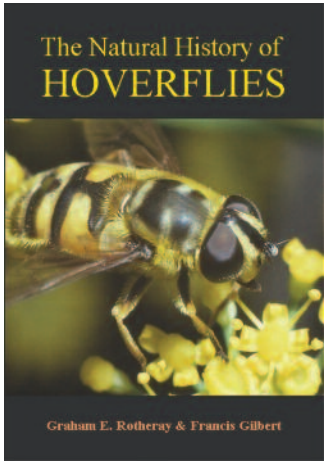


# *The Natural History of Hoverflies*

Graham E. Rotheray & Francis Gilbert. 2011.

Forrest Text, Tresaith, Wales, UK, xiii + 333 pp (with 34 colour figures, two half-tones and 22 line figures, all in the text).

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*Hoverflies are diverse and beautiful and their habits and behaviour provoke both wonder and curiosity*
Rotheray & Gilbert (2011: xi)

Hoverflies are the butterflies of the two-winged horde. With their bright colours and spectacular behaviour they offer a relatively accessible entrée to the fascinating but challenging world of the Diptera. However, at about 150,000 words, this book offers far more than a little dipterological titillation: it is a profound but also very personal introduction to the natural history of Syrphidae, based on the accumulated knowledge and experience of two leading hoverfly specialists, Graham Rotheray and Francis Gilbert. Their knowledge, they generously admit (p. xii), has also been primed and enhanced by their contact with numerous other specialists, including Chris Thompson, Martin Speight, Alan Stubbs, Jennifer Owen, Malcolm Edmunds, and the remarkable Dick Vockeroth, to mention but a few.

Following the fourteen page introduction, which discusses basics such as what hoverflies are and their four most characteristic attributes (hovering, visiting flowers, mimicry, larval biology), the rest of the book is divided into eleven chapters: adult form and function, early stages, evolution and classification, British hoverflies, colour and mimicry, relationships with flowers, syrphids as predators, syrphids as saprophages and phytophages, life-cycles and populations, habitats and communities, and finally hoverflies in ecosystem services and conservation. The book is completed with references, and species and subject indexes.

Adult form and function sounds as if it could be tedious, but it is presented in a most engaging style, including some very interesting observations on torpor and behavioural thermoregulation. The discussion of flight, so characteristic of 'hoverflies', is excellent (including the observation that the pipunculids, sister-group of the Syrphidae, may be even better aeronauts). The authors introduce an interesting biomechanical argument for the evolutionary trend to wing-vein reduction seen in the Diptera and actively flying insects generally: "Weight for weight, a single strengthened vein creates a more effective solution than two veins side by side". Given that they also acknowledge that the 'corrugation' of alternate long veins is another important contributor to wing strength, there has to be a limit to

*Spilomyia digitata*, a 'pefect' wasp mimic (photograph by Graham E. Rotheray).

vein reduction, but they do not discuss this trade off. They also point to the addition of the *vena spuria* (which has apparently been suggested to be formed at the boundary between the anterior and posterior wing compartments), and is a striking autapomorphy for the entire family.

Here and in many places in the book, there is a lack of referencing. While this is very understandable in a work of this kind, it is also frustrating, as it becomes difficult to distinguish the authors' own ideas (with which I suspect this book is replete) from existing, 'received wisdom'.

It has often been observed that entomologists are preoccupied with their genitalia. Well, you know what I mean! Apparently syrphydologists are no exception – the final six pages of Chapter 2 offer an excellent account of the almost baffling complexities of rotation, reduction, fusion and loss affecting the sclerites responsible for the endless variations observable in the syrphid male hypopygium. In this context, it is also notable that, in a way even more extreme than in butterflies, duration of copulation ($T_f$ in John Burns terminology) in the hoverflies varies enormously. As Burns also suggested for butterflies, this may relate to relative vulnerability – according to Rotheray & Gilbert, $T_f$ may last several hours in species of *Blera*, *Xylota* and *Eupeodes*, but only a few seconds in hoverflies that adopt the high-risk strategy of mating in flight (those not familiar with this aerobatic feat might like the remarkable image available at: http://en.wikipedia.org/wiki/File:Hoverflies_mating_midair.jpg).

The eternal shame of entomologists is the poverty of our knowledge of early stages. In Chapter 3, the authors estimate that life-histories remain unknown for more than 90% of the world fauna of *ca* 6000 hoverfly species. For Europe as a whole just over one-fifth are known, and in the British Isles just over half its fauna of some 260 species. In trying to address why this should be so, the authors point towards a view that adults are not only easier to find but also that, for the purposes of classification at least, "early stages are not required" (p. 45). They then rapidly disabuse us of any such notion: "The main hoverfly groups are in fact, more distinctively characterised by the structure and biology of their early stages than by adult features" (page 46).

