✓

Imperfect mimicry: a pigeon's perspective

WINAND DITTRICH[1], FRANCIS GILBERT[2], PATRICK GREEN[3], PETER McGREGOR[2] AND DAVID GREWCOCK[2]

[1] *Department of Psychology, University of Exeter, Exeter EX4 4QG, U.K.* [2] *Department of Life Science and* [3] *Department of Psychology, Nottingham University, Nottingham NG7 2RD, U.K.*

[Plate 1]

SUMMARY

Despite the dearth of field-based evidence from natural model–mimic communities, theory suggests that Batesian mimicry should have limits placed upon the model:mimic ratio for mimics to benefit. Paradoxically, hoverflies that are apparently mimics are often superabundant, many times more abundant than their supposed models. One possible solution to this paradox is that perhaps they are not mimics at all. We use discriminative operant conditioning methods to measure the similarity perceived by pigeons between wasps and various species of supposedly mimetic hoverflies, and an image processing technique to measure objective similarity. We demonstrate that pigeons rank mimics according to their similarity to a wasp model, in an orderly broadly similar to our own intuitive rankings. Thus pigeons behave as if many hoverflies are indeed wasp mimics. However, they rank the two commonest hoverflies as very similar to wasps, despite these looking decidedly poor mimics to the human eye. In these species, 'poor' mimicry may have been sustainable because it exploits some constraint in birds' visual or learning mechanisms, or some key feature used in pattern recognition. Furthermore, the relation between similarity and mimicry is nonlinear: small changes in similarity can lead to dramatic increases in the degree of mimicry.

1. INTRODUCTION

Biologists have always been fascinated by the phenomenon of mimicry in all its various forms (see Wickler 1965, 1968; Sheppard 1959, 1975; Turner 1984; Malcolm 1990). Mimicry has even been accorded the status of a paradigm of adaptive evolution by natural selection (Turner 1987; Brower 1988), although surprisingly there is still a dearth of good empirical evidence, particularly for field evidence of the protective effects of mimicry (see the review by Malcolm 1990). In defensive Batesian mimicry, the selective agent is a predator selecting amongst prey, often visually; visual mimics are palatable and gain protection by looking like other organisms that are unpalatable or unprofitable in some other way (models).

Here we are particularly interested in the evolution of imperfect mimics in a visual Batesian mimicry complex. Imperfect mimics constitute an almost completely neglected part of the problem of Batesian mimicry, as their existence is usually discounted (see, for example, Sheppard 1975, p. 182). (Their occurrence amongst Müllerian mimicry complexes is acknowledged: Sheppard 1975; Ackery & Vane-Wright 1984.) They have only rarely been addressed in the theory of mimicry (see, for example, the review by Huheey (1988)), with some notable exceptions (see, for example, Getty 1985). Even rarer are experimental studies, although there are some (see, for example, Hetz & Slobodchikoff 1988). Nearly all theoretical treatments assume that strong selection pressure on mimics in the past has resulted in close resemblance to models (Sheppard 1975; Huheey 1988), and suggest further that there is a limit to the sustainable model:mimic ratio, set by absolute abundance, model noxiousness, prey spatial distribution, and the profitability of alternative prey (Huheey 1964, 1988; Pough *et al.* 1973; Estabrook & Jespersen 1974; Luedemann *et al.* 1981).

However, paradoxically, in nature species which to the human eye appear to be poor mimics (cf. figure 1) often far outnumber both good mimics and models (see Turner 1984). This is certainly true in the mimicry complex of wasp models and hoverfly (Diptera, Syrphidae) mimics we study here (see figure 1; see also Gilbert 1986; Stubbs & Falk 1983; Owen 1981, 1991; Owen & Gilbert 1989). There are various hypotheses that can account for this discrepancy, including (Grewcock 1992): man-made habitat disturbance leading to non-natural relative abundances; potential distastefulness and hence the possibility that they

Proc. R. Soc. Lond. B (1993) **251**, 195–200
Printed in Great Britain

might be Müllerian not Batesian mimics, which are said to show less exact resemblance to one another (Sheppard 1975, p. 182–183; Ackery & Vane-Wright 1984); aposematism through unprofitability because of their flight agility; predators may perceive them as good mimics because they only get a fleeting glimpse; and finally, the possibility that they are not mimics at all, but merely have black and yellow colour patterns for some other reason. This paper addresses the last hypothesis, that perhaps these 'poor mimics' are not in fact mimics at all.

Two contradictory hypotheses suggest themselves: at one extreme, their natural predators may not perceive any similarity between them and models; at the other, they may be perceived as very good mimics, in spite of what to the human eye is a poor match. To decide between these explanations, we need two important parameters: the physical similarity between model and mimic, and the degree of mimicry, the similarity perceived by a predator. In the experiments reported here, we show that pigeons rank mimics according to their similarity to a wasp model in an order broadly similar to our own intuitive rankings (see figure 1); with two interesting exceptions, pigeons behave as if many hoverflies are indeed wasp mimics.

