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Hoverflies are imperfect mimics of wasp colouration

Christopher H. Taylor[1] · Tom Reader[1] · Francis Gilbert[1]

Abstract Many Batesian mimics are considered to be inaccurate copies of their models, including a number of hoverfly species which appear to be poor mimics of bees and wasps. This inaccuracy is surprising since more similar mimics are expected to deceive predators more frequently and therefore have greater survival. One suggested explanation is that mimics which appear inaccurate to human eyes may be perceived differently by birds, the probable agents of selection. For example, if patterns contain an ultra-violet (UV) component, this would be visible to birds but overlooked by humans. So far, indirect comparisons have been made using human and bird responses to mimetic stimuli, but direct colour measurements of mimetic hoverflies are lacking. We took spectral readings from a wide range of hoverfly and wasp patterns. They show very low reflectance in the UV range, and do not display any human-invisible colour boundaries. We modelled how the recorded spectra would be perceived by both birds and humans. While colour differences between wasps and hoverflies are slightly more distinct according to human visual abilities, bird vision is capable of discriminating the two taxa in almost all cases. We discuss a number of factors that might make the discrimination task more challenging for a predator in the field, which could explain the apparent lack of selection for accurate colour mimicry.

Keywords Spectrophotometry · Colour analysis · Visual model · Just Noticeable Difference · Batesian mimicry · Syrphidae

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Introduction

Colour is widely used by animals as a signal, for example to attract mates (Andersson 1994) or as an anti-predator warning display (Ruxton et al. 2004). However, colour is an experience as much as a physical property, and therefore the perceived signal depends on the visual and cognitive abilities of the observer (Endler 1990). For example, male blue tits (*Cyanistes caeruleus*) use an ultra-violet (UV) signal to attract a mate, which is striking to female conspecifics but invisible to humans (Andersson et al. 1998). The butterfly *Heliconius numata* displays a colourful wing pattern that conveys different signals to other butterflies and to potential predators (Llaurens et al. 2014). Cases like these demonstrate the importance of considering the signal receiver when assessing the colour component of any biological signal, and show that doing so can shed new light on well-studied systems.

Some harmless organisms attempt to deceive predators by mimicking the display of a more dangerous "model", in a process known as Batesian mimicry (Bates 1862). Mimetic displays can incorporate a range of different cues, including shape (Jones et al. 2013), pattern (Bain et al. 2007) and movement (Golding et al. 2005), but among these, colour is thought to be particularly salient to predators (Marples et al. 1994; Aronsson and Gamberale-Stille 2012; Kazemi et al. 2014). Most experimental evidence suggests that Batesian mimics should gain the greatest protection by resembling their models as accurately as possible (Dittrich et al. 1993; Lindström et al. 1997). However, to human eyes there is great variation in the degree of resemblance between mimics and models in nature, which raises the question of why the less accurate mimics persist in the face of predicted selection towards perfect resemblance (Edmunds 2000; Kikuchi and Pfennig 2013).

One proposed solution to the problem is that a perceived lack of mimetic accuracy as observed by humans might be specific to our particular visual abilities (Cuthill and Bennett 1993). If mimicry is in the "eye of the beholder", those mimics that we (as humans) consider to be inaccurate might be highly accurate when viewed by an observer with different sensory and cognitive capabilities. A key part of Cuthill and Bennett's (1993) argument was that in systems with avian predators, the birds' ability to detect UV light (Chen and Goldsmith 1986) might lead them to interpret patterns very differently to humans.

In their "eye of the beholder" hypothesis, Cuthill and Bennett (1993) make particular reference to hoverflies (Diptera: Syrphidae), which, together with their models, are a key study system for understanding the evolution of imperfect mimicry (see e.g. Dittrich et al. 1993; Azmeh et al. 1998; Holloway et al. 2002; Penney et al. 2012). The family comprises a large number of species, many of which are abundant and widespread, ranging from non-mimetic to highly accurate mimics of various hymenopteran models (bees and wasps; Apidae and Vespidae), with a wide range of accuracy in between (Gilbert 2005; Rotheray and Gilbert 2011).