Knowledge of early stages is not only of use with respect to more recondite matters of phylogenetics and evolution, but even to the seemingly more mundane matter of biological recording. The authors give the very nice example of *Callicera rufa*, so rarely encountered in the adult stage that it was given endangered status in the 1987 *UK Insect Red Data Book*. However, based on Ralph Coe's discovery of the larvae of this species in pine-tree rot-holes, *C. rufa* has since been found in numerous localities in northern Scotland, and taken off the endangered list – making the important point that the promotion of relatively common species to 'rare' status due to low encounter rate with the adults potentially diverts limited conservation resources away from more deserving causes. Chapter 4 includes numerous examples of the many fascinating peculiarities of syrphid life histories now known – but with less than 10% of species known worldwide, one can hardly guess at what remarkable early stage biology remains to be discovered.

Chapter 4 starts with an excellent introduction to the issue of what is involved, and what is possible in trying to understand the origin, evolution and diversification of any group of organisms – the interplay of history and ecology. According to previously published accounts by the authors, the (Pipunculidae + Syrphidae) form the sister-group of the higher cyclorrhaphous Diptera. This insight not only allows comparison with the other 'grade' families of the lower Cyclorrhapha (Lonchopteridae, Platypezidae, Phoridae), but also allows interesting comparisons to be drawn between the two focal groups – the pipunculids, which are parasitoids that hunt visually for their hosts (mostly leaf-hoppers and allies, but also adult craneflies), and the syrphids, which are never parasitic. The outstanding vision and flight control seen in both groups potentially represent different potentials inherent in the ancestral

"Microdontines . . . distinguished by their larval characteristics . . . develop in ant nests" (remarkable round larvae of *Microdon eggeri* in ant nest under bark of fallen pine tree: photograph by Richard Lyszkowski).

A male *Esoeristalis nemorum* displaying amazing powers of flight by hovering just above a feeding female (photograph by Ellen Rotheray).

potentials inherent in the ancestral enhancement of one or both of these systems – in the case of the syrphids, perhaps as an aid to defence against visually hunting predators. This leads to an interesting discussion of the relative 'success' of the two groups. The rest of the chapter is devoted to hoverfly phylogenetics and classification, feature evolution, and of origins. I was fascinated to learn that as many as 100 hoverfly fossils are known – testament, no doubt, to the heuristic value of the *vena spuria!*

Chapter 5, on the hoverflies of Britain and the rest of Europe, will no doubt be of particular interest to many readers of *Antenna*. But what is the exact extent of the British hoverfly fauna? The authors state that "since 1983 more species have been added to the British [list] than at any time since 1900." Although some of these appear to be recent immigrants, most are long-term residents that have simply been overlooked until now. These themes are explored in sections on resident hoverflies, summer visitors, strays or vagrants, and introductions. With respect to the last of these, the authors (p. 124) discuss the possibility that the spectacular Golden Hoverfly (*Callicera spinolae*), known in Britain only from the East Anglian region and a species of conservation concern, was quite possibly "introduced into Suffolk after the First World War" in timber imported from the continent – although they do not rule out autonomous migration. Alan Stubbs and Stephen Falk's milestone work on *British Hoverflies* (1983), together with the National Hoverfly Recording Scheme (1976) that Alan did so much to create, have been key stimuli for the flow of new discoveries about the British fauna over the past three decades. The need to place our knowledge of British hoverflies in the context of the west Palaearctic fauna as a whole is rightly emphasised.

The section on colour and mimicry addresses a number of topics, the stated aim being "to understand and explain the importance and diversity of colour patterns in the lives of hoverflies." In reality this chapter largely focuses on visual mimicry and hoverfly predation, ending with much shorter but still significant discussions on the roles of colour patterns in crypsis, thermoregulation and communication.

In my view this section of the book is not entirely successful in explaining the widely discussed issue of so-called "perfect" versus "imperfect" mimicry in the Syrphidae. This may stem in part from focusing almost entirely on the well-established theoretical distinction between Batesian and Muellerian mimicry to the exclusion of various other dynamics, together with an unjustifiably narrow definition of mimicry as something only to do with predators and predation.

The great value of this chapter, however, lies in the authors' accounts of several very important pieces of empirical research, notably those by the German biologist Gerhard Mostler and others by the Russian G.M. Dlusskii. Following discussion of what they see as the two major issues – the unexpected finding that the so-called imperfect mimics often appear far more abundant than their models, and the issue of imperfect mimicry itself, the authors come down in favour of explaining the latter by a combination of signal detection theory and the existence of multiple models. While I agree that the evidence is in favour of the hypothesis that the colour patterns of 'imperfect-mimic' hoverflies really do confer a defensive advantage due to mimicry *per se* (and not some other possible benefit), what is still lacking is a satisfactory explanation of so-called 'perfect' mimicry. Very interesting in this context is an observation due to Dlusskii reported by the authors: that spotted flycatchers are able to distinguish between social wasps and supposedly 'perfect' mimics such as the syrphid *Temnostoma vespiformis*. It appears that we have yet to discover which predators or other operators are really responsible for the more 'perfect' forms of mimicry.

