

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.

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Accepted 14 October 2005

Summary

Many hoverfly species show specific or non specific morphological resemblance to wasps (*Vespula* sp.) and it has been suggested that they also show similar flight behaviour. In this study we therefore compared the flight behaviour of wasps with that of four mimetic hoverflies, *Sericomyia silentis*, *Myathropa florea*, *Helophilus* sp. and *Syrphus* sp., by filming insects while they were foraging on an artificial array of flowers. Films were analysed to determine the routes taken, time spent hovering and flight speed. Of the four flies, only the non specific mimic,

Syrphus, showed similar flight behaviour to the wasps; it flew more slowly, and with more roundabout routes than the other flies, hesitating before landing. These results suggest that in hoverflies there is little reason to expect strict correlation between morphological and behavioural mimicry; insects may acquire the similarities to their model more-or-less independently.

Key words: flight, mimicry, Syrphidae, behaviour.

Introduction

Batesian and Müllerian mimicry are textbook cases demonstrating evolution by natural selection (Bates, 1862; Muller, 1879; Fisher, 1930; Carpenter and Ford, 1933; Cott, 1940; Wickler, 1968; Edmunds, 1974). The morphological resemblances between different species of tropical butterflies, between some spiders and ants, and between certain species of hoverflies and wasps and bees, are well known and documented (Turner, 1965; Oliveira, 1988; McIver and Stonedahl, 1993; Mallet and Gilbert, 1995; Howarth et al., 2000). The resemblances also extend to behaviour. It has often been observed that unpalatable butterflies and their mimics fly more slowly than other palatable butterflies (Chai, 1986). Srygley and coworkers have also demonstrated convergence in the wingbeat frequencies of certain ithomiine butterflies from the same Müllerian mimicry rings (Srygley and Dudley, 1993; Srygley, 1994, 1999a; Srygley and Ellington, 1999a,b). These convergences, however, are not necessarily unexpected in such closely related organisms (Brower, 1995).

Rettenmeyer (1970) predicted that behavioural mimicry would be especially important among mimics of Hymenoptera because the behaviour of their model is so conspicuous. Hoverflies that are Batesian mimics of Hymenoptera should therefore be expected to exhibit close behavioural convergence with their models. Such similarities have indeed been detected in the foraging behaviour of droneflies *Eristalis tenax* and their supposed model the honeybee *Apis mellifera*; they spend

similar amounts of time foraging on individual flowers and flying between flowers (Golding and Edmunds, 2000). Films of insects flying between flowers also showed that the droneflies behaved more like honeybees than like other flies, despite their very different ecology; they flew at similar speeds, took similar routes, and performed similar loops in their flight path. (Golding et al., 2001). Golding et al. (2001) concluded that droneflies may have adapted their behaviour to appear more like their models at a time when they are particularly vulnerable to predation (as had earlier been suggested by Dlusski, 1984), and that this is a clear case of mimetic flight behaviour.

Many other hoverflies are thought to be Batesian mimics of social wasps, gaining protection from their predators by their mimicry (Howarth et al., 2000). Some species such as *Temnostoma vespiforme* or the tropical *Milesia vespoidea* are considered very precise morphological mimics of social wasps (Wickler, 1968; Torp, 1994). In Britain there are no such perfect mimics, but there are several species that have been described as specific or non-specific wasp mimics (Howarth et al., 2000) of which four are common and widespread. *Sericomyia silentis*, is considered to be a specific wasp mimic (Howarth et al., 2000). It is a large fly of wing length 11 to 14 mm (Stubbs and Falk, 2002) which has conspicuous black and yellow markings and a pigmented leading edge to its wings. It looks particularly wasp-like when hanging upside

down whilst foraging on flowers (M.E., Y.G., personal observation) and is especially abundant in August and early September when workers of social wasps *Vespula vulgaris* are most numerous and reach their maximum size, with a wing length, like *Sericomyia* of 11–14 mm (Zahradnik, 1991).

