Hoverflies: the garden mimics

Mimicry offers protection from predators by convincing them that their target is not a juicy morsel after all. It happens in our backgardens too and the hoverfly is an expert at it.

Malcolm Edmunds

Title image: A form of *Merodon equestris* mimicking *Bombus pascuorum*

Hoverflies are probably the best known members of the insect order Diptera after houseflies, blue bottles and mosquitoes, but unlike these insects they are almost universally liked by the general public. They are popular because of their bright colours and darting flight, interspersed with hovering around garden flowers. Many of these brightly coloured hoverflies look like bees or wasps – and they use this similarity to protect themselves.

Batesian mimicry is where a palatable animal (the mimic) gains protection from resembling a noxious animal (the model) so that predators are deceived into mistaking the mimic for the model and do not attack it (Edmunds, 1974). Mimicry is far more widespread in the tropics than in temperate lands, but we have some of the most superb examples of mimicry in Britain, among the hoverflies.

Apparent Batesian mimics occur in every garden throughout the summer months, including the droneflies *Eristalis tenax*, *E. pertinax* and *E. arbustorum* all of which resemble honeybees (*Apis mellifera*) (Figure 1), the black and yellow hoverflies *Syrphus ribesii* and *S. vitripennis* which resemble social wasps (*Vespula vulgaris* and related species) (Figure 2), and the furry black and yellow and white hover-

Figure 1. Eristaline hoverflies, from left to right: *Eristalis pertinax*, *Eristalis arbustorum* (both honeybee mimics), *Helophilus pendulus* (a wasp mimic) and *Eristalis intricarius* (bumblebee mimic). These hoverflies are closely related in the subfamily Eristalinae and have a looped vein distally on the wing which is absent from many other hoverflies.

flies *Merodon equestris* and *Eristalis intricarius* (Figures 3 and 1) which resemble bumblebees. But do they actually derive protection against birds because of their similarity to hymenopterans or are they coloured like their respective models for reasons unrelated to mimicry?

Although colour is important in many insects for defence against predators, it can also be important in thermo-regulation, male-male competition and courtship. In hoverflies the abundance of species that appear to mimic hymenopterans suggests very strongly that in these species colour must have some defensive value. Seventy years ago Mostler (1935) showed that several species of birds will eat hoverflies but quickly learn to avoid attacking wasps, and they then also refuse to attack the wasp-like hoverflies *Sericomyia* and *Chrysotoxum* (Figure 2). In the same way he also showed that droneflies are protected by their resemblance to honeybees while *Volucella bombylans* is protected by its similarity to bumblebees (Figure 3).

These experiments were in an aviary, though, and obtaining proof that any hoverfly really does gain protection through Batesian mimicry in the field is not at all easy: one would need to show that birds (or other predators) kill fewer flies that mimic wasps than similar flies that do not mimic wasps.

One way of tackling this problem is to make predictions on the assumption that hoverflies are Batesian mimics and then test these predictions.

Ecology and Batesian mimicry

In 1994 Brigitte Howarth surveyed three areas of semi-natural ancient woodland in Lancashire and Cumbria each week from April until October, recording all hoverflies and hymenopterans seen on standard walks. Some were identified to species, others to a group of similarly coloured species. The five common bee and wasp groups were honeybees, social wasps, black and yellow bumblebees (*Bombus terrestris, B. lucorum* and *B. hortorum*), black, yellow and rusty-red bumblebees (*Bombus pratorum*) and brown bumblebees (*B. pascuorum*).

Her first prediction was that if hoverflies are Batesian mimics, then they should occur at the same season as the models and be rarer than the models. If they occur at other times or are commoner than the models, then birds are likely to catch a mimic and find it tasty before they have caught a model and learned to avoid insects with that colour pattern; in such cases, mimicry is unlikely to evolve.

All of the hoverflies that resembled bumblebees (including *Volucella bombylans*, *Criorhina berberina* and *Arctophila superbiens*, Figure 3) were indeed much rarer than their models, so too were the wasp-like *Sericomyia silentis* and *Chry-*

Figure 2. Wasp-like hoverflies, from left to right: *Syrphus ribesii*, *Episyrphus balteatus*, the marmalade fly (these are both 'poor' mimics), *Sericomyia silentis* and *Chrysotoxum festivum* (two 'good' mimics with more wasp-like patterns and, in *Chrysotoxum*, conspicuous antennae).

