure, and European species have not been well studied. This is a very good study of this African species.