
Mimicry profiles are affected by human-induced habitat changes

Salma Azmeh*, Jennifer Owen, Karin Sørensen, David Grewcock and Francis Gilbert

School of Biological Science, University of Nottingham, University Park, Nottingham NG7 2RD, UK

Mimicry theory predicts that mimics in a Batesian mimicry complex evolve to resemble models closely, and that there is a limit on the numbers of mimics relative to models. For hoverflies (Diptera: Syrphidae), supposed mimics of social wasps (Hymenoptera: Vespidae), neither of these is true; many mimics are imperfect and in the UK and Europe they outnumber their models manifold. We hypothesized that the high abundance of mimics relative to models in the UK may be the result not just of mimic–model dynamics, but of habitat changes caused by humans. Most of the larvae of poor mimics are aphidophagous, and changes from ancient forest to agricultural and/or urban habitats may have vastly augmented aphid numbers. Using new and literature data, we compared mimicry profiles of habitats differing in their degree of habitat disturbance. In both cases, more highly disturbed habitats had proportionally more poor mimics and fewer high-fidelity mimics than less disturbed habitats. This supports the hypothesis that habitat change has an effect on model to mimic ratios.

Keywords: Batesian mimicry; habitat disturbance; Syrphidae; wasp

1. INTRODUCTION

Mimicry has been a source of fascination for biologists ever since the beginning of modern evolutionary thought. Bates published the first adaptive explanations for mimetic relationships between species in 1862. This original theory of ‘Batesian mimicry’ described how the patterns of unpalatable species (models) can be imitated by unrelated, palatable species, affording the mimics a degree of protection from visual predators. Bates’ theory originated from his observations in Brazil of the similarities between the red-and-yellow-patterned ithomiine heliconiids and some species of pierid butterfly (Dismorphiinae), which had almost identical coloration even though Dismorphiinae are generally white. In this case, a palatable mimic is thought to deceive predators by imitating an unpalatable model. Batesian mimicry is often contrasted with Müllerian mimicry, where unpalatable species evolve to resemble one another. Recent modelling suggests that this distinction may (Turner & Speed 1996) or may not (MacDougall & Dawkins 1998) be artificial, with the two categories either distinct, or part of a continuum, depending on the assumptions made about predator behaviour.

A frequently cited example of Batesian mimicry involves the black-and-yellow patterns of social wasps (Hymenoptera: Vespidae), imitated by the unrelated hoverflies (Diptera: Syrphidae). However, this complex throws up a number of discrepancies with the predictions of Batesian mimicry. Since Bates’ time, theories about mimicry (see, for example, Fisher 1930; Sheppard 1959, 1975; Turner 1984; Malcolm 1990) contain some funda-

mental universally accepted predictions. First, a close resemblance to the model evolves owing to strong selection pressures (Fisher 1930; Sheppard 1975; Huheey 1984). However, in hoverflies, close morphological and even behavioural resemblance to wasps (see, for example, Waldbauer 1970) occurs in some species (e.g. *Temnostoma vespiforme*), but is unusual. Most common European hoverfly species have a much less faithful resemblance to their wasp models. Here, we call these ‘poor mimics’, assuming them to be mimetic since birds make mistakes similar to those of humans in distinguishing them from wasps (see Dittrich *et al.* 1993). A variety of hypotheses address this problem, including a non-mimetic aposematic function to hoverfly colour patterns, advertizing either flight agility (Srygley 1994; Pinheiro 1996) or distastefulness (Malcolm 1981, 1992), or predator perceptions of imperfect mimicry differing from human ones (Dittrich *et al.* 1993; Howse & Allen 1994).

Furthermore, mathematical models of mimicry suggest that there is a limit to the number of mimics compared with models: there may be more mimics than models in some circumstances, but even under extreme circumstances the ratio still has limits of ten mimics per model (van Brower 1960; Estabrook & Jespersen 1974; Sheppard 1975; Luedemann *et al.* 1981; Turner 1984). However, all these studies only consider perfect mimicry. In hoverflies, seemingly poor mimics often outnumber their supposed models (Gilbert 1986; Owen & Gilbert 1989; Owen 1991) by much larger factors than are allowable by any theoretical model. One possible explanation for this is a shift in the natural abundance of mimics and models owing to the artificial effects of habitat disturbance by humans (Grewcock 1992; Dittrich *et al.*

*Author for correspondence (plxsa@plnl.life.nott.ac.uk).