Predation from birds is thought to provide the main selective pressure on hoverfly colour patterns (Waldbauer 1988; Gilbert 2005; Bain et al. 2007). Bees and wasps are unpalatable to most birds due to their sting and tough cuticle (Mostler 1935), although a few specialists do prey on them despite these defences, usually by removing the sting prior to consumption (Birkhead 1974). Hoverflies do not appear to have any chemical or physical defence, being readily accepted and consumed by birds that have not previously encountered a model (Mostler 1935). Some models, such as *Apis mellifera* and *Vespula vulgaris*, are widespread in the Palearctic and overlap extensively with the ranges of many hoverfly species, while other potential models (e.g. *Ectemnius cavifrons*) are more

restricted geographically and may be present in only part of the range of a given mimic (Richards 1980). Most hoverflies, bees and wasps are also likely to overlap over a finer, microhabitat scale, with many being frequent flower visitors. In the UK, most species of hoverfly first emerge between March and May and remain active until at least September (Stubbs and Falk 2002), with workers of social Hymenoptera generally reaching peak abundance in July/August (Richards 1980).

Given the discrepancy between bird and human visual abilities, it is vital to consider avian perception of the mimetic signals (Cuthill and Bennett 1993). Suitable methods are well-developed for both collection of spectral data and its subsequent interpretation through the eyes of a particular observer (Endler 1990; Vorobyev and Osorio 1998; Endler and Mielke 2005). These methods have been used to investigate mimetic accuracy in animals such as fish (Cheney and Marshall 2009), butterflies (Llaurens et al. 2014) and salamanders (Kraemer and Adams 2014), but to our knowledge, detailed colour analysis is lacking for hoverflies and their hymenopteran models.

Most animals, including birds, are thought to perceive the chromatic (hue and saturation) and achromatic (brightness) components of colour separately, and the information in these different channels may be used in different contexts by the signal receiver (Giurfa et al. 1997; Osorio et al. 1999). Chromatic stimuli are useful for comparison among disparate objects, as the chromatic properties do not change much under different illumination conditions. Achromatic signals are strongly affected by illumination, but are useful for detecting local changes in spectral properties, such as at the border between two colour patches (Osorio et al. 1999). From this, we predict two possible ways in which spectral properties could be used by an observer to discriminate between models and mimics. The absolute values of chromatic stimuli could be important, as birds have been shown to learn and recognise particular colour combinations in potential prey (Svádová et al. 2009; Aronsson and Gamberale-Stille 2012; Kazemi et al. 2014). For achromatic stimuli, the absolute values are less likely to be relevant, since they are difficult to compare for samples that are separated in space and time (Osorio et al. 1999). However, the achromatic contrast between colour patches within a single pattern will be easier to detect, and could form an important signal (Aronsson and Gamberale-Stille 2013).

In this study, we present data on both chromatic and achromatic components of the colours of wasp-mimicking hoverflies and their potential models, confirming that there is no "hidden" signal in the patterns of either taxon. Then, we interpret the colours through the eyes of avian predators and estimate the level of mimetic accuracy that is achieved. In doing so, we show that mimicry of wasp colours by hoverflies is, to varying degrees, imperfect.

