



Why are wasps so intimidating: field experiments on hunting dragonflies (Odonata: *Aeshna grandis*)

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(Received 30 September 2002; initial acceptance 8 November 2002;
final acceptance 25 December 2002; MS. number: 7487)

The mechanisms of aposematism (unprofitability of prey combined with a conspicuous signal) have mainly been studied with reference to vertebrate predators, especially birds. We investigated whether dragonflies, *Aeshna grandis*, avoid attacking wasps, *Vespula norvegica*, which are an unprofitable group of prey for most predators. As a control we used flies that were painted either black or with yellow and black stripes. The dragonflies showed greater aversion to wasps than to flies. Black-and-yellow-striped flies were avoided more than black ones, suggesting that aposematic coloration on a harmless fly provides a selective advantage against invertebrate predators. There was no significant difference in reactions to black-painted and black-and-yellow wasps, indicating that, in addition to coloration, some other feature in wasps might deter predators. In further experiments we offered dragonflies artificial prey items in which the candidate warning signals (coloration, odour and shape) were tested separately while other confounding factors were kept constant. The dragonflies avoided more black-and-yellow prey items than solid black or solid yellow ones. However, we found no influence of wasp odour on dragonfly hunting. Dragonflies were slightly, but not significantly, more reluctant to attack wasp-shaped prey items than fly-shaped ones. Our results suggest that the typical black-and-yellow stripes of wasps, possibly combined with their unique shape, make dragonflies avoid wasps. Since black-and-yellow stripes alone significantly decreased attack rate, we conclude that even profitable prey species (i.e. Batesian mimics) are able to exploit the dragonflies' avoidance of wasps.

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Unpalatable or otherwise unprofitable prey species sometimes advertise their unsuitability to predators with bright coloration or some other feature (Poulton 1890; Cott 1940; Edmunds 1974), a phenomenon called aposematism. Warning colours are assumed to enhance the effectiveness of other warning signals by exploiting predator-learning mechanisms (Gittleman & Harvey 1980; Roper & Wistow 1986; Roper & Redston 1987; Schuler & Roper 1992). Conspicuous warning coloration reportedly facilitates the process of predator learning and prolongs the time that the predator remembers the conspicuous colour pattern that broadcasts the unprofitability of the prey (Guilford 1986, 1990). If the predator is able to learn the signal of unprofitability, an opportunity opens for a cheater to exploit this avoidance. This phenomenon, where a palatable species mimics an unpalatable one, is called Batesian mimicry (Bates 1862; Brower 1960; Papageorgis 1974; Mallet & Singer 1987; Brown 1988; Mappes & Alatalo 1997a).

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Originally, it was assumed that predator avoidance of an aposematic prey type could result only from knowledge gained through unpleasant encounters (e.g. Cott 1940). However, predators (birds) may also have an unlearned ability to avoid conspicuously coloured prey types (Smith 1975; Schuler & Hesse 1985; Roper & Cook 1989; Rowe & Guilford 1996). The predators may, for example, show avoidance behaviour towards black, yellow or red prey types presented to the predator for the first time and a simultaneous preference for green, blue or brown prey (Schuler & Hesse 1985; Kovach 1987; Roper & Cook 1989; Mastrota & Mench 1994; Rowe & Guilford 1996; Lindström et al. 1999a). Innate avoidance also often occurs when the prey is highly poisonous to the predator, as in the case of lethally toxic sea snakes, *Pelamis platurus*, innately avoided by green-backed herons, *Butorides striatus*, great egrets, *Casmerodius albus*, and snowy egrets, *Egretta thula* (Caldwell & Rubinoff 1983).

Both the ecological and the evolutionary determinants of aposematism have been repeatedly studied using vertebrate predators (great tit, *Parus major*: e.g. Alatalo & Mappes 1996; chicken, *Gallus domesticus*: e.g. Gittleman & Harvey 1980; toad, *Bufo terrestris*: Brower et al. 1970;

ameiva lizard, *Ameiva ameiva*: Boyden 1976; cod, *Gadus morhua*: Tullroth 1998; garter snake, *Thamnophis radix*: Terrick et al. 1995). There are at least two obvious reasons for this. First, as the feature to advertise the aposematic nature of the prey type is, in many cases, colour pattern, the potential predators must have colour vision or at least see colour contrasts. Second, to work as a protection mechanism for the prey, aposematism requires a predator to learn and remember. Vertebrates, especially birds, most often meet both of these requirements.