2. MATERIALS AND METHODS

We used pigeons to represent generalized avian predators; although pigeons are not insectivorous, bird visual systems are known to be highly conservative (Hodos 1972). There is also evidence that pigeons are readily able to classify insects in a taxonomically relevant way (W. Dittrich, F. Gilbert, P. McGregor, P. Green & D. Grewcock, unpublished results). Pigeons were trained to discriminate between sets of photographic slides of wasps and non-mimetic flies, and then tested for generalization to slides of supposedly mimetic hoverflies (see figure 1).

We obtained 12 retired racing pigeons, with no previous experimental history: they were maintained at 85% of the *ad libitum* body mass on a 14 h:10 h light:dark cycle with water and grit continuously available other than in the test apparatus. Pigeons were assigned randomly to three categories before the start of the experiment: wasp$^+$, the presence of wasp images was the positive stimulus; fly$^+$, the presence of non-mimetic flies was the positive stimulus (this is analogous to the natural situation); and pseudocategory, 40 randomly chosen slides of wasps and non-mimetic flies (20 of each) were arbitrarily classified as positive stimuli. The last category was included as a control for memorization of individual images (Vaughan & Greene 1984).

We used a one-key operant chamber, with colour slides being back-projected from a Kodak S-RA2000 random access projector onto the response key. A shutter, operated by a rotary solenoid, controlled the presentation of images. In addition to the response key, the panel carried an aperture that gave access to a solenoid-operated food hopper containing the reward, a mixture of food grains. An Apple II microcomputer controlled events and recorded responses.

Pigeons were first trained by standard methods (see Dittrich & Lea 1993) to find food in the hopper, and then to peck at the illuminated centre key. The schedule of reinforcement was a fixed interval of 20 s, with a 10 s delay after each food reinforcement during which the shutter closed and the projector moved to a new random position (no slides present at this stage). (Full details of the methods will be published elsewhere.) Discrimination training then began, using 40 slides of different individual wasps (*Vespula vulgaris* and *V. rufa*: see figure 1*a*) and 40 slides of different individuals of non-mimetic flies (these included 1–3 slides of different individuals of various Dipteran species (*Rhagio*, *Tabanus*, *Tachina*, *Sarcophaga*, *Scathophaga*, etc.), including some hoverflies that are not wasp mimics (*Eristalis tenax* (a honeybee mimic), *Xylota sylvarum*, *Chrysogaster* spp.)). On each slide there was an image of a single insect, always in the same central position, photographed against an identical and homogeneous blue background. All specimens were photographed at the same magnification, so that size as well as pattern cues were available, although size differences were not substantial. In each session all 80 slides were used, each projected once for 20 s. In the case of a positive stimulus, the end of a 20 s period or the next peck caused the shutter to close and the bird to be reinforced. In the case of a negative stimulus, after 20 s of stimulus presentation the shutter closed and the houselight turned off regardless of the bird's behaviour. A new pseudorandom stimulus sequence was generated for every session. Training continued until performance reached a criterion of five successful sessions after learning the discrimination.

Significant discrimination was assessed by the *rho* statistic (Herrnstein *et al.* 1976), and occurred in both wasp$^+$ and fly$^+$ groups after only two sessions, but never occurred in the pseudocategory group. Two conclusions can be drawn: first, that a pigeon's behaviour was not influenced by any pre-existing aversion to wasps or wasp-like patterns (cf. discussion in Guilford 1990); and second, that, although pigeons can remember a large number of individual images and respond to them adequately (Vaughan & Greene 1984), the complete lack of discrimination in the pseudocategory group shows that successful discrimination did not depend on memory for individual images.

We then used a new set of 260 colour slides, each of a different individual wasp, non-mimetic fly, mimetic hoverfly (see figure 1*c*, *e*, *g*), or non-insect control (a black polygon), in a series of experiments to test the trained pigeons' generalization to other images. The photographic format of these test slides was the same for all but one experiment: in this last experiment, we tested whether discrimination was maintained with a set of 48 photographs taken in the field. These natural pictures (see figure 1*b*, *d*, *h*) showed the insect as the focal object in the centre, but size and orientation were uncontrolled, against a wide variety of natural backgrounds.