1993). Evidence for the influence of human disturbance on mimicry dynamics already exists in a different context (Linares 1997).

In this paper, we address the problem of the relative abundances of models and mimics in hoverflies. Specifically, we test the idea that the very high relative abundance of poor mimics is a direct result of anthropogenic habitat disturbance. If mimics are common relative to models, their mimicry should gradually be lost, because predators learn if colour patterns do not indicate noxiousness (Turner 1984). In hoverflies, poor wasp mimics are much more abundant than high-fidelity mimics, but their relative abundance may be artificially inflated by human-induced changes to habitats. If in the past mimics were not so common, it could be that the mimicry has simply not been lost yet.

The potential reasons for changes in hoverfly relative abundances are connected with larval food resources; whereas adults all feed on pollen and nectar, larval feeding habits vary remarkably widely (see Rotheray 1993). Most of the common poor-mimic species are aphidophagous as larvae (e.g. *Syrphus* spp.), whereas many good mimics feed as larvae in tree holes or rotting wood (e.g. *Temnostoma* spp.). Most Palaearctic hoverflies are species of open glades in forested habitats (Speight *et al.* 1975; Speight 1983), and their colour patterns probably evolved in the ancient forests that covered the Palaearctic, now mostly changed to the urban–agricultural landscapes common in Western Europe. These landscape changes may also have hugely boosted abundance of aphids, because aphids are also insects of open or edge habitats (Dixon 1973). Although this hypothesis does not directly address the issue of why poor mimicry exists, it does provide an explanation for the current relative abundance of poor mimics to good mimics, and also the abundance of poor mimics relative to models.

We test the disturbed-habitat hypothesis by comparing median mimetic similarities of hoverfly communities in sites varying in their degree of disturbance. Hoverfly abundances are measured in each site (either our own, or literature data), and plotted against calculated similarity values to produce ‘mimicry profiles’. The prediction is that in undisturbed sites, the median similarity is greater than in disturbed habitats. Less disturbed habitats supported proportionally more good mimics, suggesting a significant role of habitat disturbance in the relative abundance of mimetic hoverflies.

2. MATERIALS AND METHODS

We tested whether poor mimics have increased in frequency and hence changed the relative abundances of good and poor mimics. Mimicry profiles were contrasted for sites differing in degree of disturbance, by measuring the frequency distributions of hoverfly taxa and converting them into frequency distributions of mimetic similarity by measuring similarity of each taxon to wasps. Our own and literature data on relative abundances were analysed, by comparing the median mimetic similarities of hoverflies in different types of habitat.

(a) *Measuring similarity to wasps*

Model–mimic similarity in abdominal pattern only was measured, because behavioural mimicry is difficult to quantify.

The model used in all cases was *Vespa vulgaris*, the commonest wasp type at all three sites and therefore the presumed model. We used the method of Ditttrich *et al.* (1993) because they established, by means of photographs and bit-mapped images, that humans, pigeons and computers all largely agreed in their assessments of relative similarities. Although pigeons can see ultraviolet (UV) light, and normal photographs do not record the UV patterns (Cuthill & Bennett 1993), UV photography of the relevant hoverfly species shows that there are no extra UV components of the colour patterns (Gentle 1995; P. R. Green, L. Gentle, P. K. McGregor, T. Peake, F. Gilbert and W. Ditttrich, unpublished data).

To measure the similarity of a hoverfly species to *V. vulgaris*, a photograph of a specimen was scanned into a PC. Pictures were obtained from specimens from the Natural History Museum (London) and from colour plates (Torp 1994). Images were standardized in size to a height of 100 pixels, and reduced to a standard set of seven colours (RGB values in brackets): black (0, 0, 0), dark orange (230, 255, 255), orange (240, 155, 25), yellow (255, 204, 102), pale yellow (255, 255, 153), grey (204, 204, 204) and white (255, 255, 255). Each hoverfly abdomen was compared with a standard wasp image by means of the image analysis technique described in Ditttrich *et al.* (1993; see also Grewcock 1992). The technique generates a single-value percentage description of the similarity between two patterns, achieved by comparing images pixel by pixel, and measuring the Euclidean distance apart of each pair of corresponding pixels in red–green–blue colour space. The images are shifted slightly to obtain the maximal match between them. (For a fuller explanation of how the similarity value is calculated, see Ditttrich *et al.* (1993).)