Along with vertebrate predators, certain groups of invertebrates actively forage on other invertebrates and select prey by vision (mantids: Berenbaum & Miliczky 1984; Bowditch & Bultman 1993; dragonflies: Baird 1991; Frye & Oldberg 1995). For example, Berenbaum & Miliczky's (1984) experiment suggests that an invertebrate predator, a mantid, can learn to avoid an aposematic animal, a milkweed bug, and that this avoidance is beneficial to the predator.

Dragonflies (Odonata) are a numerous group of medium-sized or large visually hunting insects (Askew 1988). A hunting dragonfly bases its decision to attack on the visual features of the prey (Mokrushov 1972; Edman & Haeger 1974; Rowe 1987; Hatto 1994; Baird 1991). The first stimulus to trigger the hunting mode of a dragonfly is usually the movement of the prey (Frye & Oldberg 1995). To check whether the potential prey item meets the criteria of acceptability, dragonflies often come close to or touch potential prey in flight (Pajunen 1964; Parr 1983). After locating the moving prey the dragonfly apparently estimates its size. Certain species reportedly reject potential prey as too large (Corbet 1999), whereas some prefer relatively large prey (Edman & Haeger 1974) or avoid potential prey below a certain size (Baird 1991). In a few cases dragonflies attack objects larger than themselves, for example individuals of larger dragonfly species and even birds (Stearns 1961). Along with prey size, prey shape is also known to play a part in the prey selection of dragonflies (Corbet 1999).

Females of certain dragonfly species choose their mates by using colour cues (Corbet 1999) and dragonflies are able to perceive ultraviolet reflection (Horvath 1995; Yong & Osorio 1996). Although it seems likely that colour and ultraviolet vision is a general phenomenon among dragonflies, no experiments have been carried out to see whether they use these abilities in prey selection.

Different interactions have been reported in studies on dragonflies and aposematic prey. The field observations of O'Donnell (1996) suggest that the dragonfly *Gynacantha nervosa* Rambur avoids the wasps *Polybia aequatorialis* Zavattari and *Mischocyttarus* sp. as prey. In contrast, Rowe (1987) reported that some large dragonfly species actively forage on bees and wasps. Furthermore, White & Sexton's (1989) experimental results suggest that the dragonfly *Hagenius brevistylus* preys on aposematically coloured monarch butterflies (Danidae), leaving the most poisonous part of the butterfly, the wings, untouched. These differences in interactions between dragonflies and their potential aposematic prey are probably due to the range of toxicity in the prey and to the local counteradaptations of dragonflies and their prey. The observations of

O'Donnell (1996), Rowe (1987) and White & Sexton (1989) offer valuable information about the interactions between dragonflies and aposematic prey but do not provide convincing evidence that the aposematic signals affect the hunting behaviour of dragonflies.

We investigated whether the brown hawkler dragonfly, *Aeshna grandis*, avoids the wasp *Vespula norvegica* as prey and which cues the dragonfly uses in decision making while hunting. We carried out four field experiments using free-flying dragonflies as predators. We first tested whether dragonflies avoid wasps more than they do flies, and then tested the relative effect of wasp colour, shape and odour on the observed avoidance.

METHODS

Study Area and Predator Species

We carried out experiments in the surroundings of Konnevesi research station (62°37'N, 26°20'E) in central Finland during August 1999 and June–August 2000.

Brown hawkers live in water during the larval stage and disperse away from the water after emerging (Askew 1988). Like most species of dragonflies, hawkers spend their 'maiden flight' mainly feeding on other flying insects in warm, sunlit spots in woodlands. We conducted the experiments in these swarming spots. Because both mature and immature dragonflies are reported to forage in these swarming spots (Askew 1988), we used both age groups in our study. Brown hawkers are fairly common in central Finland. They are suitable for our study because they are large enough (69–76 mm total body length) to attack and eat wasp-sized flying prey. We have observed them hunting mainly flies but also butterflies (e.g. genus *Pieris*) and occasionally flying beetles. Furthermore, their flight period is long, from the end of June to early October (personal observations).