Each test session consisted of 80 trials. In each, a subset of 80 slides was used. Of the slides, 40 (20 positive and 20 negative) were chosen from the training stimuli, 20 slides

---

DESCRIPTION OF PLATE 1

Figure 1. Examples of standard (*a*, *c*, *e*, *g*) and natural (*b*, *d*, *h*, *i*) slides used in the discrimination experiments using pigeons trained by operant conditioning methods. (*a*, *b*) *Vespula vulgaris*, (*c*) *Temnostoma vespiforme*, (*d*) *Episyrphus balteatus*, (*e*, *f*) *Syrphus ribesii*, (*g*, *h*) *Scaeva pyrastri*, and (*i*) *Temnostoma alternans*. Using the standard slides, most people agree that there is a rank order of mimetic quality, from (*c*) *Temnostoma* to (*e*) *Syrphus* to (*g*) *Scaeva*. (*f*) is a natural slide of *Syrphus ribesii*. Photographs were taken by David Fox (*b*, *h*), John French (*d*) and Francis Gilbert (*f*, *i*).

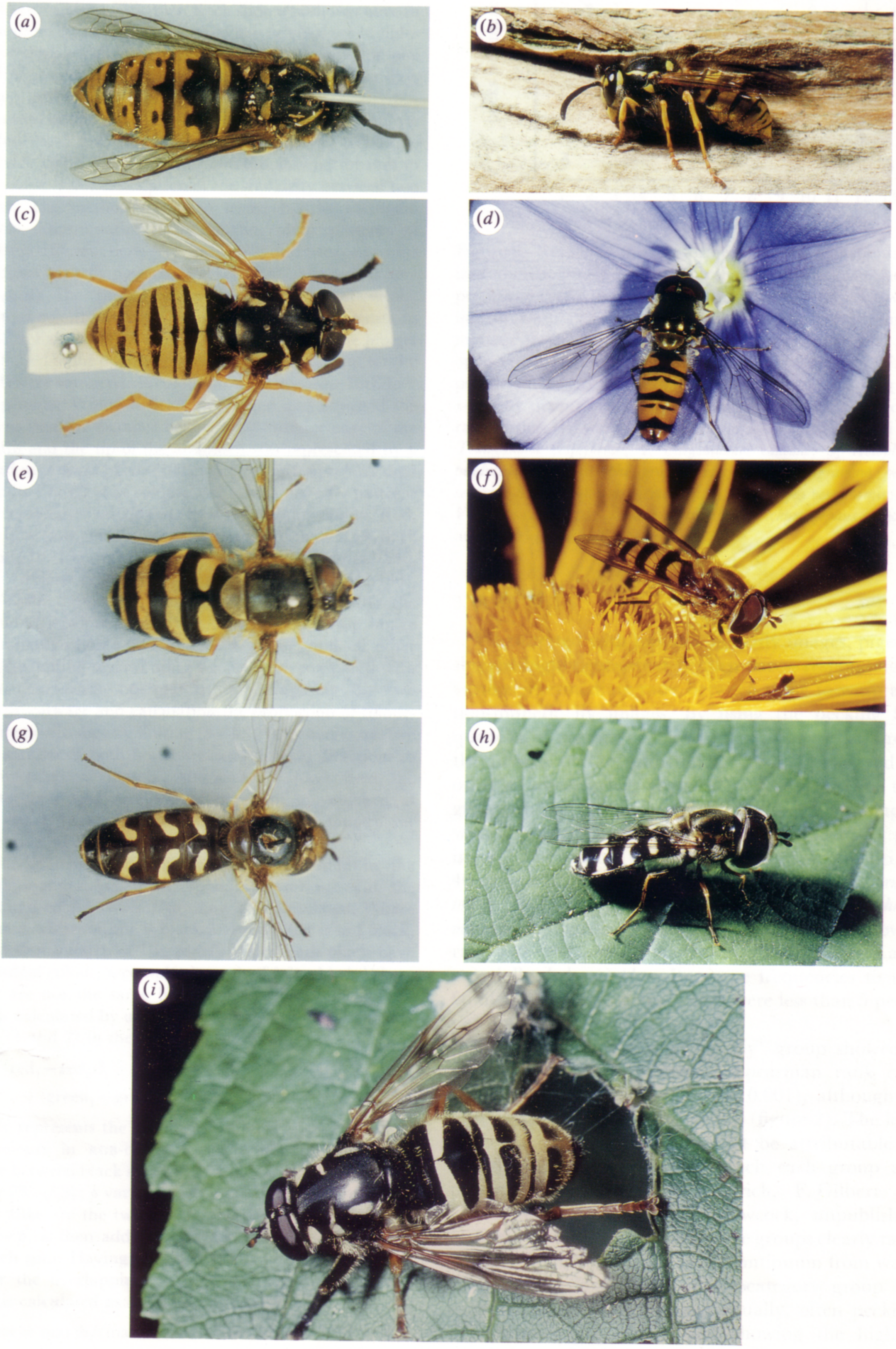

Figure 1. For description see opposite.

were novel exemplars of the original insect species, and the remaining 20 slides were novel exemplars of mimetic hoverflies or non-mimetic flies. Each slide was shown once in a test session. After four test sessions the original set of slides and the initial training contingencies were given for one retraining session. Sessions were normally given one per day, four days per week.