Materials and methods

Specimens

Insects were collected using a hand net from wild communities in Nottinghamshire, UK and surrounding areas, during July to September 2014. Target insects were any hoverflies or stinging Hymenoptera bearing a two-colour (typically yellow and black) pattern (Fig. 1), but excluding bumblebees and their putative mimics because they are very likely part of a different mimicry ring (Gilbert 2005), and their hairiness makes taking reliable
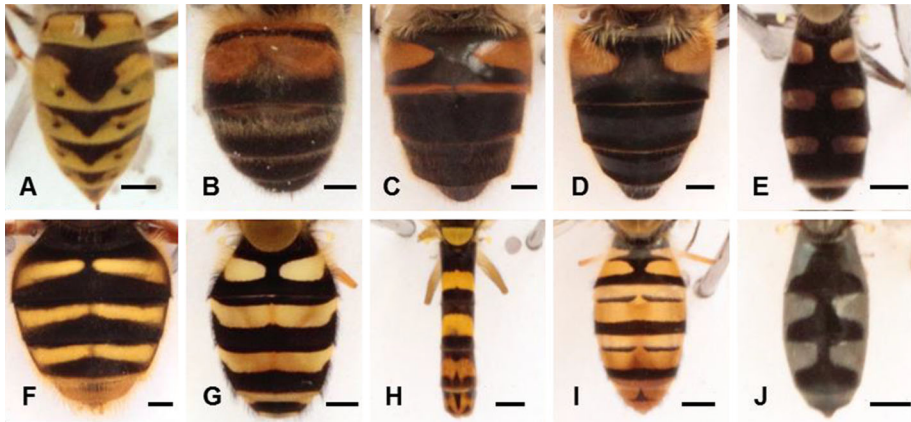
Fig. 1 Examples of *colour* and pattern variation in hymenopteran (**a**, **b**) and hoverfly (**c**–**j**) abdominal patterns. *Scale bars* each show 1 mm. **a** *Vesupla vulgaris*. **b** *Apis mellifera*. **c** *Eristalis tenax*. **d** *Eristalis pertinax*. **e** *Melangyna labiatarum*. **f** *Sericomyia silentis*. **g** *Syrphus ribesii*. **h** *Sphaerophoria scripta*. **i** *Episyrphus balteatus*. **j** *Platycheirus albimanus*. (Color figure online)

colour measurements difficult. A total of 247 individuals were identified to species level and sexed using relevant keys (Richards 1980; Stubbs and Falk 2002).

Specimens were euthanised by freezing for 10–20 min on the day of capture and then pinned. Colour measurements (see below) were taken within 1 h of death to minimise any colour changes that might occur (colours of some species fade during the days following death: C Taylor, pers. obs.).

Eight different model species were sampled, but only four were found more than twice: *Apis mellifera* (N = 14), *Vespula vulgaris* (N = 10), *V. germanica* (N = 3) and *Vespa crabro* (N = 5). We know from both theory (Getty 1985) and experiments (Lindström et al. 1997) that a model's importance in shaping predator behaviour increases with its abundance, and therefore we have excluded rare models (N < 3) from the bulk of the analysis. However, for comparison, we also conducted a repeat analysis using all eight model species.

Spectrophotometry

Reflectance measurements were taken using a 100 µm bifurcating optic fibre probe (Ocean Optics, Dunedin, FL, USA, custom spec) with one fibre connected to a pulsed xenon light source (Ocean Optics PX-2) and the other to a spectrophotometer (Ocean Optics USB 2000+ UV–VIS–ES). The probe was held steady and targeted using a micro-manipulator (Prior, Cambridge, UK). The probe was fixed at an angle of 45° to horizontal, and the patch under measurement was placed as close to horizontal as possible. A custom-made aluminium probe cover cut off at an angle of 45° aided with this alignment, and also helped to maintain a constant distance (approximately 2 mm) between the specimen and the probe (Endler 1990). The light source pulsed at a frequency of 50 Hz and spectral readings were integrated over 10 pulses, or 200 ms. Measurements were recorded for wavelengths over the range 300–700 nm at intervals of 0.4 nm. Measurements were taken in relation to a white standard (Ocean Optics WS-1 Diffuse Reflectance Standard) and recalibrated to the standard after approximately every four specimens in order to account for lamp drift. All

measurements were taken in a dark room with the xenon lamp being the only source of light.

Pilot testing revealed that readings taken from within 0.2 mm of a colour border were inaccurate (see Electronic Supplementary Material) and we therefore targeted the centres of insect colour patches that were at least 0.5 mm in width. In order to check that, in doing so, we did not overlook any colour boundaries invisible to humans, we moved the probe across adjacent areas and monitored any changes to the spectral read-out in real time. We recorded an example of such a process in the form of a transect along the abdomen of an individual of *Helophilus hybridus*, with intervals of 0.2 mm.

For each hoverfly or wasp specimen, we took spectral readings from both 'black' (low reflectance, black or dark red/brown to human eyes) and 'coloured' (higher reflectance, usually yellow or orange to human eyes) patches of the abdomen where possible. In a few cases, patches of one type were too small to take accurate readings and therefore we only recorded spectra of the predominant patch type in those cases. At least three readings were taken for both of the patch types (where present), ideally taken from different patches on different abdominal tergites, again limited in cases where patches were small or absent on some tergites.