Wasp Avoidance Experiment

We carried out a wasp avoidance experiment during daylight hours (1100–1700 hours) on 7 sunny days in August 1999 (3, 4, 5, 6, 9, 17 and 18 August).

We caught wasps and flies (Sargophagidae) with a butterfly net from the meadows surrounding the Konnevesi research station on either the day before or the same day that they were used, to ensure that they were still alive and fresh. We stored them in a refrigerator at 7–10°C until we tested them.

We painted the prey to produce four groups: (1) black flies; (2) black-and-yellow flies; (3) black wasps; (4) black-and-yellow wasps. We applied the paint with a thin brush after stunning the prey items with carbon dioxide in a test-tube. We painted three black stripes on the normally dark abdomen of the flies in treatment 1 and three yellow stripes with nontoxic Decorlack paint (Marabu, Dusseldorf, Germany) on the abdomen of the flies in treatment 2. We painted the normally yellow parts of the wasps in treatment 3 black, to remove the characteristic black-and-yellow coloration that is generally considered to be aposematic. The wasps of treatment 4 were given

three black stripes on the naturally black parts of their abdomen, so their coloration was similar to their natural one.

We measured the reflectance of the black and yellow paints (three times) and compared them with the natural reflectance of black and yellow stripes ($N=3$ of each colour) of five wasps. We did this to ensure that the spectral reflectance curves of the natural coloration and of the paint were similar, that is, that the yellow paint was really yellow and that, for example, no unexpected ultraviolet peaks would affect the results. All reflectance was recorded in the range 360–700 nm at 5-nm intervals using a spectroradiometer (Light Touch Software 1.04a, EG&G Gamma Scientific GS3100 Radiometer, Gamma Scientific, San Diego, U.S.A.). We measured the reflectance as a proportion of the light reflected from a calibrated 98% white standard (LabSphere). The yellow paint showed the peak reflectance around 600 nm and the shape of the reflectance curve and the peak reflectance were identical to those of the yellow stripes on the wasps. Both black paint and the black stripes of wasps gave flat reflectance curves.

To minimize confounding effects of prey size, we weighed the prey items and used only those weighing between 45 and 70 mg. Others were released immediately after catching and weighing. The individuals that met the size criteria were systematically divided by weight into four treatments (black flies: $\bar{X} \pm SD = 64.8 \pm 7.9$ mg; black-and-yellow flies: 67.4 ± 7.3 mg; black wasps: 71.7 ± 14.6 mg; black-and-yellow wasps: 67.6 ± 5.3 mg). There was no significant difference between these four groups either in weight ($F_{3,40} = 0.959$, $P = 0.422$) or in variance ($P = 0.254$). If a dragonfly attacked and damaged a prey item, we replaced it with a fresh one. However, we never presented one prey individual to more than four dragonflies. The total number of dragonflies that encountered wasps and flies was 79 (black flies: 23; black-and-yellow wasps: 20; black wasps: 19; black-and-yellow wasps: 17).

We offered the prey one at a time attached to a piece of thin fishing line 2 m long. After being painting and while prey were still unconscious and easy to handle, they were attached to the fishing line with a drop of instant glue. We first glued a piece of black paper (about 2×2 mm) on to the end of the fishing line to facilitate the attachment of the line to the dorsal side of the thorax of a prey animal. We then bound the other end of the fishing line to a fishing rod 2.5 m long. The prey items attached to the fishing line flew for a while but soon became exhausted and did not attempt to fly when later offered to the swarming brown hawkers. The only movements were the side-to-side swings and nods that the holder of the fishing rod made to provoke the dragonflies when offering the prey. We were aware that this way of offering the prey to dragonflies may bias the results, so to minimize this bias, we practised moving the fishing rod in a consistent way. We also took turns to offer prey items to dragonflies and there were always two of us to score observations of attacks. Since the prey items were nearly immobile when offered to the predator, there were no characteristic ways of flying or flying sounds to affect the hunting responses of the dragonflies.