Some hoverflies are obvious mimics of honeybees (*Apis* spp.), bumblebees (*Bombus* spp.), or other hymenopteran models; such species (e.g. *Eristalis* spp., *Volucella bombylans*) were excluded from the analysis. Similarity values were not calculated for every species, but rather for exemplar species representing a colour-pattern group, usually comprising a genus or part of a genus. Species were only allocated to a colour-pattern group if it was known that their abdominal pattern was identical or almost identical to that of the exemplar species. A small minority of species whose appearance was unknown, or whose image was unavailable, were not used in the analysis. To take size differences between hoverflies into account, the similarity values were scaled by each hoverfly’s difference in size from the wasp model.

There is some variation within hoverfly species in abdominal colour pattern (see, for example, Holloway *et al.* 1997). In this study, just one individual from each species was compared to a wasp image, but differences between colour-pattern groups were much larger than within-species variation.

(b) *New data on hoverfly abundance*

Hoverfly abundances were recorded in May and June from three areas: the Far East of Russia (pristine forest habitat), Bialowieza, Poland (undisturbed forest habitat) and Leicester, UK (highly disturbed habitat). Waldbauer & LaBerge (1985) suggest that Batesian mimics time their emergence to when fledgling birds have learned to avoid models, and this does not necessarily coincide with the emergence of the models themselves. We therefore restricted the analysis to mimic abundance, and did not include model numbers.

Data on a pristine site were gathered from forested areas surrounding Komsomolsk-na-Amure in the Far East of Russia. This is true virgin mixed forest, with huge areas of woodland occasionally punctuated by human disturbance, at approximately

the same latitude as central Britain (50°32' N, 136°59' E). During six weeks in May and June 1997, numbers of hoverflies and wasps of all types were counted during 10-min periods at flowers throughout the day (07.00–16.00). Flowers were patchily distributed through the forest, mostly in well-lit forest gaps such as disused roads, paths or railway lines. Ideally, individual hoverflies would be marked (Holloway & McCaffery 1990) or removed from the population when measuring abundance, to avoid counting the same individuals twice. However, this would have confounded the counting method by disturbing the hoverflies feeding in the patch. To avoid counting the same individuals in different patches, we used many different areas within the sites, 1–100 km apart. Within these subsites, almost all patches were separated by a minimum of 50 m. Some data from June 1995 are also included, collected during census walks.

The most undisturbed mixed-forest habitat in Western Europe is the Bialowieza forest (1250 km²) in Poland and Belarus, part of which (47 km²) is a UNESCO-protected World Heritage site. It was in glades and small open areas around this protected area that the data on hoverfly abundance were collected. The forest is also at about the same latitude as the British study site (52°41' N, 23°50' E). Data were collected during six weeks in May and June 1996, after a preliminary survey of the habitat for suitability (Sørensen & Gilbert 1997).

The third set of data came from a long-term Malaise trap study (partly published in Owen (1991)) of a suburban garden in Leicester, UK (52°38' N, 1°05' W), well stocked with a variety of flowers suitable for adult hoverfly feeding (see Owen 1991). Most of the UK should naturally have a climax vegetation of mixed forest, now long since disappeared, so this was classified as a highly disturbed site. A 23-year data set (1972–1994) was used from catches of hoverflies in the trap, and abundances from May and June were extracted for comparison.