Spectral analysis

Analysis was carried out in R version 3.1.2 (R Core Team 2014) making use of the package 'pavo' for spectral processing and visual models (Maia et al. 2013). Noise was removed from the spectra using loess smoothing over a span of 0.4. Any smoothed spectra showing negative reflectance values, which can occasionally result from noise or a drift in calibration, were adjusted by adding a constant to the spectrum such that the minimum reflectance value was zero. "Brightness" was calculated as the mean reflectance value across the whole spectrum (300–700 nm).

Given that the main selective pressure on hoverfly mimicry is considered to come from passerine birds (Dlusski 1984; Gilbert 2005) but that no single species stands out as an obvious candidate, we modelled the colour perception on a generalised 'UV-type' retina, with four cone types (U, S, M and L) with peak sensitivity at 372, 456, 544 and 609 nm respectively (Ödeen and Håstad 2003; Maia et al. 2013). Achromatic stimulation was based on a blue tit double cone with peak sensitivity of 566 nm. We used models of photon catch to calculate cone stimulation values for each spectrum (Vorobyev and Osorio 1998; Maia et al. 2013). Given the wide range of species included in this study, it is not possible to record precise illumination conditions that will be valid for all sampled individuals; however all were collected from locations with low canopy cover, and therefore we modelled illumination as 'D65', which is representative of daylight in open areas (Endler 1993). We then used receptor noise models to calculate the chromatic (ΔS) or achromatic (ΔL) contrast between a given pair of spectra, with units of 'Just Noticeable Differences' or JNDs (Vorobyev and Osorio 1998; Maia et al. 2013), and based on a Weber fraction (a measure of signal to noise ratio) of 0.06 (Olsson et al. 2015).

In accordance with the way in which birds are thought to perceive spectral information (Osorio et al. 1999), we analysed chromatic and achromatic components of the signals separately. To compare the chromatic properties of patterns from a pair of species, we treated black and coloured patch types separately, and calculated ΔS for each. We then made the assumption that, in attempting to discriminate two patterns, a predator will attend to the patch type within the patterns that shows the larger difference. Thus the chromatic

distance within a given model-mimic pairing was taken as the larger of the ΔS values for black and coloured patches.

As achromatic signals are typically used to detect within-pattern variation (Osorio et al. 1999), we calculated the within-pattern achromatic contrast (ΔL) between the black and coloured patches for each individual insect. We then calculated the absolute difference between model and mimic in values of within-pattern contrast as a measure of achromatic distance.

We repeated the model-mimic comparisons using a different visual model based on human vision, in order to examine any differences from bird perception. Human cone sensitivity data was taken from Stockman and Sharpe (2000) and we assumed a Weber fraction of 0.018 (Wyszecki and Stiles 2000). Achromatic stimulation was calculated as the sum of M and L cones (Wyszecki and Stiles 2000). To compare achromatic perception between the two systems, we regressed human against avian estimates of within-pattern contrast across the insect species sampled, with the intercept fixed at zero. The slope value gives an estimate for the ratio in achromatic sensitivity between birds and human. We carried out similar regressions on chromatic contrast data, with separate regressions for the four different model species and for the two patch types (these eight sets of data could not be pooled as they are not independent of each other).

Results

We examined spectra from 209 individual hoverflies of 33 species, and 38 individual Hymenoptera of eight species, sampling both "black" (very low reflectance) and "coloured" (higher reflectance; usually yellow or orange) patch types within the pattern. At no point did we detect a marked change in spectral properties of any individual that did not correspond to a human-visible boundary (see example with *Helophilus pendulus*, Fig. 2). None of the patterns sampled has a strong UV component in either the coloured or black patches (Fig. 3).