We scored attack intensity on a five-point scale: (1) the dragonfly paused near the prey but did not touch it; (2) the dragonfly touched the prey but did not grab it with its forefeet; (3) the dragonfly grabbed the prey with its forefeet for less than 2 s and then released it; (4) the dragonfly grabbed the prey with its forefeet for more than 2 s but did not kill it; (5) the dragonfly seized the prey and killed it (in these cases the hawker also usually ate at least part of the prey).

We recorded 27 encounters between brown hawkers and black flies, 24 with black-and-yellow flies, 24 with black wasps and 25 with black-and-yellow wasps.

As soon as one of the swarming brown hawkers encountered a prey item, we observed and scored its responses, then moved to another swarming spot at least 500 m away, except when we were certain that two different dragonfly individuals encountered the prey at the same spot. We never visited the same swarming spot twice. We thus made sure that each hawker was used only once and avoided pseudoreplication. The flies and wasps that survived the dragonflies' attacks were killed by keeping them in the freezer for ca. 1 h.

Coloration Experiment

We carried out the coloration experiment between 1100 and 1700 hours on 10 sunny days between 11 June and 31 August 2000. We evaluated the effects of prey coloration alone on the responses of hunting dragonflies. As prey, we used cylindrical pieces of rubber (0.5×0.4 cm) that were painted black, yellow or black-and-yellow striped with odourless paints. We attached the artificial prey items to fishing line with a 1.5-cm piece of iron wire.

The procedure for offering prey was the same as in the wasp avoidance experiment. We recorded attack intensity on a three-point scale: (1) the dragonfly paused near the prey but did not touch it; (2) the dragonfly touched the prey item but did not grab it with its forefeet; (3) the dragonfly grabbed the prey item with its forefeet.

We recorded 33 encounters between brown hawkers and black prey items, 35 with yellow prey items and 32 with black-and-yellow striped prey items.

Wasp Odour Experiment

We conducted the wasp odour experiment between 1100 and 1700 hours on 5 sunny days between 11 June and 31 August 2000. Our aim was to investigate whether the characteristic odour of the wasp affected the hawkers' hunting behaviour. As prey, we used pieces of soft plastic foam ($0.5 \times 0.5 \times 0.5$ cm). First, we stunned five prey animals (wasps or flies) with carbon dioxide, then mashed them with a glass rod in a test-tube with a drop of water. We did this on each day to make sure the odour of the insects was fresh. We then dipped a piece of foam into the wasp or fly liquid to make the odour stick to the artificial prey. Prey items were attached to fishing line with a 1.5-cm piece of iron wire. The procedure for offering the prey and for recording attack intensity was

the same as in the coloration experiment. We recorded 17 encounters between hawkers and artificial prey dipped in fly liquid and 20 between hawkers and prey dipped in wasp liquid.

Wasp Shape Experiment

We conducted the wasp shape experiment between 1100 and 1700 hours on 5 sunny days between 11 June and 31 August 2000. We investigated whether the characteristic shape of a wasp alone affects dragonflies' attack response. As prey items we used wasps and flies that were first killed by freezing, dried with a hair drier and then painted solid black with odourless paint. Thus, no coloration or odour could affect the dragonflies' responses. Before drying and painting them, we weighed the prey items so as to choose wasps and flies that were the same size (67.0–68.0 mg). Procedures for offering prey and recording attack intensity were the same as for the coloration experiment. We recorded 30 encounters between brown hawkers and fly-shaped prey items and 30 with wasp-shaped prey items.

Data Analysis

Since the data on predator responses were categorical, we used nonparametric statistics. All *P* values are for two-tailed tests. There was no effect of sex of the dragonflies, day, or the time of day (all *P* values >0.40) on attack intensity. We therefore omitted these variables from the analysis.