(c) Literature data

We also obtained data from publications containing European hoverfly abundance or frequency data (see Appendix A on the Royal Society web site at http://www.pubs.royalsoc.ac.uk/publish/pro_bs/dec98pb1.htm). Each study site was classified into one of four broad habitat categories: ancient undisturbed forest, ancient disturbed woodland, recent disturbed woodland, or highly disturbed habitat (urban parks and gardens). In total, 117 data sets were compared, representing very wide variation in methods used for surveying hoverflies (time of year, scale of study, etc.). We could not be certain that *Vespa vulgaris* was the dominant model in all cases: however, good mimics of other wasps (e.g. *Polistes* spp.) rate highly on our similarity scale, and we aimed to test only broad differences between habitat categories in terms of mimicry profile. Appropriate similarity values were assigned to each individual in every hoverfly community (again only including those species that to human eyes appear candidates for wasp mimics), and a median similarity calculated. Where data were given in abundance form, (i.e. in abundance categories, for example 'rare', 'frequent'), these were converted to frequency form (i.e. actual numbers) by using a set of conversion factors. Each set was scaled approximately exponentially between frequencies of 1 and 100, varying according to the number of categories used in a data set. The factors were as follows (least abundant category first): seven abundance categories (×2, ×4, ×10, ×20, ×50, ×100), six (×2, ×6, ×15, ×40, ×100), five (×3, ×10, ×30, ×100), four (×3, ×20, ×80), three (×5, ×50) and two (×7).

We tested the *a priori* hypothesis that anthropogenic disturbance artificially boosts the relative abundance of poor mimics

(because these are largely aphidophages). This predicts that the average median similarities will fall into the rank order: undisturbed forest > ancient woodland > recent disturbed woodland > disturbed urban habitats.

The correct and most powerful test for this is a one-tailed ANOVA for an ordered expectation, still very uncommon in the ecology and evolution literature (see Gaines & Rice 1990). Because we cannot assume normality, we need a non-parametric version of this ANOVA for ordered expectations; such a test is available in the form of a 'specific ANOVA' (as advocated in the integrated non-parametric system of Meddis (1984); see also Barnard *et al.* (1993) for a simplified account), otherwise known as Jonckheere's test for ordered alternatives (see Siegel & Castellan 1988). Using the median similarity from each site as the raw data, we calculated the rank sums R_i for each group ($i=1-4$), and then calculated a \mathcal{Z} -score according to the formula

$$\mathcal{Z} = (L - E) / \sqrt{V},$$

where $L = \sum \lambda_i R_i$,

$E = (N + 1) \sum n_i \lambda_i / 2$, and

$$V = (N + 1) [N \sum n_i \lambda_i^2 - (\sum n_i \lambda_i)^2] / 12.$$

(λ_i , predicted order for the groups; n_i , sample size for each group, $N = \sum n_i$). \mathcal{Z} -scores greater than 1.64 are adjudged to be significant at the 5% level.

3. RESULTS

Similarity values were obtained for 60 exemplar species, describing 99% of individuals from Leicester, 91% from Poland, and 85% from Russia. For the data from the literature, the similarity values covered on average $94 \pm 1\%$ of the data. For our own data, the peak in abundance moved to higher similarity values as the habitat became less disturbed (figure 1*a-c*). In Leicester, the similarity value range with highest frequency was 5–15% similarity to models, whereas in Poland the highest frequency was in the 15–25% range. In Russia the peak frequency had moved even higher, to 25–35% similarity.

The whole population tended to have higher similarity values in the less disturbed habitats; in the Leicester data set almost half of the hoverflies had similarity values of 15% or below, whereas Poland and Russia had only 5% and 10%, respectively, in this category. Conversely, the Leicester community had only 1% of individuals with 45% similarity or above, whereas Poland had 38% and Russia had 16%. This resulted in a higher overall median similarity in the undisturbed habitats: 36.9% similarity in Poland and 34.5% in Russia, compared with 17.3% in Britain.

For the overall test of the hypothesis, there was a trend of lower median similarity with increased habitat disturbance (figure 2); statistically, the predicted pattern of similarity with habitat type did indeed occur ($\mathcal{Z}=1.69$, $p < 0.05$). There is a large jump in mean similarity between truly undisturbed forest and all the disturbed categories, indicating the sensitivity of hoverfly communities to disturbance. This is further underlined by excluding the data for pristine forests; the remaining three categories fall into the predicted order, but the pattern is not significant ($\mathcal{Z}=1.19$, $p > 0.05$).