Human "Just Noticeable Difference" (JND) estimates for within-pattern achromatic contrast (ΔL) are related to but considerably higher than the avian equivalents (slope = 4.4, $r^2 = 0.996$, $p < 0.001$). Human and avian JND estimates for chromatic similarity (ΔS) are closer to each other, but human values are usually higher. Slopes for black patches range from 0.88 to 1.41, and for coloured patches from 1.19 to 1.94 (all $r^2 > 0.75$, $p < 0.001$; Fig. 4). Hence, the colour differences that we perceive among model and mimic species are generally rather larger than those evident to avian predators.

All remaining values in the results section are calculated with respect to avian vision. The four main model species (those with $N \geq 3$) are distinguishable from each other in terms of their spectra (Fig. 3). For coloured patches, chromatic contrast ranges from 2 to 12 JNDs (Table S1). Differences among black patches are smaller, ranging from 0.6 to 4.7, with the largest differences being between *Vespa crabro* and the other three models. The three vespid species (*Vespa crabro*, *Vespula vulgaris* and *V. germanica*) have similar levels of within-pattern achromatic contrast (ΔL = 40–45 JNDs), whereas contrast for *Apis mellifera* is much lower (ΔL = 22; Table 1).

All of the mimic species sampled are theoretically distinguishable from each of the four main model species in chromatic terms, although some have ΔS values only just larger than one (e.g. *Episyrphus balteatus* differs from *A. mellifera* by ΔS = 1.3; Table 1,
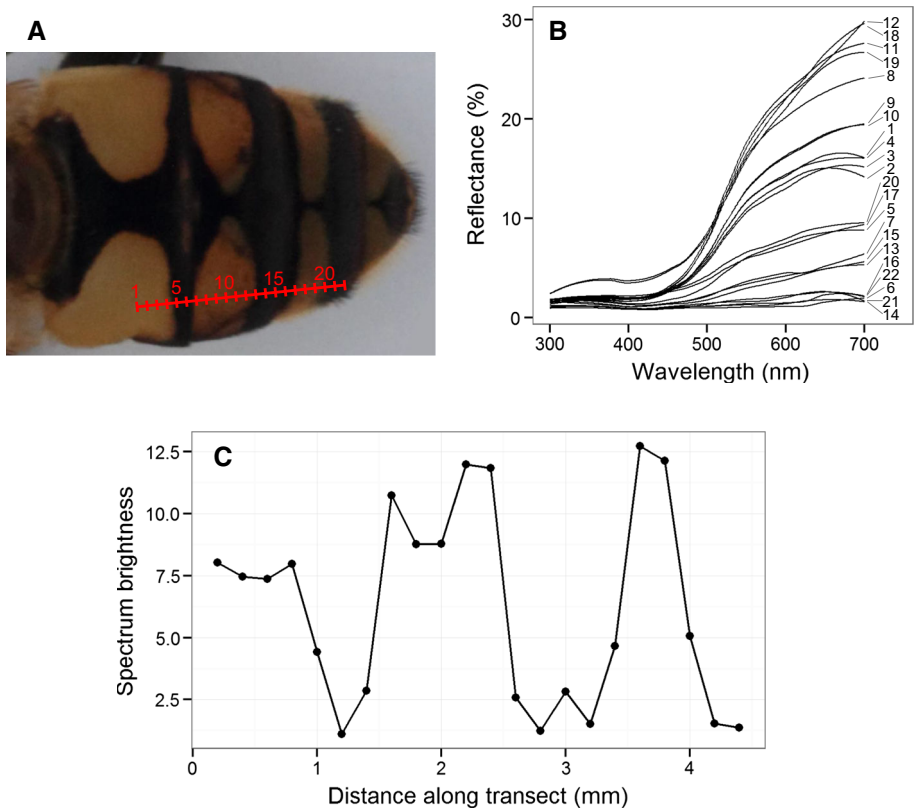
Fig. 2 Colour variation along a transect on an abdomen of *Helophilus hybridus*. **a** The abdomen, with locations of spectral readings shown in *red*. **b** All 22 spectra from the transect. **c** Variation in spectral brightness along the transect. (Color figure online)

Figs. S2 and S3). The species sampled are split roughly half and half between being most similar to *A. mellifera* (15) and *Vespula vulgaris* (14), with two being closest to *Vespa crabro* and two to *Vespula germanica*.