Figure 3. Bumblebee mimics, from top left to bottom right: *Criorhina berberina* typical form mimicking *Bombus terrestris*, *Criorhina berberina oxyacanthae* mimicking *Bombus pascuorum*, a form of *Merodon equestris* mimicking *Bombus pascuorum*, *Cheilosia illustrata* mimicking *Bombus pratorum*, *Volucella bombylans typica* mimicking *Bombus lapidarius* and *Volucella bombylans plumata* mimicking *Bombus terrestris*.

sotoxum spp. (Howarth and Edmunds, 2000). These are all insects that bear a very close resemblance to their models so can be called 'good mimics'. But the yellow and black *Helophilus* spp. (Figure 1) and *Syrphus* spp. and the orange and black *Episyrphus balteatus* (Figure 2) were all much more numerous than their supposed wasp models, as also were droneflies compared with their honeybee models. To the human eye many of these abundant hoverflies (particularly the wasp-like ones) are not as similar to their supposed models as are the rarer 'good mimics' so they can be referred to as 'poor mimics'.

Dittrich *et al*. (1993) trained pigeons to avoid pictures of wasps but to peck at flies, and found that the yellow and black hoverflies that looked like wasps were better protected than black flies. But pigeons attacked the orange and black *Episyrphus balteatus* the least, even though to our eyes it is a 'poor mimic'. This work suggests that these apparently poor mimics may still be protected by Batesian mimicry because birds perceive them differently from humans.

More recently Azmeh *et al* (1998) found that these very abundant but poorly mimetic wasp-like hoverflies are not so common in ancient forests of Poland and Russia as they are in secondary forests, fields and gardens, so it is possible that they have increased due to human-induced changes to the environment. If true, then the protection they receive may be minimal and mimicry may be breaking down. However, many years ago Jane Brower (1960), using mealworm prey with caged birds, showed that if a model is sufficiently nasty then mimics can still gain some protection even when they outnumber the model by nine to one. So do superabundant droneflies and wasp-like hoverflies indeed benefit from Batesian mimicry?

In her survey work Brigitte Howarth made a second prediction: that if mimicry occurs then hoverfly numbers should be positively related to numbers of their supposed models. If there is no mimicry then there should be no necessary relationship between dronefly and honeybee numbers. In collaboration with Francis Gilbert this was tested by means of a General Linear Model (GLM) to explore how dronefly numbers were related to a variety of environmental factors (see Table 1). As one would expect, dronefly numbers were significantly affected by time of year, habitat (woodland, scrub or pasture), temperature and other hoverflies (more droneflies were present on warm days and when other flies were also common). However, there was also a significant positive relationship to numbers of honeybees but a negative relationship to numbers of other hymenopterans (Howarth *et al*, 2004). This is precisely what one would expect if droneflies are indeed mimicking honeybees. There were similar positive relationships between numbers of the smaller honeybee mimic *Eristalis arbustorum* and honeybee numbers, and between both *Syrphus* spp. and *Episyrphus balteatus* numbers and social wasp numbers.

All of these hoverflies are often more numerous than their models, but it is difficult to think of a good reason why this correlation should occur unless the hoverflies are indeed gaining protection through Batesian mimicry. Similar significant positive relationships between hoverfly numbers and model numbers were found for several of the 'good mimics' (Table 2), but not for all of them. Perhaps the numbers of these insects are too small for there to be any additional advantage to be gained from evolving similar activity patterns to the model.

An exception to this relationship for the superabundant hoverflies is *Helophilus* spp.: numbers of *Helophilus* are not related to numbers of social wasps (which they resemble in colour), but when the GLM was run again with the five main hymenopteran groups separately it was found that *Helophilus* numbers are significantly and positively related to numbers of honeybees. One possible reason for this relationship is that *Helophilus* is closely related to the honeybee mimics *Eristalis tenax*, *E. pertinax* and *E. arbustorum*, and there may simply not have been enough time or sufficient selective advantage to be gained from altering this ancestral pattern after *Helophilus* evolved its wasp-like colouration. When the GLM for the bumblebee mimic *Eristalis intricarius* was run again with honeybees and the three bumblebee taxa separately there was a significant positive relationship with honeybee numbers for males but not for females; this is consistent with the hypothesis that ancestral droneflies were honeybee mimics but some have since evolved a morphological resemblance to social wasps or to bumblebees.