To assess similarity in a relatively objective manner, we have developed and extended an image analysis technique (Grewcock 1992) that compares two-dimensional images to yield a single-value description of the similarity between two patterns. The method has been tested by the successful statistical discrimination between the colour patterns of wasps from different nests (Nevison 1989) and between wasps and various hoverfly patterns (Parker 1990). We used it here to quantify the similarity between model and mimic abdominal colour patterns. By using field-guide illustrations (Stubbs & Falk 1983) as a basis, or in some cases the images actually used in the operant conditioning experiments, tergite patterns were scanned into colour bitmaps. By using BitEdit™ running under Windows 3.1™, we edited and adjusted the images so that the distance between the anterior edge of the scutellum and the tip of the abdomen was represented by a standard number of pixels (100), and the pattern represented by a limited number of colours. All British hoverfly patterns can be represented adequately by a set of eight colours (Red, Green, Blue (RGB) values in parentheses): black (0, 0, 0), dark red (160, 10, 15), red–orange (215, 100, 20), orange (240, 155, 25), yellow (255, 255, 0), pale yellow (240, 240, 130), cream (230, 240, 200), and grey (180, 240, 180): the background is white (255, 255, 255). A single wasp image was randomly chosen as a reference image, and all other images (including several other wasps) were compared with it. The comparison operates by superimposing the two images in software and calculating the proportion of colour-matching pixels, slightly shifting (5–10%) the images relative to one another in both horizontal and vertical directions to find the maximal match. Although we have used the computer-generated RGB values here for convenience, it would also be possible to use Endler's (1990) four-colour classification.

Colour matches and mismatches are recorded in the following manner. When corresponding pixels are both the background colour (white), nothing is accumulated. Where only one is white, or one is black and the other is not black, a complete mismatch of 1 is added. When both pixels have the identical colour, a complete match of 1 is added. Where colours are not the same but do not include black, their match is calculated by using the RGB values for the two pixel colours (1 and 2) in the following manner:

$$p = \sqrt{[(\mathrm{red}_1 - \mathrm{red}_2)^2 + (\mathrm{green}_1 - \mathrm{green}_2)^2 + (\mathrm{blue}_1 - \mathrm{blue}_2)^2]}/(255\sqrt{3});$$

p merely represents the euclidean distance apart of the two pixel colours in RGB-colour space relative to the same distance between black and white (and hence whose distance apart is $255\sqrt{3}$); p varies between 0 and 1, the larger it is, the less alike are the two colours. Hence having calculated this, $(1-p)$ is then added to the match sum, and p to the mismatch sum. Having obtained the match and mismatch sum for the overlapping pictures, the similarity between images is calculated as:

$$\text{similarity} = \text{match}/(\text{match} + \text{mismatch}).$$

This results in a relatively objective estimate of image similarity to a wasp exemplar, either including or excluding size effects (by adjusting image sizes either to the standard width of 100 pixels or to be proportional to their real size). We use only images standardized for size.

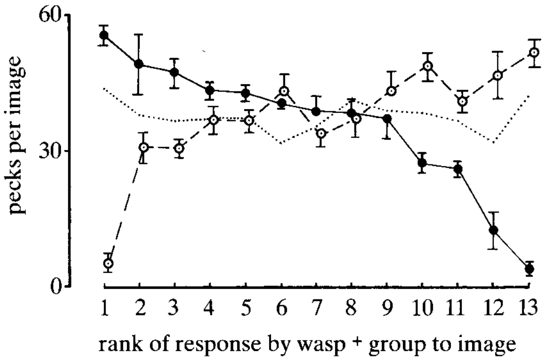

Figure 2. Results of the test for generalization to standardized mimetic images. The graph shows the number of pecks per image (±s.e.) given by pigeons trained to peck at wasp images (wasp$^+$, solid line and filled circles), or to peck at non-mimetic fly and not to wasp images (fly$^+$, broken line and open circles). The dotted line shows the responses of the pseudocategory control group. Species are ranked along the x-axis by the mean response of the wasp$^+$ group, and are, in rank order: 1, wasps (*Vespula* spp.); 2, *Syrphus ribesii*; 3, *Temnostoma vespiforme*; 4, *Chrysotoxum cautum*; 5, *Helophilus pendulus*; 6, *Epistrophe grossulariae*; 7, *Xanthogramma pedissequum*; 8, *Chrysotoxum bicinctum*; 9, *Sphecomyia vespiformis*; 10, *Volucella zonaria*; 11, *Scaeva pyrastri*; 12, *Ischyrosyrphus glaucius*; and 13, non-mimetic hoverflies.