Achromatic differences span a wider range of values than chromatic differences, and are usually larger than the latter (Fig. 5). The hoverflies generally show lower within-pattern contrast than the Hymenoptera (Fig. S4), but some model-mimic pairings were highly similar in achromatic terms, with five mimics differing from their closest model by $\Delta L < 1$ (Table 1). When mimics are allocated to models according to the lowest achromatic difference, we find twelve mimics of *Vespula vulgaris*, ten mimics of *A. mellifera*, ten of *Vespa crabro* and one of *Vespula germanica*. Agreement between the chromatic and achromatic measures is poor—the closest model in chromatic terms matches the achromatic for only 14 of the 33 mimics (Table 1).

We repeated the above analysis taking into account all eight sampled species of Hymenoptera, including those with very low abundance. Results in this re-analysis were very similar, with only nine of 33 hoverfly species having one of these rare species as their closest model (Table S2).
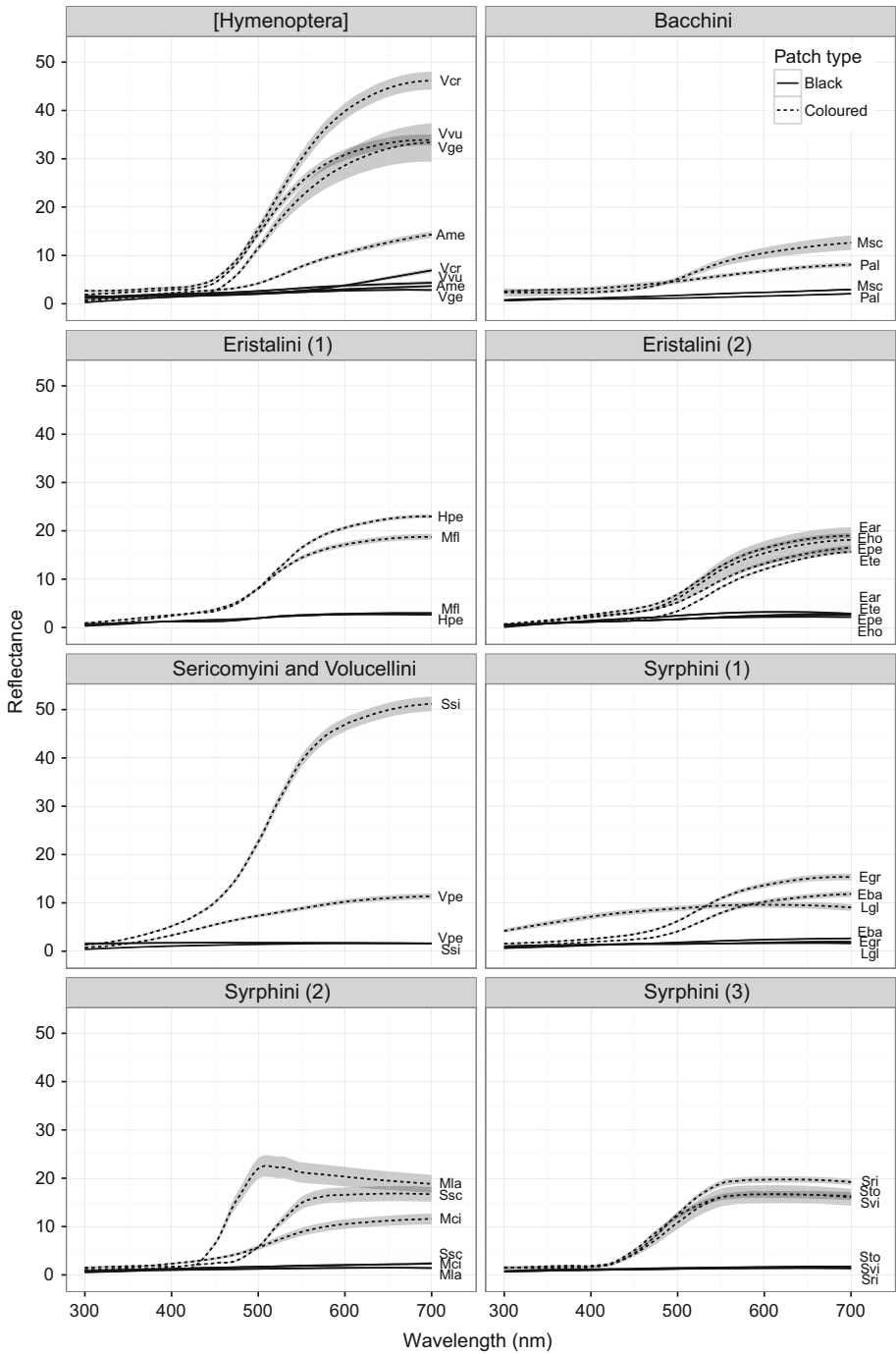
Fig. 3 Reflectance spectra for all sampled species with N > 3. *Solid* and *dashed lines* show means for *black* and *coloured* patches respectively, *shaded areas* show standard error. For species abbreviations, see Table 1
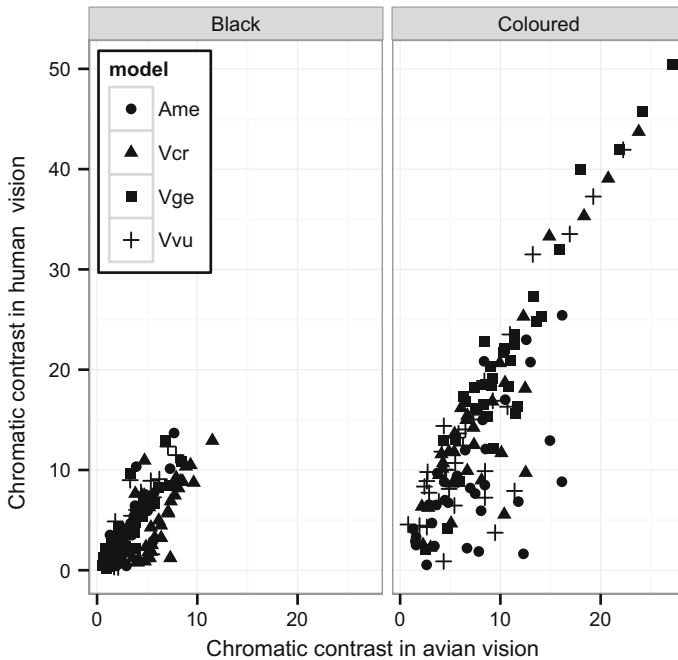
Fig. 4 Comparison of estimates of chromatic contrast as calculated in models based on avian and human vision. *Each point* represents a single model-mimic pairing. Values are in units of Just Noticeable Difference. The *two panels* show data on *black* and *coloured* patch types separately. For model abbreviations, see Table 1