The following chapter, on flowers and pollination, reflects the alternative vernacular name for the Syrphidae: flower flies. It commences with a brief but very nice review of the history of our understanding of the role of insects in pollination, from the initially discredited work of Christian Sprengel (1750–1816), via Charles Darwin to the current realisation initiated by Fritz Schneider's work in the late 1940s that pollen-feeding is vital to the fecundity of both sexes of many species of Syrphidae. Nectar and honeydew are mainly energy sources for flight. And, rather like butterflies and many other insects, various hoverflies also feed on plant sap, obtain salts and other minerals from dung, urine and mud, and drink plain water.

*Blera fallax*, an endangered British hoverfly thought to have been an early coloniser of Britain after the last ice age. (Photograph by Ellen Rotheray)

Chapter 7 goes on to look at a number of issues concerning the relationships between Syrphidae and flowers, both entomophilous and anemophilous, how the insects find them, specificity and preferences, factors affecting the utilisation of nectar versus pollen, foraging behaviour, hoverflies as pollinators (apparently significant, even in comparison to honeybees) and, intriguingly, "flowers as more than food" – mainly as sites for mate location and courtship, but also for shelter and thermoregulation. In high latitudes and mountains it seems that heliotropic flowers may offer hoverflies a particular important heat resource.

The following two chapters address the three major feeding ways of larval hoverflies: predation (Chapter 8) and saprophagy and phytophagy. The predators include the remarkable Microdontinae that feed on ant brood, the numerous familiar Syrphinae that prey on aphids and coccids, but sometimes even on beetle larvae and adult insects, and a few specialised members of the Eristalinae that prey on aquatic insect larvae in pitcher plants or, as in the case of *Volucella*, on the brood of social bees and wasps.

The final three chapters look at the population biology and ecology of hoverflies, with the last mainly devoted to the ecological services that hoverflies offer to humans – notably as pollinators, as predators of aphids and other plant bugs, of mosquito larvae, in weed control, and in the clean-up of organic wastes. Against this good-guy roll-call we have to set the fact that a few phytophagous species can cause significant economic damage, including the narcissus bulb flies (*Merodon* spp.), which can attack onions and other economically important plants as well as ornamental bulbs, and *Cheilosia* spp. on artichokes – most likely opportunistic host-switching from native Asteraceae such as burdock. The last part of Chapter 12 addresses various conservation issues, finally concluding (page 303): ". . . who can resist the lure of these curiously energetic little insects, so richly endowed in colours, beneficial qualities, survival mechanisms and biological phenomena?"

What did I like least about this work? At times the authors seem uncertain of their audience. I am not sure someone willing to read such a substantial account of a single family of flies needs to be told that insect bodies are divided into head, thorax and abdomen (page 20). Typos seem relatively few, but I did notice that the pointed-wing flies on Figure 4.2 have suffered some form of family suffix-ectomy and also been called, rather awkwardly, "pointed winged flies", while in the same figure the Phoridae have be shorn of their 'h'. Some of the original line drawings are rather un-aesthetic to my taste, and the book does not handle well – it is a constant battle to keep it open at a given page, unless you are prepared to do some real violence to the spine. The work is completed by 170 references – which may sound a lot, but is not really sufficient for the very extensive content.

What did I like most? Almost all of it! This is what I call a 'real' book – it's not a pot-boiler, but an account that flows directly from the authors' profound personal knowledge and great enthusiasm for these wonderful insects. Moreover, the approach of highlighting the major biological features of the group, and then refining these issues in the form of a series of interrelated questions at the beginning of key chapters, offers an excellent model for anyone wanting to write a book about the general biology of any group of organisms.

This last point raises a challenge to which some readers of this review might respond. The commissioning editor would like to see this book become the first in a series on the scientific natural history of a variety of insect groups. To match *Hoverflies*, additional works would ideally come from equally knowledgeable and passionate authors. However, texts even less than half the length of this work, from about 60–70,000 words upwards, would be welcome.

Forrest Text (http://www.forrestext.co.uk) specialise in short-run digitally printed books, with a strong emphasis on biological subjects. This publication method keeps initial costs low, a huge help with getting specialised works of this sort into print. Anyone interested in making an insect natural history book proposal to Forrest Text should contact Bryan Sherwood (bryansherwood@ymail.com).

In final conclusion, this is a most notable contribution to the entomological literature. Anyone with an interest in the natural history of Diptera in general, and obviously Syrphidae in particular, amateur or academic, should have a copy of this book.

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Please note: there is a duplication of five words at the foot of page 141 / top of page 142 [or is this a case of perfect mimicry?].