RESULTS

Wasp Avoidance Experiment

Attack intensity of predators depended on whether the prey was a wasp or a fly (Mann–Whitney *U* test: $Z = -2.84$, $N_1 = 43$, $N_2 = 36$, $P = 0.005$). The intensity of attacks on wasps was low and did not differ between the two colour groups (black and black-yellow; $Z = -0.161$, $N_1 = 19$, $N_2 = 17$, $P = 0.925$). In contrast, black-and-yellow stripes significantly decreased attack intensity on flies ($Z = -2.55$, $N_1 = 23$, $N_2 = 20$, $P = 0.011$; Fig. 1). We found no significant relation between prey mass and attack intensity (flies: $r_s = -0.38$, $N = 43$, $P = 0.811$; wasps: $r_s = -0.16$, $N = 36$, $P = 0.359$).

Coloration Experiment

The colour of the artificial prey item significantly affected the responses of the dragonflies ($H_2 = 6.77$, $P = 0.034$). In pairwise comparisons predator responses were significantly more intense to black and to yellow prey items than the black-and-yellow ones ($Z = 2.417$, $N_1 = 32$, $N_2 = 33$, $P = 0.048$ after sequential Bonferroni correction). However, we found no significant differences between responses to black items and yellow items ($Z = -1.756$, $N_1 = 33$, $N_2 = 35$, $P = 0.158$) or between responses to yellow items and black-and-yellow items

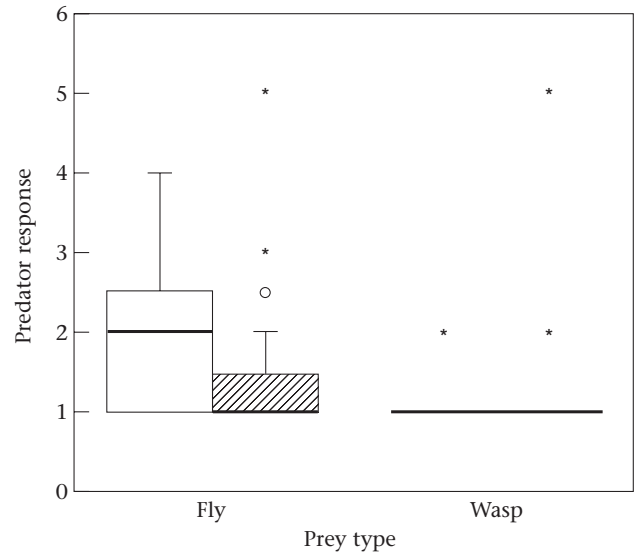


Figure 1. Responses of dragonfly predators (1=ignore, 5=kill) to black (□) and black-and-yellow (▨) wasps and flies. Lines show medians and boxes represent interquartile ranges which contain 50% of values. Whiskers show the highest and lowest values without the outliers. O: Outliers; *: extremes.

($Z = -0.925$, $N_1 = 32$, $N_2 = 35$, $P = 0.355$ after sequential Bonferroni correction; Fig. 2a). Thus, the results are in accordance with the wasp avoidance experiment where we found that having black-and-yellow stripes defended flies against dragonflies. The results of the coloration experiment show that colour itself significantly affects the predator's response.

Wasp Odour Experiment

We found no significant difference between the responses of dragonflies to wasp and fly odours ($Z = -0.130$, $N_1 = 17$, $N_2 = 20$, $P = 0.916$; Fig. 2b). This result suggests that hawkers do not use odour as a cue when deciding whether to attack wasps.

Wasp Shape Experiment

We found a nonsignificant tendency for dragonflies to attack fly-shaped more than wasp-shaped prey ($Z = 1.816$, $N_1 = 30$, $N_2 = 30$, $P = 0.069$; Fig. 2c). Thus, the reluctance of dragonflies to attack wasps may be partly caused by their characteristic shape.

DISCUSSION

In the wasp avoidance experiment, the brown hawkers avoided wasps significantly more than they did flies (Fig. 1). The features most likely to trigger this avoidance are colour, shape, odour, taste, sound and way of moving. A combination of two or more of these features is also possible (Rowe 1999).

