Hoverfly mimicry deceives humans

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(Accepted 11 January 2005)

Abstract
It is believed that the resemblance of many hoverflies to stinging hymenopterans is a case of Batesian mimicry, though there is little experimental evidence that it is effective in protecting them from predators. In this study the effectiveness of hoverfly mimicry was investigated for humans by presenting groups of university students and schoolchildren with a questionnaire which included pictures of stinging hymenopterans, mimetic hoverflies and dipteran controls. More people thought that the mimics would sting than either of the control flies, though fewer than those who thought that the mimics’ hymenopteran models would sting. This showed that the hoverflies’ mimicry worked but was not 100% effective. More people thought that the good mimics would sting than poor mimics which were black and yellow, showing that the reaction was not just due to their warning coloration. Students’ identification skills were poor; only 77%, 66% and 50% were able to correctly identify wasps, bumblebees and honeybees, respectively, but even knowledgeable students were confused by mimetic hoverflies. Significantly more of the students who had been stung thought that the Hymenoptera would sting and identified Hymenoptera correctly. Students who thought a hymenopteran would sting were in turn more likely to think that its mimic would sting. This suggests that the mimicry is partly mediated by experience. However, even students who had never been stung showed the same pattern of discrimination as those who had, suggesting that information is also passed on culturally. These results suggest that mimicry is effective and might help hoverflies avoid predation by birds but, as many of the subjects said they would kill a stinging insect, this would actually increase their chances of being killed by humans.

Key words: Batesian mimicry, hoverflies, deception, Hymenoptera

INTRODUCTION
Many hoverflies (Diptera: Syrphidae) resemble bees and wasps and this is regarded as a textbook case of Batesian mimicry (Edmunds, 1974). It is believed that the mimicry protects hoverflies from their predators, which have learned to avoid stinging Hymenoptera. However, only a very few studies have attempted to answer the crucial question of whether the mimicry fools the natural predators of hoverflies which include toads (Brower & Brower 1962, 1965), dragonflies (Beatty 1950; Kauppinen & Mappes, 2003), wasps (Pickard, 1975) and birds (Torp, 1994). Such studies are difficult to carry out in natural surroundings with free-living predators, though Kauppinen & Mappes (2003) did investigate the responses of free-living dragonflies to wasps and sarcophagid flies which had been painted different colours. Similarly, captive studies using birds are hard to perform, particularly those investigating social insects which are orientated to their nest; such experiments are also subject to ethical problems.

Human beings also have good reasons to recognize hymenopterans that frequently sting them. Humans could therefore be used as a model species to test the effectiveness of hoverfly mimicry, just as Sherratt, Rashed & Beatty (2004) investigated the effectiveness of locomotor mimicry in simulated ‘prey’ on a computer screen. Humans have the advantages that they are easier to deal with experimentally than the natural predators, yet have eyesight with comparable acuity. Another advantage of using humans is that they can be quizzed not only on their reactions to the insects, but also on their
past experiences and knowledge. It should therefore be possible to test one of the main predictions of mimicry theory: that experience of being stung should increase aversion to both the models and their mimics.

Our experience suggested that hoverfly mimicry is effective to humans, and Atkins (1948) has described many anecdotes of the mimicry fooling both beekeepers and entomologists. However, no quantitative study had been performed to confirm whether hoverfly mimics deceive humans, and entomologists rightly point out that hoverflies can readily be distinguished from bees and wasps as they have only one pair of wings, shorter antennae and no wasp-waist.

This study was therefore designed to test the ability of non-specialist humans to distinguish between photographs of stinging Hymenoptera and non-stinging Diptera, and to investigate the effects of gender and experience of being stung on the effectiveness of the mimicry of hoverflies.