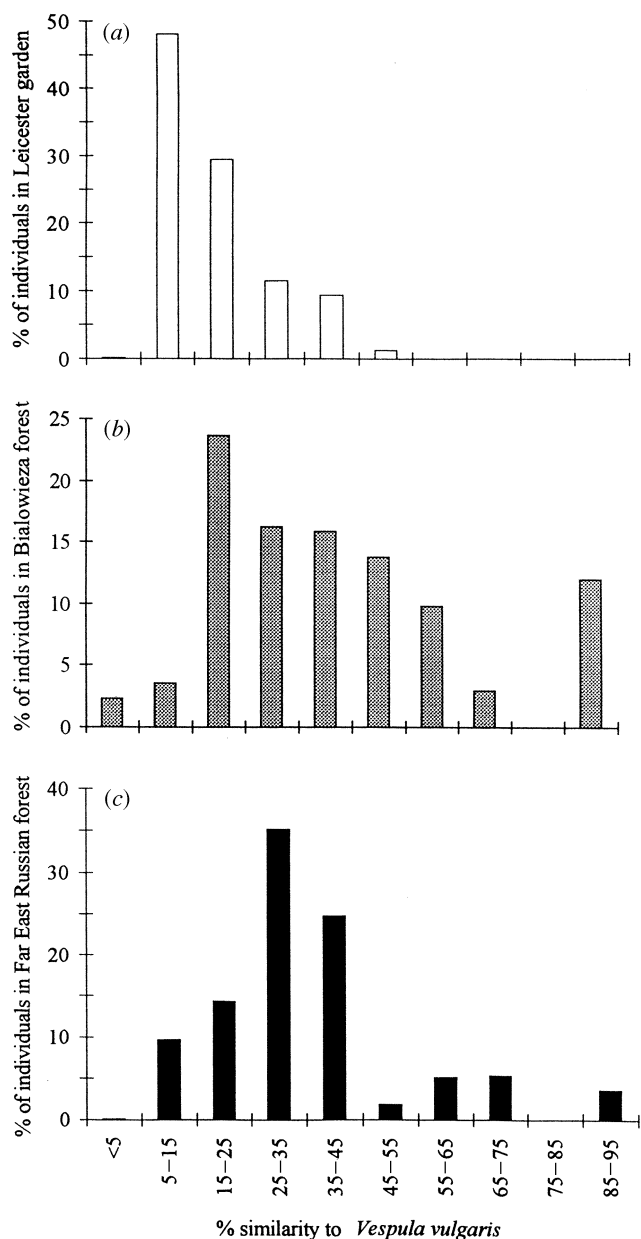


Figure 1. Abundance of hoverflies categorized by degree of similarity to *Vespula vulgaris*, in (a) a Leicester garden in June 1972–1994, (b) Bialowieza forest, Poland, in June 1996 and (c) Russian Far East forest, in June 1995 and 1997.

4. DISCUSSION

This study demonstrates that the disturbance of forest habitats has a large effect on the relative frequencies of hoverfly species. A shift towards lower similarities to wasps was found when habitats were disturbed. This suggests a reason why so many poor mimics may be present in the highly disturbed landscapes of Western Europe: the change to urban and agricultural environments has increased food resources for the larvae of poor mimics, while decreasing them for good mimics. Indeed, in Leicester, there were no high-fidelity mimics at all over the 23 years of the study.

The paradox of mimics outnumbering models could therefore be explained thus. Evolution of colour patterns owing to changes in model:mimic ratios may be slow

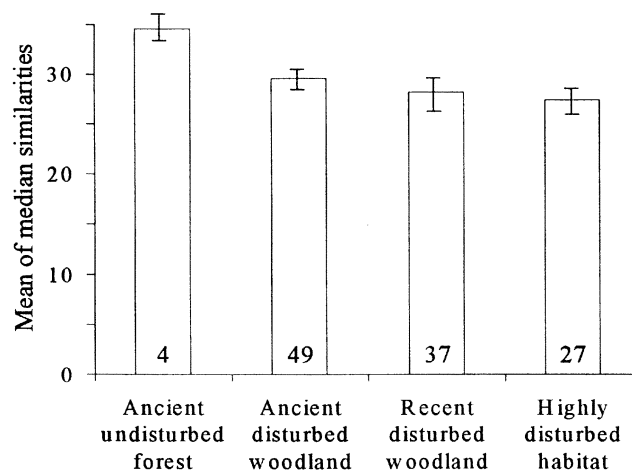


Figure 2. Similarity of hoverflies to wasp model *Vespula vulgaris* in four habitat categories. Similarity values are means of the median similarities of all sets of data within each category. Numbers in columns indicate sample sizes (the number of data sets) in each category. The similarities follow the predicted monotonic pattern.