We eliminated sound and way of moving by offering inactive prey items to the predator. The taste of the prey

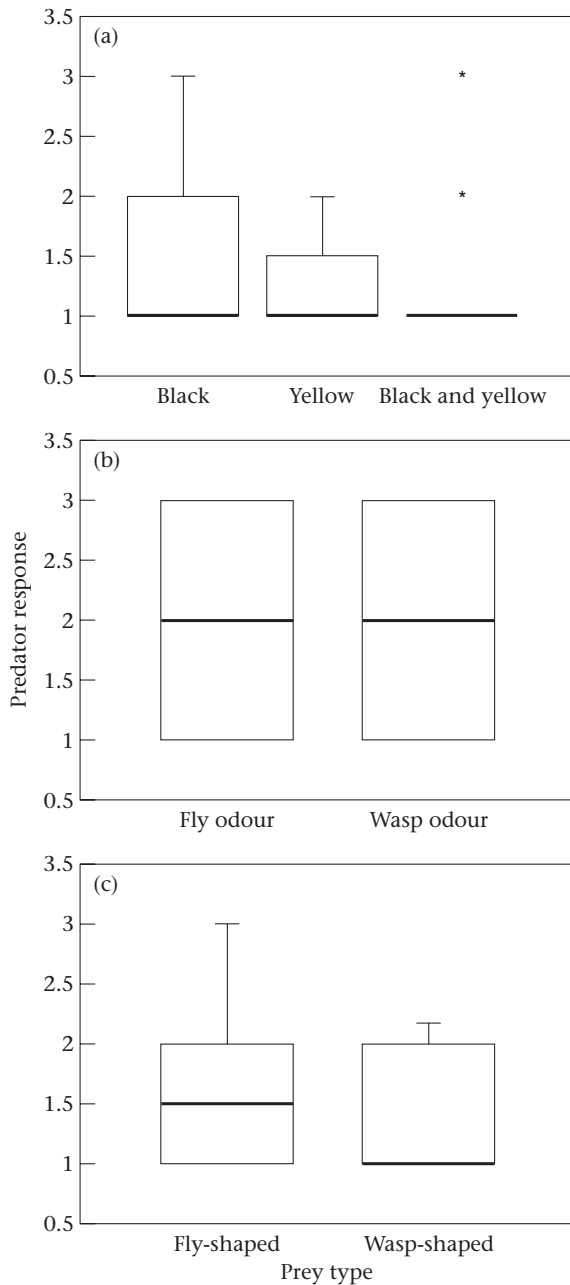


Figure 2. Responses of dragonfly predator (1=ignore, 2=touch, 3=grab) to artificial prey items with different (a) colours, (b) odours and (c) shapes. Lines show medians and boxes represent inter-quartile ranges which contain 50% of values. Whiskers show the highest and lowest values without the outliers. *: Extremes.

had no effect on attack intensity, because in the wasp avoidance experiment the majority of the dragonflies rejected the wasps before ever touching them. The role of these three features in the wasp signalling system remains unclear. The results of the odour experiment also suggest that the wasp's odour has no effect on attack intensity (Fig. 2b). Thus, the possible features causing wasp avoidance in the wasp avoidance experiment could have been only the wasp's colour or shape.

In the wasp avoidance experiment, there was a significant interaction between the colour and the species of the prey: the black-and-yellow colour significantly decreased the dragonflies' attack intensity on the flies but not on wasps (Fig. 1). Furthermore, in the coloration experiment where other wasp features were excluded, dragonflies avoided black-and-yellow prey items significantly more than they did black ones (Fig. 2a). These results suggest first that hawkers see colours, which is in line with earlier studies (e.g. Corbet 1999). Second, the colour of the potential prey item can apparently be used as an aposematic cue by a hunting dragonfly. Almost all other studies of aposematism have used vertebrate predators (e.g. Brower et al. 1970; Gittleman & Harvey 1980; Alatalo & Mappes 1996). Our results, however, support those of some earlier studies (e.g. Berenbaum & Miliczky 1984; Bowdish & Bultman 1993), suggesting that aposematic cues might also protect against an invertebrate predator.