MATERIALS AND METHODS

Subjects were given 1 of 2 colour plates containing 8 photographs (50 x 50 mm) of insects (c. 20 mm long) in natural poses on flowers or leaves. There were 3 stinging hymenopterans: bumblebee Bombus pascuorum, honeybee Apis mellifera, and social wasp Vespa vulgaris; their respective hoverfly mimics Arctophila superbiens, Eristalis tenax and Sericomyia silentis; and 2 control flies: a yellow and black hoverfly that is considered to be a poor wasp mimic (either Episyrphus balteatus or Helophilus pendulus), and a non-mimetic fly (either the hoverfly Cheilosia albitarsus or a muscid fly). The subjects were asked to look at the plates for 1–2 min and make quick decisions about which insects they thought would sting. They were also asked their age; gender; whether they had been stung by wasps, honeybees or bumblebees; and whether they would kill stinging insects. In 1998–99, 2000 and 2003 the questionnaires were given to a total of 1051 first year undergraduate biology students from 3 universities (University of Central Lancashire, University of Manchester and Manchester Metropolitan University), 94% of whom were between 19 and 25 years of age. At each date, half the students were given plate 1 and half plate 2. In 2003, a final section was added to the questionnaires to investigate students’ actual knowledge of Hymenoptera. This included a third plate with 3 larger photographs (80 x 60 mm) of a social wasp Vespa vulgaris, a honeybee Apis mellifera, and a bumblebee Bombus lucorum (each c. 30 mm long), which they were asked to name. This part was completed by 276 students.

The experiment was also repeated on 629 schoolchildren (age range 13–16 years) from 16 schools. Of these, 353 14- to 16-year-olds completed the final section testing their identification skills. The results from these schoolchildren are summarized here for comparison but will be analysed elsewhere to investigate age-related effects.

RESULTS

People’s perceptions of whether insects would sting

The results for both the students and the schoolchildren are summarized in Fig. 1, using the three year-groups as replicates for the students. In both cases it can be seen that more people thought that the hymenopterans would sting than that their supposed mimics would do, but more people thought that the three fly mimics would sting than that either of the control flies would sting. The results for children were similar to those of the students except that for all of the insects, relatively more children thought that they would sting. These results showed that the mimicry was at least partially effective for both groups. More people thought wasps and their mimics would sting than either bees or bumblebees and their mimics, and more thought the black and yellow control fly would sting than the black control fly. These results suggest that people’s decisions about whether an insect might sting were probably based only partly on possession of yellow

Fig. 1. The percentages of people who identified insects as likely to sting: (a) first year undergraduate students; (b) schoolchildren in key stage years 9, 10 and 11. The results for the students are the means (SE) from 6 year-groups; each set of photographs was shown to three of the groups. The results from the schoolchildren are aggregated data. Solid bars, models; hatched bars, hoverfly mimics; open bars, dipteran controls.
and black warning coloration; the overall appearance of insects must also play a part. A three-way ANOVA was carried out on the student data for the three model and mimic pairs to further investigate the effectiveness of the mimicry. This would determine whether using different photographs had had an effect on people’s decisions, whether particular mimicry groups were more feared than others, and whether models were more feared than mimics. It was found that there was no significant difference in the students’ responses to the two plates ($F_{1, 24} = 0.399, P = 0.534$), which showed that the results did not depend on the details of the pictures they were shown. However, more students thought models would sting than mimics ($F_{1, 24} = 23.28, P < 0.001$), confirming that the mimicry was not 100% effective. The ANOVA also showed different responses to the three model:mimic pairings ($F_{2, 24} = 4.69, P < 0.001$); more people thought the wasp and its mimic would sting, followed by the honeybee pairing, and the bumblebee pair. Only one interaction was significant, between plates and mimicry pairs ($F_{2, 24} = 7.64, P = 0.003$), showing that the difference between the mimicry pairs was not the same for the two plates.

**People’s experience of being stung**

Perceptions about which hymenopterans would sting were generally in agreement with personal experience. More people reported being stung by wasps (63% of students and 62% of schoolchildren) than by other Hymenoptera, just as more thought the wasp would sting (see Fig. 1). However, more people reported being stung by bumblebees (19% of students and 25% of schoolchildren) than by honeybees (13% of students and 9% of schoolchildren), even though more people thought honeybees would sting than bumblebees.

More male than female students reported being stung by wasps (69% vs 55%; $\chi^2 = 21.69, P < 0.001$) and honeybees (24% vs 10%; $\chi^2 = 20.81, P < 0.001$), but there was no significant difference for bumblebees.