Table 1. Results of General Linear Model showing that there are significant relationships (deviances) between dronefly numbers (*Eristalis tenax* & *E. pertinax*) and all six variables, and that for three of the four covariates the relationship is positive. Thus there are more droneflies when it is warm, when there are more honeybees and when there are more hoverflies present. The six variables listed account for 65% of the variance in dronefly numbers.

Variable	Deviance	d.f.	*P*	Slope of covariate
Month	63.6	5	<0.001	
Habitat	177.0	7	<0.001	
Temperature	37.8	1	<0.001	+
Numbers of honeybees	7.0	1	<0.01	+
Numbers of other hymenopterans	29.4	1	<0.001	-
Numbers of other hoverflies	119.4	1	<0.001	+
residual	460.7	196		
total	1306.0	212		

% variance accounted for = 100 * (1306 - 460.7)/1306 = 65%
P – probability; d.f. – degrees of freedom.

Behaviour and Batesian mimicry

We can also predict that if a hoverfly gains protection from mimicry then its foraging behaviour should be similar to that of its supposed model. If there is no mimicry then its behaviour should be more like that of other hoverflies. Yvonne Golding measured the times droneflies and other insects spent on flowers (either feeding or resting), and the times they took flying from one flower to another. She studied the feeding and flying times for insects on eight plants making 16 comparisons in all; of these the times for droneflies did not differ significantly from those of honeybees in 13 instances whereas they very often differed from the times for bumblebees, other hoverflies and muscid flies (Table 3, Figure 4) (Golding and Edmunds, 2000). The conclusion from this work was that droneflies have modified their foraging behaviour to be more like that of their honeybee models than of other hoverflies, yet droneflies are feeding only themselves while honeybees are collecting food for the colony. The most plausible reason why this should have occurred is because it enhances their similarity to bees and hence their chances of avoiding being eaten by birds through Batesian mimicry.

Have droneflies altered their flight behaviour to resemble honeybees in other ways? When honeybees fly away from a flower after collecting pollen, they clean pollen from their body and push it into the pollen baskets on their hind legs. The large dronefly *Eristalis tenax* dangles its hind legs when in flight very much like a honeybee, but of course it has no pollen baskets, so this behaviour may have survival value by enhancing its resemblance to a honeybee. In collaboration with Roland Ennos,

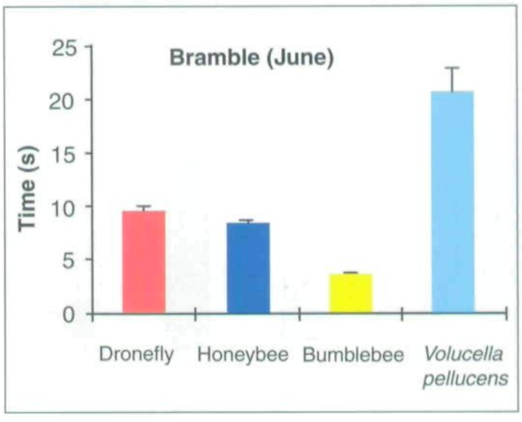

Figure 4. Times (seconds) spent resting or feeding on bramble flowers by different insects: droneflies and honeybees spend similar lengths of time; bumblebees spend significantly less time on each flower while the hoverfly *Vollucella pellucens* spends significantly more time.

Table 2. Results from the General Linear Model for supposed hoverfly mimics showing the deviances of the model covariates, their significance and slope. For ten of the species the deviances and slope show that hoverfly numbers are significantly and positively related to the numbers of their supposed model, which is consistent with the hypothesis that they are indeed gaining protection through Batesian mimicry.

Mimic	Batesian model	Deviance of model covariate[1]	Slope
Bee mimics			
Eristalis tenax/pertinax	honeybees	7.0**	+
Eristalis arbustorum	honeybees	23.8***	+
Cheilosia pagana	*Lasioglossum* bees	0.7	+
Wasp mimics			
Syrphus ribesii	social wasps	14.8***	+
Episyrphus balteatus	social wasps	5.3*	+
Helophilus pendulus	social wasps	39.7[2]	-
Sericomyia silentis	social wasps	0.2	+
Myathropa florea	social wasps	0.8	+
Xanthogramma citrofasciatum	*Nomada* bees,	14.4***	+
	yellow & black solitary wasps	6.7*	+
Bumblebee mimics			
Cheilosia illustrata	all bumblebees	4.2*	+
Arctophila superbiens	brown bumblebees	0.3	+
Criorhina berberina	black, yellow & rusty-red bumblebees	1.7	+
C.b. var. *oxyacanthae*	brown bumblebees	2.3	+
Criorhina floccosa	brown bumblebees	1.1	+
Eristalis intricarius ♀	black & yellow bumblebees	5.7**	+
E. intricarius ♂	black, yellow & rusty-red bumblebees	5.1*	+
Volucella bombylans var. *plumata*	black & yellow bumblebees	3.7*	+