The intensity of the hawkers' attacks on wasps was generally low regardless of whether they were black or black and yellow, suggesting that the possible effects of wasp colour were diluted by some other feature. This result leads to consideration of the role of the wasps' shape as a cue of toxicity. Although shape did not make a significant difference, dragonflies tended to attack the wasp-shaped prey items less intensely than the fly-shaped ones (Fig. 2c). Thus, the wasps' shape could have given them some protection in the wasp avoidance experiment, where they did not carry their characteristic warning coloration.

Aposematic signals of potential prey animals are sometimes composed of several cues. For example, certain coccinellid beetles carry a multicomponent signal consisting of colour, taste and odour (Marples et al. 1994). These signals may be targeted at different types of predators (i.e. odour against mammals and colours against birds, Cott 1940; Endler 1988). However, odour together with colour is more effective against chicks than colour alone, even if chicks can learn to avoid colour without the odour (Marples & Roper 1996; Rowe & Guilford 1996; Roper & Marples 1997). Our results suggest that wasps carry a multicomponent signal where colour and the unique shape, at least, work as aposematic cues. Whether this avoidance is learnt or has a genetic basis needs to be tested in separate experiments. The wasp's aposematic cues may also include its way of moving, its flying sound or its taste, and all of these need further investigation.

One possibility is that the observed advantage gained by the black-and-yellow flies was the so-called novelty effect. Several authors have suggested that predators might be wary of attacking novel prey (e.g. Coppinger 1969, 1970; Schlenoff 1984; Marples & Brakefield 1995; Mappes & Alatalo 1997b; Marples et al. 1998; Marples & Kelly 1999; Lindström et al. 2001). This is reported to be caused by the conservative nature of many predators when searching for and selecting their prey. On the other hand, novel, aposematic prey may suffer from increased predation risk because of their increased visibility (Harvey et al. 1982; Guilford 1990; Lindström et al. 1999b). However, although the black-and-yellow flies in the wasp avoidance experiment could, to some extent, be

considered novel prey (no animals are naturally coloured exactly like them), their actual novelty is open to question because of the large number of dipteran and hymenopteran insects that naturally have a black-and-yellow coloration.

In Batesian mimicry, palatable prey gain protection against predators by advertising signals or features (coloration, shape, flying pattern) similar to their unpalatable model (Bates 1862; Brower 1960; Papageorgis 1974; Mallet & Singer 1987; Brown 1988; Mappes & Alatalo 1997a; Srygley & Kingsolver 2000). A classic case of Batesian mimicry is the mimic-model relationship between certain hoverfly (Syrphidae) and wasp species (e.g. Edmunds 2000; Howarth & Edmunds 2000). Wasps and hoverflies are also a classic example of poor resemblance between models and their mimics since, paradoxically, the commonest species of hoverflies often just weakly resemble their models in their yellow-black coloration or other features (body shape or striping of colours). The question then arises 'How is it possible that natural selection can produce such an imperfection among nonprotected mimics?' Several hypotheses have been presented to explain this paradox (Edmunds 2000) and these are not mutually exclusive. The black-and-yellow flies in our avoidance experiment were poor, hoverfly-like Batesian mimics of wasps. Our artificial wasp mimic was fairly effective even though the signal was imperfect and other features offered no similarities. Black-and-yellow stripes helped to protect the fly even if coloration alone did not seem to be the crucial feature for the wasp model (Fig. 1). This may support Ditttrich *et al.*'s (1993) suggestion that when the model species is highly unprofitable for the predator, even imperfect mimicry offers significant protection against predation. Our results also suggest that, in addition to vertebrate predators (Rowe & Guilford 1996), invertebrate predators can use multiple cues together or separately when making foraging decisions about aposematic prey.

Acknowledgments

We thank Helinä Nisu for helping to stun and paint the wasps and flies. Konnevesi Research Station provided nice working facilities. We are grateful to Leena Lindström, Nicola Marples and an anonymous referee for their valuable criticism and comments on the manuscript. Maxine Iverse kindly corrected the language. The Academy of the Finland financed the study (project no. 44140).

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