Three other common hoverflies: *Syrphus* sp. (wing length 7.25–11.5 mm), *Helophilus* sp. (wing length 8.5–11.25 mm) and *Myathropa florea* (wing length 7–12 mm) are considered to be non-specific mimics of wasps (Howarth et al., 2000). They are all smaller than social wasps (Stubbs and Falk, 2002) but have similar black and yellow markings on the abdomen and yellow and black legs, while *Helophilus* also has yellow longitudinal stripes on the thorax.

It might be expected that all these flies, and especially the better mimic, *Sericomyia*, would show mimetic flight behaviour to wasps: in particular that they might mimic the slow speed, and characteristic zigzag orientation movements which wasps use when leaving their nest or approaching foraging sites (Gaul, 1951; Collett and Lehrer, 1993).

There are indeed many anecdotal reports that some hoverfly species appear wasp-like in flight (Wickler, 1968; Stubbs and Falk, 1983; Morgan and Heinrich, 1987; Azmeh, 1999; Howarth et al., 2000), but few studies have empirically measured these behaviours. In this study, therefore, we compared the flight behaviour when foraging on flowers of the social wasp *Vespula vulgaris* and the four supposed hoverfly mimics to determine whether these species showed mimetic flight behaviour. We analysed gross aspects of flight, including velocity, flight routes and time spent hovering; such behaviours will all be highly visible to potential predators.

Materials and methods

The method was adapted from that of Golding et al. (2001). Free-flying insect were filmed while foraging on flowers of ivy *Hedera helix*, black knapweed *Centaurea nigra* and devil's bit scabious *Succisa pratensis* at the University of Manchester Botanical Grounds and at Latterbarrow, a nature reserve in South Cumbria, UK. The flower heads were arranged 10 cm apart in a 4×3 array. The flower stalks passed through holes drilled in a Perspex sheet into a water reservoir below. The arrays, which were frequently moved around, were placed near to mature, naturally growing patches of the experimental flowers, which were visited by our target insects. All flights were out of doors. The behaviour was captured by a digital video camera (Canon XM1, 20×) mounted on a tripod, approx. 150 cm away from the array, which was directly facing it. Parallax even at the edges of the array were calculated to result in errors in velocity of less than 1%. A commentary made at the time helped to identify different species. The filming was carried out on warm, calm days in August and September 2003 and 2004.

The insects were social wasps (*Vespula vulgaris* L.) and their black and yellow hoverfly mimics: *Sericomyia silentis* Harris; *Myathropa florea* L.; *Helophilus* (two very similar species, *pendulus* L. and the much rarer *hybridus* Loew); and

Syrphus (two very similar species, *ribesii* L. and the much rarer *vitripennis* Meigen). Because it proved impossible to distinguish between the sister species in the field, they were classified as either *Helophilus* sp. or *Syrphus* sp. This is justified because, as other authors (Stubbs and Falk, 1983; Howarth et al., 2000) have noted, these species not only look similar but behave in a similar manner. In total 109 flights between flowers 10 cm apart were captured that were performed by 53 individuals of the five species. For analysis, each flight was taken as an independent observation. This was justified because for all but *Helophilus* (where one individual made nine flights) each individual made only one to four flights. Because different individuals behaved in similar ways, a separate analysis, using mean figures for individual insects, gave almost identical results.

The flight trajectories that insects took between the flowers were established by stopping the film frame by frame and marking the position of the head on transparent OHP film. From the OHP films the total distance flown between each flower was measured by following the path with a digital map measurer. The precise straight-line distance between the point the insect took off from one flower and landing on an adjacent flower 10 cm away was also measured. This allowed the ratio of distance travelled by the insect to the shortest distance between flowers (the deviation) to be calculated (see also Chai and Srygley, 1990). The average speeds at which the insects flew between flowers were calculated by dividing the total distance by the time spent flying, knowing that each frame represented a time lapse of 0.04 s. Time spent hovering was excluded from the calculations of flight velocities. Hovering was identified as episodes when the insects moved less than 2 mm per frame (a speed of less than 5 cm s⁻¹).

Results were tested for normality using the Kolmogorov-Smirnov test. All except hovering time proved to be normally distributed. The means for the different species were compared using a one-way ANOVA. A *post hoc* Dunnett C test was then carried out to detect which, if any, of the fly genera showed different flight behaviour from their presumed wasp model.