* - $P < 0.05$; ** - $P < 0.01$; *** - $P < 0.001$

[1] All probabilities were halved in accordance with the one-tailed nature of the hypothesis being tested

[2] Not significant because one-tailed tests were adopted, and this slope is negative

Yvonne Golding analysed flight behaviour further (Golding *et al*, 2001). First she manipulated a patch of everlasting daisies so that the flower heads were at almost the same level, then she set a video camera above the patch. The flight paths between flowers of various insects visiting the patch were filmed and analysed by stopping the film frame-by-frame and plotting the position of the insects on acetate sheets. The flight paths and speeds of the insects were then calculated.

The results (Figures 5 and 6) showed that muscids fly much faster than honeybees and droneflies while the wasp-like *Syrphus ribesii* spends more time hovering in the air. Flying honeybees often execute loops in their flight and droneflies do so as well, but *Syrphus* and muscids rarely perform loops. But why do bees loop?

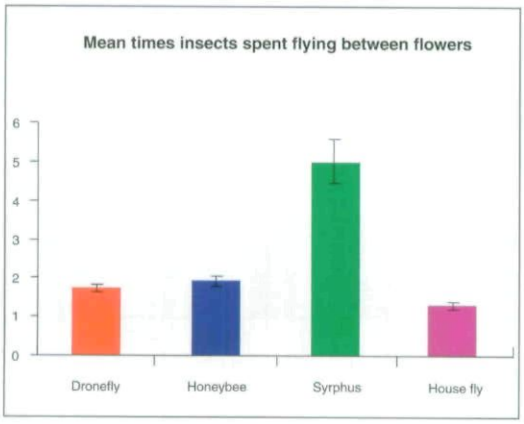

Figure 5. Times (seconds) taken for different insects to fly from one everlasting daisy flower to another: honeybees and droneflies take similar lengths of time but *Syrphus ribesii* takes significantly more time and houseflies take significantly less.

Newly released homing pigeons characteristically fly around for a few minutes before heading off in the direction of their home, presumably they take this time to orientate themselves in relation to the sun or other cues in the sky. Honeybees may do the same: the looping may give them a few moments to 'get their bearings' before flying off in the right direction. The looping flight of droneflies may then have no specific function related to orientation or obtaining food but simply increase their mimetic resemblance to a honeybee.

Similar experiments showed that *Syrphus ribesii* has very similar flight behaviour to social wasps – it flies at similar speeds and follows similar flight paths – but the other wasp-mimics *Sericomyia silentis* and *Helophilus* sp. do not (Golding *et al,* 2005).

Conclusions

The pattern that emerges from all of these studies is that the ecology and behaviour of many bee- and wasp-like hoverflies is very similar to that of their supposed models which supports the hypothesis that they do indeed gain protection through Batesian mimicry. Hoverfly mimicry of honeybees, bumblebees and social wasps involves similarity of colour, morphology, behaviour, ecology and phenology. But each species of hoverfly has evolved a different spectrum of these adaptations. So long as predatory birds are deceived by the resemblance to hymenopterans, the mimetic patterns, habits or behaviour will persist – and give increased fascination to us human observers of these delightful and beautiful insects.

References

Azmeh S, Owen J, Sorensen K, Grewcock D and Gilbert F (1998) Mimicry profiles are affected by human-induced habitat changes. *Proceedings of the Royal Society of London B*, 265, 2285-2290.

Brower J V Z (1960) Experimental studies of mimicry. 4. The reactions of starlings to different proportions of models and mimics. *American Naturalist*, 94, 271-282

Dittrich W, Gilbert F, Green P, McGregor P and Grewcock D (1993) Imperfect mimicry: a pigeon's perspective. *Proceedings of the Royal Society of London B*, 251, 195-200.