**People’s ability to identify Hymenoptera**

Students proved poor at identifying stinging Hymenoptera from the large plates; 77% identified wasps correctly, but only 66% correctly identified the bumblebee and 50% the honeybee. The schoolchildren performed significantly better than students at identifying wasps (84% correct; $\chi^2 = 5.48, P < 0.05$) though there was no significant difference for honeybees (56% correct) or bumblebees (64% correct).

Logistic regression analysis showed that students who reported being stung by a wasp were more likely than students who had not been stung to correctly identify the wasp photo (87% vs 66%; $B = 1.485, P < 0.001$). Similarly those stung by bumblebees were more likely than other students to correctly identify the bumblebee photo (92% vs 62%; $B = 2.012, P = 0.002$). Being stung by a honeybee had no significant effect on the ability of students’ to correctly identify the photo of a honeybee.

**People’s reactions to stinging insects**

People proved surprisingly belligerent towards stinging insects; 53% of students and 71% of schoolchildren said they would try to kill an insect if they thought it would sting. More males (57% students and 78% schoolchildren) than females (50% students and 64% schoolchildren) would be prepared to do so. However, there was no difference between people who had been stung and those who had not been stung, in their willingness to kill insects.

**Factors affecting students’ perceptions of insects**

The student data were combined into one large dataset in SPSS. Logistic regression analysis was then carried out to determine how the students’ perception of whether an insect species would sting depended on the plate used, their gender, their previous experience of being stung, and whether they thought other species of Hymenoptera would sting. Age was not investigated because so many of the students were between 19 and 25 years old. Effects that were significant were further investigated by cross-tabulation analysis to determine the percentages involved.

**Perceptions of the Hymenoptera**

The main factor which influenced students’ perceptions of the Hymenoptera was their personal experience; students were more likely to think a hymenopteran would sting if they had previously been stung by that species. Of people who had been stung by a wasp, 88% thought the wasp would sting compared with 79% of those who had not (B = 0.537; P = 0.002). Figures for honeybees were 64% vs 52% (B = 0.534; P = 0.008) and for bumblebees 56% and 45% (B = 0.379; P = 0.024).

The only other significant factors were that students who thought a bumblebee would sting were more likely than other students to think a honeybee would sting (62% vs 46%; B = 0.671; P < 0.001) and students who thought a honeybee would sting were more likely than other students to think a bumblebee would sting (55% vs 39%).

**Perceptions of the hoverfly mimics**

The main factor that influenced students’ perception of the hoverfly mimics was their perceptions of the model; students were more likely to think a hoverfly would sting if they also thought its model would sting. For instance, 76% of students who thought that the wasp would sting also thought the wasp mimic would sting, compared with 63% of students who did not think the wasp would sting (B = 0.574; P = 0.003). Figures for the honeybee
mimic were 57% and 32% \((B = 1.050; P < 0.001)\) and for the bumblebee mimic were 44% and 20% \((B = 1.129; P < 0.001)\).

The only other significant factor was that fewer students who had been stung by a wasp thought the bumblebee mimic would sting (30%) than students who had not been stung by a wasp (35%) \((B = -0.314; P = 0.040)\).

**How are these perceptions influenced by knowledge?**

In the cases for which we had data about students’ abilities to identify Hymenoptera, further logistic regression analysis was carried out. Surprisingly this analysis showed that the ability of students to identify hymenopterans did not significantly affect their perception about whether hymenopterans or their mimics would sting.

**DISCUSSION**

Despite the rather unnatural nature of the test and the small (but larger than life size) photographs, the primary finding of the survey was extremely clear; mimetic hoverflies can fool humans, though their mimicry is not 100% effective. More people thought the good mimetic hoverflies would sting than the poor mimic and the non-mimetic control flies, though fewer than the hymenopterans. Ideally a wider range of controls should have been used with different amounts of black and yellow and different patterns to test which factors influence people’s perceptions. Nevertheless, the results do seem to show that people’s decisions about whether an insect might sting are based on more than just its possession of yellow and black warning coloration, just as Kauppinen & Mappes (2003) found for dragonflies. Other factors such as overall body shape and the precise details of the coloration pattern must play a part, and this could be the focus for further study.