3. RESULTS

When tested with mimetic hoverfly images, pigeons showed highly consistent performances, responding at various intermediate rates between those to wasp and non-mimetic fly images. By using the pecking frequencies of pigeons of the wasp$^+$ group, we can order the images of the mimetic hoverflies in descending order of mean values (figure 2). As expected for this group, the greatest response was to the wasp images, with a pecking frequency of more than 55 pecks per image. The images of seven hoverfly species elicited 40–50 pecks per image: *Syrphus*, *Temnostoma*, *Chrysotoxum*, *Helophilus*, *Epistrophe*, *Xanthogramma* and *Sphecomyia*. The pigeons pecked with substantially lower rates (10–30 pecks per image) at *Volucella*, *Scaeva* and especially *Ischyrosyrphus*. Response frequencies to unfamiliar non-mimetic fly images were less than 5 pecks per image.

Furthermore, pigeons of the fly$^+$ group showed a very similar set of responses (Spearman rank correlation, $r_s = -0.88$, $n = 13$, $p < 0.001$), although as expected in the opposite direction (figure 2). The less-than-exact correspondence might be attributable to slightly different cues upon which each group apparently concentrates (W. Dittrich, F. Gilbert, P. Green, P. McGregor & D. Grewcock, unpublished results). Thus birds from both these groups clearly rank mimetic images along the same continuum from wasp to non-mimetic fly. The pseudocategory group responded to all images almost equally, often pecking 35–40 times per image, and showing the highest pecking rates for the most familiar images of wasps and non-mimetic flies.

Remarkably, in the visually highly complex situation of insects in the field, pigeons were still able to find the relevant features which they had previously acquired

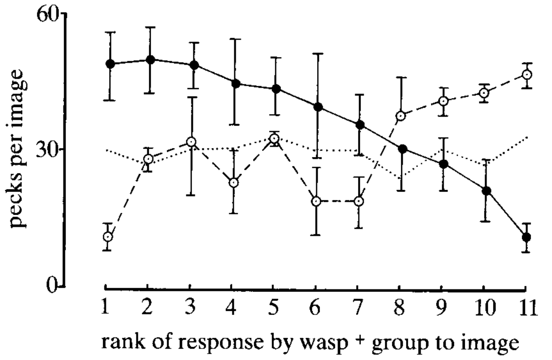

Figure 3. Results of the test for generalization to images of mimetic hoverflies taken in natural surroundings. Symbols and arrangement as in figure 2. Rank order of species along the x-axis is: 1, wasps (*Vespula* spp.); 2, *Episyrphus balteatus*; 3, *Chrysotoxum arcuatum*; 4, *Sericomyia silentis*; 5, *Epistrophe eligans*; 6, *Helophilus trivittatus*; 7, *Myiatropa florea*; 8, *Volucella zonaria*; 9, *Scaeva pyrastri*; 10, *Volucella pellucens*; and 11, various other hoverflies (*Ischyrosyrphus glaucius*, *Leucozona lucorum*, *Eristalis* spp. and *Xylota segnis*).

during discrimination learning; thus they were well able to transfer this ability to unfamiliar stimuli, in this case either the same or novel species in an unknown natural setting. Birds of the wasp$^+$ and fly$^+$ groups significantly discriminated between totally novel wasp and hoverfly images photographed in their natural habitat. Although the equivalence in the results of the two groups was not as high as in the mimicry experiment with a homogeneous background and controlled posture, there remains a highly significant negative correlation between them ($r_s = -0.76$, $n = 12$, $p = 0.011$). It was again possible to order the different images in terms of their response frequencies (figure 3), and for those species in common the order is highly comparable to the order previously achieved (cf. figure 2: $r_s = 0.91$, $n = 14$, $p < 0.001$). Once again the pseudocategory group failed to discriminate between wasps and non-mimetic insects.

What is the relation between a relatively objective measure of pattern similarity and mimicry, as measured by the pigeons' responses? We use the results of the image analysis to relate similarity to the average degree of mimicry as assessed by the pigeons (figure 4). We present only the results for images adjusted to equal sizes because there is less scatter to the fitted curves (W. Dittrich, F. Gilbert, P. Green, P. McGregor & D. Grewcock, unpublished results), consistent with our experimental evidence that pigeons use pattern rather than size cues (figure 3).

4. DISCUSSION

In these experiments, a group of pigeons rapidly acquired successful discrimination between images of wasps and non-mimetic flies. When tested with images of mimetic hoverflies, the pigeons' responses ranked the images along a continuum from wasp-like to fly-like, providing a measure of the degree of mimicry for each hoverfly species, i.e. of the pigeons' perception of the pattern similarity between wasp model and hoverfly mimic. When related to an objective similarity, this now creates a powerful tool with which to investigate the evolution of these patterns, and a vital component of models of the evolution of mimicry. Imperfect mimicry as established by the birds themselves is clearly present in these flies, and requires an explanation.