Edmunds M (1974) *Defence in animals: a survey of anti-predator defences*. Longman, Harlow.

Golding Y C and Edmunds M (2000) Behavioural mimicry of honeybees (*Apis mellifera*) by droneflies (*Eristalis* spp., Diptera, Syrphidae). *Proceedings of the Royal Society of London B*, 267, 903-909.

Golding Y C, Ennos A R and Edmunds M (2001) Similarity in flight behaviour between the honeybee *Apis mellifera* (Hymenoptera: Apidae) and its presumed mimic, the dronefly *Eristalis tenax* (Diptera: Syrphidae). *Journal of Experimental Biology*, 204, 139-145.

Golding Y C, Edmunds M and Ennos A R (2005) Flight behaviour during foraging of the social wasp *Vespula vulgaris* (Hymenoptera: Vespidae) and four mimetic hoverflies (Diptera: Syrphidae) *Sericomyia silentis*, *Myathropa florea*, *Helophilus* sp. and *Syrphus* sp. *Journal of Experimental Biology*, 208, 4523-4527.

Howarth B and Edmunds M (2000) The phenology of Syrphidae (Diptera): are they Batesian mimics of Hymenoptera? *Biological Journal of the Linnean Society*, 71, 437-457.

Howarth B, Edmunds M and Gilbert F (2004) Does the abundance of hoverfly (Syrphidae) mimics depend on the numbers of their hymenopteran models? *Evolution*, 58, 367-375.

Mostler G (1935) Beobachtungen zur Frage der Wespenmimikry. *Zeitschrift f r Morphologie und kologie der Tiere*, 29, 381-454.

Further reading

Stubbs A E and Falk S J (1983) *British Hoverflies: an Illustrated Identification Guide*, British Entomological & Natural History Society, London.

Howarth B, Clee C and Edmunds M (2000) The mimicry between British Syrphidae (Diptera) and aculeate Hymenoptera. *British Journal of Entomology and Natural History*, 13, 1-39.

Edmunds M (2000) Why are there good and poor mimics ? *Biological Journal of the Linnean Society*, 70, 459-466.

Figure 6. Percentage of time spent hovering in front of flowers by different insects: *Syrphus ribesii* spends more time hovering than do either droneflies or honeybees, while houseflies do not hover at all.

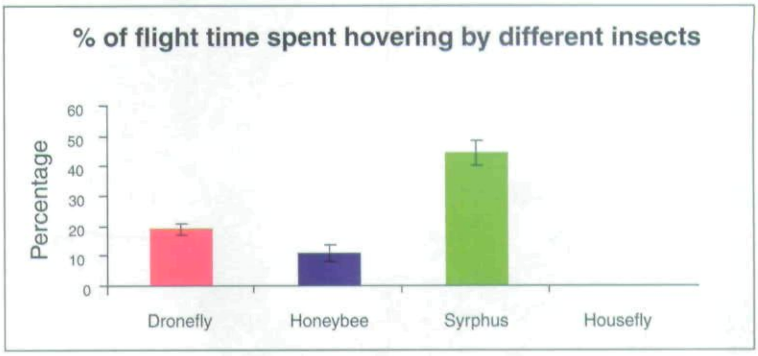

Table 3. The mean times of droneflies feeding on flowers and flying between flowers are very similar to the times for honeybees but not to those for bumblebees.
+ - significant difference
– - no significant difference

Flower	honeybee feeding	(model) flying	bumblebee feeding	(control) flying
Bramble (June) (*Rubus fruticosus*)	–	–	+	+
Bramble (July) (*Rubus fruticosus*)	–	–	+	+
Snowberry (*Symphoricarpus albus*)	–	–	no	control
Everlasting daisy (*Helichrysum bracteum*)	–	–	+	–
Michaelmas daisy (*Aster novi-belgii*)	+	–	+	+
Goldilocks (*Aster linosyris*)	–	+	no	control
Knapweed (*Centaurea nigra*)	–	–	+	–
Rosebay willowherb (*Chamerion angustifolium*)	+	–	+	+

Malcolm Edmunds is Emeritus Professor of Zoology at the University of Central Lancashire. His research interests are the biology and taxonomy of opisthobranch molluscs and the antipredator defences of animals. He has published on the defences of hawkmoth caterpillars, mimetic butterflies, praying mantids, sea slugs, ant-mimicking spiders and hoverflies. Email: medmunds@uclan.ac.uk