Results

Are there differences in insect flight behaviour among different flower species?

We were only able to capture film of social wasps flying between ivy flowers and of *Myathropa* flying on knapweed flowers. *Syrphus* flew between ivy, devil's bit scabious and knapweed: a one-way ANOVA showed no differences in the speeds individuals flew between these three flower species ($F_{2,24}=1.677$; $P=0.210$) or the routes they took between them ($F_{2,24}=0.262$; $P=0.771$). The other hoverflies flew on just knapweed and devils bit scabious. For *Sericomyia* a two-sample *t*-test (equal variances; 10 flights on each flower species) showed there was no difference in the speed they flew between flowers of the two genera ($t_{18}=0.508$; $P=0.612$) or the routes they took ($t_{18}=0.214$; $P=0.833$). For *Helophilus* (unequal variances – four flights on knapweed; 21 flights on devil's bit

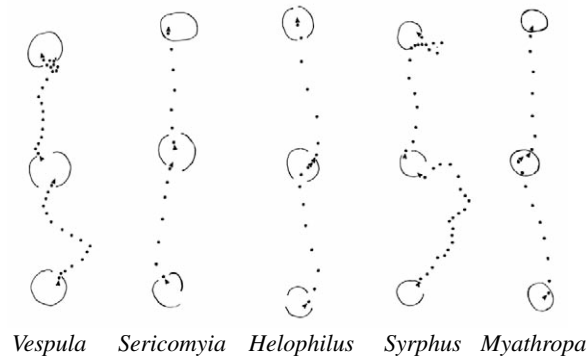


Fig. 1. Typical flight trajectories of the five genera of insect. Flowers (circles) were placed 10 cm apart, and the position of each fly was recorded at 0.04 s intervals (dots) from video recordings.

scabious) there was no difference in the routes they took ($t_{23}=0.862$; $P=0.397$) but there was a difference in the speeds they flew between the flowers of the two genera ($t_{23}=5.026$; $P=0.005$); they flew slower between knapweed flowers, averaging 0.228 m s^{-1} compared with 0.310 m s^{-1} between devil's bit scabious flowers. We have no explanation for this but it should be noted that we recorded only four flights between knapweed flowers.

Flight trajectories

Typical flight trajectories of the five genera are shown in Fig. 1. It can be seen that of the hoverflies, only *Syrphus* showed a similar path to the wasp, flying slowly in an indirect way between flowers, noticeably slowing and pausing before alighting. The other three species flew fast and straight between flowers.

Do insects take different routes between flowers?

Mean deviations of the five genera are shown in Fig. 2. The ANOVA showed that there was a significant difference

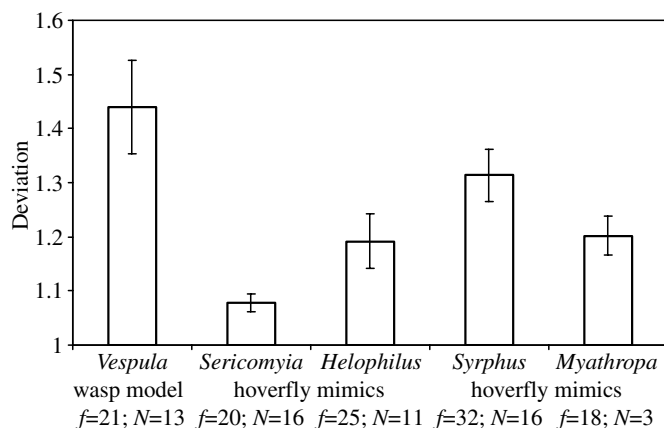


Fig. 2. Deviations (means \pm S.E.M.) in the flight path (actual/straight-line distance) taken by insects between flowers placed 10 cm apart for the five genera of insect examined. The numbers of flights, f , analysed for each genera are also shown, along with the number of insects, N .