There may be a similar spectrum of mimicry among sympatric assemblages of Müllerian mimics (danaine butterflies): the suggested explanation here was the 'generalisation series' (Ackery & Van Wright 1984). The idea is that contact with a few species across this series causes predators to generalize to the entire spectrum. This mechanism cannot work, of course, with a series of Batesian mimics.

Alternatively, Duncan & Sheppard (1965) suggested that, if the model is very noxious, there would be little selection pressure to improve mimetic quality beyond a certain degree. In contrast, where the model is only slightly noxious, there is continuing selection until the mimic is indistinguishable from the model. This could have happened in the case of the Syrphidae. Bumblebees are more cautious in stinging attackers, and could therefore be described as less noxious than wasps, which readily sting. There are many bumblebee mimics amongst the syrphids, all of which are extremely good mimics to the human eye (see Stubbs & Falk 1983). The contrast with wasp mimics is striking.

However, the relative abundances of model and mimic in this system are clearly not explicable using normal Batesian mimicry theory. As de Ruiter (1952) demonstrated, birds will switch feeding behaviour to concentrate upon mimics if these are found to be palatable. In nature, palatable hoverfly mimics will be encountered many times more frequently than wasps. Just how noxious do wasps have to be in order that predators never take a chance and sample a black and yellow insect? Various attempts to answer this question suggest that the combination of a really foul model and a predator that learns quickly and remembers for a long time might provide 'significant' protection at only 10% model frequency (Brower 1960; Brower *et al.* 1970; Pough *et al.* 1973), but these all used perfect mimics.

The fact that pigeons are able to generalize their training discrimination to the natural slides (Figure 3) demonstrates two things. First, the mimicry ranking as identified by the pigeons is a very stable one; and secondly, that discrimination does not occur via a single feature, but is a composite of many features forming the polymorphous concept (Lea & Harrison 1978) of a fly or a wasp that is used to classify these insects. In particular, discrimination does not rely on size, orientation or brightness alone, nor does it even use size as an important cue. This is interesting because human subjects learn very quickly to discriminate between wasp or bee models and hoverfly mimics, but rely mainly on size (Grewcock 1992). There are additional data relevant here concerning the visual recognition of insects in non-human primates. There is strong evidence that macaque monkeys primarily use form and contrast cues. Furthermore, their response intensity towards wasp-like patterns directly depends on

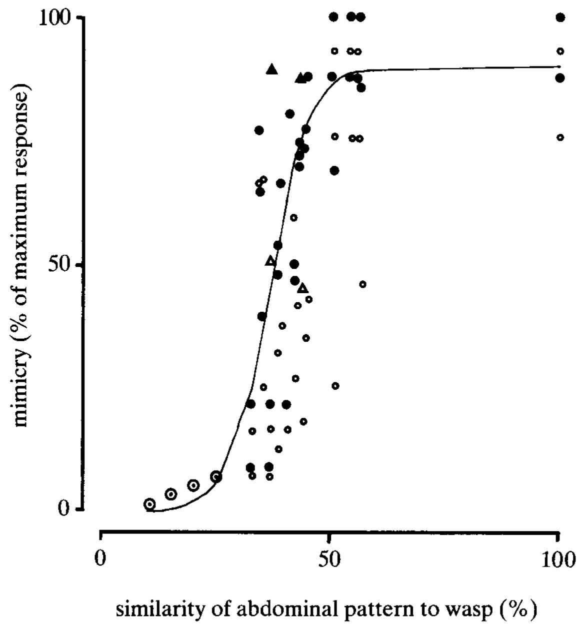

Figure 4. Relation between similarity to one single wasp exemplar (measured by image comparison) and mimicry (assessed by the response of trained pigeons to images). Logistic curves have been fitted, by using nonlinear least squares with the Marquardt method, implemented by the STATGRAPHICS statistical package. R^2 values cited below are the proportion of variance explained by the model. To fit similar curves, mimicry estimates (i.e. pigeon response rates, M) for the wasp$^+$ group were adjusted to range from 0–100% by applying the transformation $M \cdot 100/M_{\max}$. To fit data for the fly$^+$ group onto the same graph, mimicry estimates were inverted and changed to the same range by applying the transformation $(M_{\max}-M)\cdot 100/M_{\max}$. Four extra points were added to form the left-hand tail of the curve to allow the curve fitting (open circles with central dots), making $n = 36$ in all. The logistic curve fitted was of the form: mimicry $= a/[1+b.\exp\,(-c.\text{similarity})]$. wasp$^+$ group (filled circles), $a = 90$, $b = 7400$, $c = 0.24$ ($R^2 = 0.71$). fly$^+$ group (open circles), $a = 86$, $b = 210$, $c = 0.12$ ($R^2 = 0.59$). Filled triangles (wasp$^+$ group) and open triangles (fly$^+$ group) are the points for the species *Episyrphus balteatus* and *Syrphus ribesii*.

the completeness or similarity of wasp-like insects as well as their previous experiences with wasps (Dittrich 1988).