(Turner 1984) so mimicry patterns now seen in disturbed habitats may be in the process of being lost. Predator pressure is the factor that would cause mimicry to be lost by natural selection. Here, habitat disturbance may have overtaken it in its role of regulating mimic abundance, although it may eventually catch up.

Theoretical models of mimicry (Huheey 1964; Pough *et al.* 1973; Estabrook & Jespersen 1974) are generally based on measures of abundance, model noxiousness, spatial distribution of prey and the profitability of alternative prey. These parameters, however, are rarely measured in the field. More extensive studies of frequency data, including model frequencies, would provide further elucidation of the complex systems described here.

In this study, the Russian forest was less disturbed than the Bialowieza forest in Poland, where human activity does exist in most areas outside the central strict reserve. The hoverflies in Poland, however, had a higher mean similarity to wasps, and the distribution of similarity values was generally further to the right (figure 1*b,c*). This might be due to stochastic differences between years (see Owen 1991) because these studies covered only one to two seasons: in the Russian Far East, 1997 in particular was a poor year for hoverflies owing to a previous series of dry seasons. It should be noted, however, that the peak in hoverfly abundance was at a higher similarity value than in Poland. This type of problem emphasizes the usefulness of (i) long-term data sets such as the Leicester one, and (ii) the type of large-scale literature survey used here, which gives a general picture despite variation in many aspects of the studies.

Only wasp mimics have been considered in this paper. Bee mimics also exist, but are easier to account for; they have a good resemblance to their models, and are rarer relative to them (Owen 1991), in part because of the occurrence of different mimetic morphs. An area for further study would be to measure model abundance relative to mimics. In this study, we concentrated on proportions of mimics relative to one another, as abundance of

even high-fidelity mimics does not appear to correlate with abundance of wasp models in the short-term (B. Howarth, personal communication).

Even in the untouched environments surveyed here, there are still many poor mimics, although they are proportionally fewer than in disturbed habitats. Their presence still requires some explanation, but this is a neglected area of research into mimicry. Lindström *et al.* (1997) suggest that imperfect Batesian mimics can survive where models are common and highly noxious. Data on wasps throughout the year could show whether wasps are frequent enough to explain the presence of imperfect mimics, but this is unlikely in Britain, where on average mimics outnumber *Vespa vulgaris* models by a ratio of 9.6:1 (J. Owen, unpublished data). Wasp stings may be very harmful to a bird predator, and high noxiousness may therefore play a role.

The viewpoint of the predator is also vital in considering this problem; an innate tendency to avoid black-and-yellow patterns could exist (Schuler & Hesse 1985), in which case perfection of the patterns would be less important. Howse & Allen (1994) have suggested that there is ambiguity in the imperfect pattern, which confuses the predator, allowing time for escape. Predator perception is also important in considering the similarity-measuring technique. Dittrich *et al.* (1993) found that although pigeons generally rated similarity to wasps in the same way as both humans and the image-analysis technique, there were exceptions; two supposedly poor mimics were rated highly by the birds. If this is true of many species, it could alter the significance of these results, by assigning more good mimics to disturbed habitats.

A different explanation for poor mimics is that their colour patterns are aposematic in their own right. Pinheiro (1996) found evidence for the evolution of aposematism unrelated to palatability, but related to flight escape agility, in two species of *Morpho* butterfly. Hoverflies are renowned for their flight agility, and this is therefore a possible factor, currently under investigation (S. Azmeh, unpublished data).

Our results demonstrate that human-derived habitat change does alter the relative frequencies of good and poor mimics, and hence probably of mimics and models. This needs to be borne in mind when using community data to test ideas about the evolution of mimetic complexes, because data from any but pristine habitats could be misleading.

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