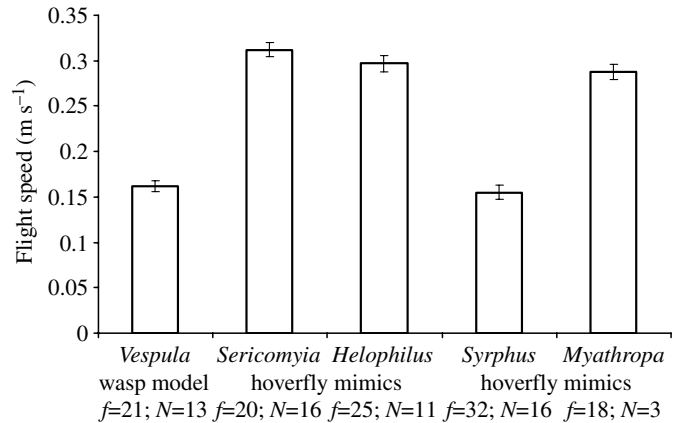


Fig. 3. Flight speeds (means \pm S.E.M.) between flowers placed 10 cm apart, of the five genera of insect examined. The numbers of flights, f , analysed for each genera are also shown, along with the number of insects, N .

between species ($F_{4,105}=6.633$; $P<0.001$). The Dunnett C test, comparing each hoverfly mimic with the model, failed to show a significant difference between the wasp and *Syrphus* ($P=0.305$) but did show significant differences between the wasp and *Sericomyia* ($P<0.001$); *Helophilus* ($P=0.003$) and *Myathropa* ($P=0.016$).

Do insects fly at different speeds between flowers?

Mean flight speeds of the five genera are shown in Fig. 3. The ANOVA showed that there was a significant difference between species ($F_{4,105}=92.421$; $P<0.001$). The Dunnett C test, comparing each hoverfly mimic with the model, failed to show a significant difference between the wasp and *Syrphus* ($P=0.999$) but did show significant differences between the wasp and the other three hoverflies ($P<0.001$ in each case).

How much time do insects spend in hovering?

Helophilus hovered on three occasions out of 25 flights, each bout of hovering occupying three to five frames (i.e. 0.12–0.16 s), whereas *Syrphus* hovered on 17 occasions out of 35 flights with each bout taking between five and 15 frames (0.2–0.6 s). *Sericomyia* and *Myathropa* were never observed to hover during 20 and 18 flight sequences, respectively. Wasps were classed as hovering only once in 21 flights, i.e. when the side-to-side movements of the insect in front of flowers were so small that it appeared to be hovering. A Chi-squared test showed that these differences in frequency of hovering between genera were indeed significant ($\chi^2_{4}=50.3$; $P<0.001$).

Discussion

The 10 cm arrays of flowers used in this study were an improvement on the natural arrays of flowers used by Golding et al. (2001) because they ensured that the flights each insect took were of almost exactly the same distance, so were more readily comparable with each other. The flowers were also

more nearly in a single plane, so could be analysed with more confidence using just a single film.

The results were very clear. *Syrphus* sp. showed more similar flight behaviour to its wasp model than did the other three hoverfly mimics, both in the speed flown between flowers, and in the routes taken; it flew more slowly and deviated more from a straight line, like the wasp. In particular there were similarities between *Syrphus* and *Vespa* in their behaviour just before landing. The wasps moved from side to side in front of flowers before alighting on them to feed, giving an overall impression of a jerky zigzag movement (see Fig. 1). This is consistent with orientation flights of social wasps approaching a feeder as described by Collet and Lehrer (1993). *Syrphus* individuals also invariably hesitated before alighting on flowers, sometimes moving from side to side as if inspecting the flowers before landing (see Fig. 1), at other times moving so little that these episodes were recorded as hovering. *Syrphus* was the only hoverfly in this study to do this, although it can also be observed in the smaller black and orange-yellow hoverfly *Episyrphus balteatus*. Our other hoverflies rarely hovered, seeming to fly without hesitation from one flower to another.