It is also interesting to note that deviations from a line of best fit in figure 4 are much smaller in the wasp$^+$ group. This is probably because this group was trained to peck at a much more unified set of images (all *Vespula* wasps) than the other group (many different kinds of non-mimetic flies). An important implication of the sigmoidal curve is that hoverflies can improve dramatically their degree of mimicry for a small increase in similarity to a wasp model. This does not agree with our own assessments, and thus human perception of mimicry is an unreliable guide to the function of colour patterns. The use of objective similarity calibrated against birds' mimicry rankings provides an important new solution to this problem. This result should now be incorporated into models of the evolution of mimicry.

The most surprising result of this study is also one of the most interesting for ideas about mimicry. It concerns the response of pigeons of the wasp$^+$ group to two of the commonest species of hoverfly, *Syrphus ribesii* (figure 1*f*) and *Episyrphus balteatus* (figure 1*d*). Neither can be regarded as successful wasp mimics by human standards; most human observers consider much rarer species such as *Temnostoma* (figure 1*i*), *Sphecomyia* or *Chrysotoxum cautum* as much more wasp-like. However, *S. ribesii* and *E. balteatus* can be superabundant in particular years (Owen 1981, 1991; Owen & Gilbert 1989), thus these apparently poor mimics can be much more common (hundreds to thousands of times more common) than both their models and 'much better mimics'. A partial resolution of this apparent paradox is suggested by the pigeons' assessment of their degree of mimicry, which places them as the most wasp-like of all the hoverflies we presented (see figures 3 and 4). To a pigeon, therefore, these hoverflies are not poor mimics at all, but the best. The question of why the visual systems of humans and pigeons reach such different conclusions remains open, but the answer is likely to lie in visual or learning constraints in the way in which birds classify their prey, processes possibly exploited by these patterns. This could be a factor in the undoubted 'success' of these two hoverflies (i.e. their high abundance), but again underlines the problem that the theory of the evolution of mimicry has in accounting for the relative abundances of this model–mimic complex (see discussion in Turner (1984)).

Thus humans may overestimate the ability of predators in making discriminations. It then follows that we may be under-estimating the frequency and significance of mimicry in nature, especially as mimetic effects need not necessarily depend upon obviously noxious or dangerous species: models may simply be unprofitable. Thus mimicry may be a much more pervasive feature of nature than is generally realized. If this is true then the general paucity of good experimental data on mimicry becomes even more unfortunate.

This study has underlined the importance of considering perception from the viewpoint of the potential predator rather than humans: mimicry seems indeed to be in the eye of the beholder.

Winand Dittrich was supported by a Feodor-Lynen Fellowship from the Alexander von Humboldt Stiftung and the University of Exeter Research Fund; David Grewcock was supported by a NERC Studentship. We thank Stephen Lea (Exeter), Peter Usherwood (Nottingham) and Peter Davies (Nottingham) for their support of this work. We thank especially David Fox (Nottingham) for loan of his 48 field-taken photographs, Brian Case for taking the standard photographs, Phil Gurr for masking the photographs, and Tim Brailsford and Rebecca Luck for their ideas for improving the mechanics of obtaining bitmaps, and for helping in capturing and editing images. We thank also Bryan Clarke and Dick Vane-Wright for very helpful suggestions on the manuscript. The Alexander von Humboldt Stiftung provided support for reproducing the colour plate.

REFERENCES

Ackery, P. R. & Vane-Wright, R. I. 1984 *Milkweed butterflies: their cladistics and biology*. London: British Museum (Natural History).

Brower, J. van Z. 1960 Experimental studies of mimicry. IV. The reactions of starlings to different proportions of models and mimics. *Am. Nat.* **94**, 271–282.

Brower, L. P. 1988 Preface. *Am. Nat.* **131** (Suppl.), 1–3.

Brower, L. P., Pough, F. H. & Meck, H. R. 1970 Theoretical investigations of automimicry. I. Single trial learning. *Proc. natn. Acad. Sci. U.S.A.* **66**, 1059–1066.

Dittrich, W. 1988 Wie klassifizieren Javaneraffen (*Macaca fascicularis*) natürliche Muster? *Ethologie* **77**, 187–208.

Dittrich, W. & Lea, S. E. G. 1993 Motion as a natural category for pigeons: generalization and a feature-positive effect. *J. exp. Analysis Behav.* **59** (1). (In the press.)