The association between the students’ perception of each hymenopteran and its mimic further supports the idea that it is Batesian mimicry that is responsible for making people think that the hoverflies will sting; if people think the model hymenopterans will sting, they are more likely also to think that the mimics will sting.

The results also suggest that the students had to some extent learned about hymenopterans from experience. If they had been stung by a hymenopteran they were more likely to be able to identify it from a photo and to recognize it as likely to sting. Since there is a relationship between students’ perceptions of hoverflies and their models, this made the students who had been stung marginally more likely than those who not been stung to think that both wasp mimics (76% vs 71%) and honeybee mimics (54% vs 44%), but not bumblebee mimics (30% vs 31%) would sting.

However, the fact that the 30% of people who had never been stung were almost as good at distinguishing stinging insects as those who had been stung supports the idea that our fear and knowledge of stinging insects are also passed on culturally. It must be said, though, that the students’ knowledge of the insects was remarkably poor, with many students in particular unable to distinguish correctly between honeybees and bumblebees. This may help account for the fact that more people said they had been stung by bumblebees than by honeybees, whereas more people thought that the honeybees in the pictures would sting. It might also explain the finding that students were more likely to think a honeybee would sting if they thought a bumblebee would sting. Considering the ubiquity of these species and their potential threat to humans, it is astonishing that half the students could not identify a honeybee, a third could not identify a bumblebee, and a quarter could not identify a wasp. Since these were biology students, this could be seen as a damning indictment of natural history education within the subject. They actually performed worse than much younger schoolchildren who had not specialized in biology.

Another interesting, if surprising, finding was that being able to identify correctly the Hymenoptera from the third plate did not improve students’ ability to distinguish between models and mimics on the first two plates. This shows that mimicry could work even for experienced predators; given several insects to scan over a short time (similar to the situation of predators in the wild), even knowledgeable humans (and presumably other predators) can become confused, and tend to avoid the mimics.

The finding that people are deceived by the hoverfly mimics lends credibility to the idea that the mimicry of honeybees by droneflies *Eristalis* spp. is the origin of the ancient *Bugonia* myth (Atkins, 1948). This stated that honeybees originate by spontaneous generation from the carcasses of decaying animals. In the biblical story in which Samson found a swarm of bees in the body of a lion he had killed (Judges xiv 8), the insects were probably droneflies, attracted to the putrefying corpse to lay their eggs. Ancient people, confused by the morphological (Howarth, Clee & Edmunds, 2000) and behavioural similarities of hoverflies (Golding & Edmunds, 2000; Golding, Ennos & Edmunds, 2001) to hymenopterans, could easily be led into thinking that droneflies emerging from a corpse were in fact bees. Even today hoverfly mimicry can fool large numbers of people. In summer 2004, swarms of the hoverfly *Episyrphus balteatus*, which we have used as a poor mimic, caused panic among the population of south-east England (Wainwright, 2004), who confused them with wasps.

What does this study tell us about the protective value of mimicry in hoverflies? Though birds can detect ultraviolet (Cuthill & Bennett, 1993), there is little evidence that Hymenoptera or hoverflies are reflective in the UV. Birds and primates have comparable visual acuity, and there is evidence that that pigeons and humans may perceive wasp mimicry by hoverflies in a similar way (Dittrich *et al.*, 1993). Our study therefore suggests that mimicry in hoverflies may be adequate to fool bird predators and protect them from bird predation, just as the study of Kauppinen & Mattes (2003) suggested that it might prevent them being eaten by dragonflies. On the other
hand specialist predators of hymenopterans such as bee-eaters also eat hoverflies and may indeed be more attracted to them than to non-mimetic flies. Today, the fact that hoverfly mimicry can fool humans may have a conservation downside, too; 53% of students and 71% of schoolchildren said they would try to kill an insect if they thought it would sting. Mimetic hoverflies may therefore be almost as likely to be killed as wasps and bees, either by being swatted or by being sprayed with our ever-increasing arsenal of insecticides.

**Acknowledgements**

We would like to thank an anonymous referee for suggesting the use of logistic regression in the analysis.

**REFERENCES**