There is no obvious reason why *Syrphus* (and *E. balteatus*) should adopt this zig zagging behaviour as they are neither predatory (as adults) nor aposematic. They may be inspecting the flowers for predatory crab spiders which sit about on flowers waiting for prey, or indeed for wasps, but if this was the case we should also expect *Helophilus* and *Myathropa*, which are similar-sized flies, to hover more frequently. An obvious remaining explanation is that *Syrphus* has modified its flight behaviour to resemble that of wasps, just as droneflies have modified their flight behaviour to resemble that of honeybees (Golding et al., 2001). The zigzagging behaviour could be readily achieved by both the wasp and the fly by altering the dorsal and ventral end points of their wingbeat without having to alter the orientation of their bodies (Ennos, 1989; Dudley, 2000). There is certainly no reason to believe that, as in mimetic butterflies, the flight resemblance is due to their morphological resemblance. *Syrphus* is much smaller than social wasps; Diptera have a quite different flight apparatus from Hymenoptera; and *Syrphus* is capable of extremely precise flight (Ellington, 1984).

So why should an apparently imprecise mimic of wasps show such good flight mimicry while the three other hoverflies, of which at least one (*Sericomyia*) appears a better morphological mimic, did not? One reason might be that the bird predators of hoverflies see them in a different way from entomologists. Dittrich et al. (1993) demonstrated, for instance, that to pigeons that were shown slides of insects, *Syrphus ribesii* appeared more similar to wasps than *Helophilus pendulus*. Clearly, pigeons are not insectivorous birds, so these results may not be very relevant to real life, but it could be that *Syrphus ribesii* is to insectivorous birds an excellent mimic both morphologically and behaviourally.

Another reason may be that different aspects of mimicry, both morphological and behavioural, may not be closely linked. *Syrphus* may compensate for a poor resemblance to its

model by showing better flight mimicry. In contrast, the specific mimic *Sericomyia*, may be protected adequately by its morphological resemblance and its extremely wasp-like behaviour when foraging on flowers. Taking faster more direct paths between flowers, which would increase the speed and efficiency of foraging, may not, therefore, significantly compromise its mimicry.

Several pieces of evidence make this explanation plausible. First, droneflies, which are also non-specific mimics, in their case of honeybees (Howarth et al., 2000), also show good flight mimicry (Golding et al., 2001). Second, it fits in with observations of the behaviour of these flies when startled. *Sericomyia* adopts jerky zig-zag flight when alarmed, so it may adapt its flight behaviour to appear more wasp-like only when directly threatened. Howarth et al. (2000) suggest this is also the case for *Helophilus*. By contrast, *Syrphus* will fly off very rapidly if threatened by a sudden movement, showing it has retained its ability for fast flight; we recorded a mean velocity of 1.47 m s^{-1} over the first 29 cm of one such escape flight, and an acceleration of over 20 m s^{-2} . We plan to further investigate alarmed flight behaviour of hoverflies to test this hypothesis.

This line of argument suggests that in hoverflies the evolution of behavioural mimicry may precede, as well as follow, the evolution of precise morphological mimicry. Kassarov (2003) suggested in relation to butterfly mimicry, that birds may detect movement better than the fine details of pattern and coloration. Therefore a hoverfly that shows a small degree of morphological similarity, may face stronger selection pressure for behavioural convergence than morphological convergence. It may also be 'easier' genetically to change behaviour than to change morphology. An individual animal can alter its behaviour as a result of some experience (e.g. birds can learn to avoid wasps), and some altered behaviours may result in behavioural mimicry. Only later does such an acquired behaviour become incorporated into the animal's genome.

That behavioural mimicry may be unlinked to morphological mimicry is also suggested by a behavioural convergence shared by all four of these quite different hoverfly species; they all make large amplitude dorsoventral movements of their abdomen while they are foraging on flowers. These movements, which are absent in non-mimetic flies, superficially resemble the ventilation movements of the abdomens of Hymenoptera (Heinrich, 1979). A probable explanation for these movements in hoverflies is that they improve their resemblance to hymenopterans and that by emphasising the abdomen and further displaying their warning coloration, they suggest that they might also be able to sting. Clearly, further studies of other mimetic hoverflies and other mimetic behaviours are required to uncover the relative roles of morphological and behavioural mimicry.

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