Duncan, C. J. & Sheppard, P. M. 1965 Sensory discrimination and its role in the evolution of mimicry. *Behaviour* **24**, 269–282.

Endler, J. A. 1990 On the measurement and classification of colour in studies of animal colour patterns. *Biol. J. Linn. Soc.* **41**, 315–352.

Estabrook, G. F. & Jespersen, D. C. 1974 Strategy for a predator encountering a model-mimic system. *Am. Nat.* **108**, 443–457.

Getty, T. 1985 Discriminability and the sigmoid functional response: how optimal foragers could stabilize model-mimic complexes. *Am. Nat.* **125**, 239–256.

Gilbert, F. S. 1986 *Hoverflies*. Cambridge Naturalists Handbooks 5. Cambridge University Press.

Grewcock, D. A. 1992 The hoverflies: a case of 'poor' mimicry? PhD thesis, Nottingham University.

Guildford, T. 1990 The evolution of aposematism. In *Insect defences* (ed. D. L. Evans & J. O. Schmidt), pp. 23–61. State University of New York.

Herrnstein, R. J., Loveland, D. H. & Cable, C. 1976 Natural concepts in pigeons. *J. exp. Psychol. Anim. Behav. Process.* **2**, 285.

Hetz, M. & Slobodchikoff, C. N. 1988 Predation pressure on an imperfect Batesian mimicry complex in the presence of alternative prey. *Oecologia* **76**, 570–573.

Hodos, W. 1972 Vision and the visual system: a bird's eye view. In *Progr. Psychobiol. physiol. Psychol.* **6** (ed. J. M. Sprague & A. N. Epstein), pp. 29–62. London: Academic Press.

Huheey, J. E. 1964 Studies of warning coloration and mimicry. IV. A mathematical model of model-mimic frequencies. *Ecology* **45**, 185–188.

Huheey, J. E. 1988 Mathematical models of mimicry. *Am. Nat.* **131** (Suppl.), 22–41.

Lea, S. E. G. & Harrison, S. N. 1978 Discrimination of polymorphous stimulus sets by pigeons. *Q. Jl. exp. Psychol.* **30**, 521–537.

Luedeman, J. K., McMorris, F. R. & Warner, D. D. 1981 Predators encountering a model-mimic system with alternative prey. *Am. Nat.* **117**, 1040–1048.

Malcolm, S. B. 1990 Mimicry: status of a classical evolutionary paradigm. *Trends Ecol. Evol.* **5**, 57–62.

Nevison, C. M. 1989 Objective measures of model similarity within and between wasp nests. BSc Honours thesis, Nottingham University.

Owen, J. 1981 Trophic variety and abundance of hoverflies (Diptera, Syrphidae) in an English suburban garden. *Holarct. Ecol.* **4**, 221–228.

Owen, J. 1991 *Ecology of a garden*. Cambridge University Press.

Owen, J. & Gilbert, F. S. 1989 On the abundance of hoverflies (Diptera, Syrphidae). *Oikos* **55**, 183–193.

Parker, J. 1990 *Mimicry in hoverflies*. BSc Honours thesis, Nottingham University.

Pough, F. H., Brower, L. P., Meck, H. R. & Kessell, S. R. 1973 Theoretical investigations of automimicry: multiple-trial learning and the palatability spectrum. *Proc. natn. Acad. Sci. U.S.A.* **70**, 2261–2265.

de Ruiter, L. 1952 Some experiments on the camouflage of stick caterpillars. *Behaviour* **4**, 222–232.

Sheppard, P. M. 1959 The evolution of mimicry: a problem in ecology and genetics. *Cold Spring Harb. Symp. quant. Biol.* **24**, 131–140.

Sheppard, P. M. 1975 *Natural selection and heredity*, 4th edn. London: Hutchinson.

Stubbs, A. E. & Falk, S. 1983 *British hoverflies: an illustrated guide*. London: British Entomological & Natural History Society.

Turner, J. R. G. 1984 Darwin's coffin and Doctor Pangloss – do adaptationist models explain mimicry? In *Evolutionary ecology* (ed. B. Shorrocks), pp. 313–361. Oxford: Blackwell.

Turner, J. R. G. 1987 The evolutionary dynamics of Batesian and Müllerian mimicry: similarities and differences. *Ecol. Ent.* **12**, 81–95.

Vaughan, W. & Greene, S. L. 1984 Pigeons' visual memory capacity. *J. exp. Psychol. Anim. Behav. Process.* **10**, 256.

Wickler, W. 1965 Mimicry and the evolution of animal communication. *Nature, Lond.* **208**, 519–521.

Wickler, W. 1968 *Mimicry in plants and animals*. London: Weidenfeld & Nicholson.

Received 7 December 1992; accepted 21 December 1992

Plate 1 was printed by George Over Ltd, Rugby and London, U.K.