Discussion

This study represents the first attempt to characterise, in detail, the colours of hoverflies and their hymenopteran models. From our measurements of insect specimens, we find no evidence that there are pattern elements or colour boundaries in either hoverflies or their models that are invisible to the human eye, a fact which until now has only been indirectly inferred (Green et al. 1999; Penney et al. 2012). Our estimates of colour similarity according to the sensory abilities of humans and birds correlated closely with one another.

Model and mimic colours were usually less distinct (smaller JND values) when calculated using the avian as opposed to the human visual model. This tallies well with recent behavioural data, which have shown that humans are at least as good at discriminating colours as chickens are, thanks to lower levels of receptor noise (Olsson et al. 2015). Nonetheless, none of the mimics differs from its nearest model by less than one avian JND, which implies that, in the eyes of birds, any given mimic-model pair should in theory be distinguishable in terms of colour (Vorobyev and Osorio 1998).

A number of researchers have speculated that a threshold of one JND may not be realistic in a natural context, instead adopting higher threshold values in the range two to four (Siddiqi et al. 2004; Feeney et al. 2014; Limeri and Morehouse 2014). There is no behavioural evidence to support the choice of a particular threshold other than one (Olsson et al. 2015) but there are a number of factors which might make the discrimination task more difficult for a predator in the wild than in the controlled laboratory settings on which

Fig. 5 Comparison of chromatic and achromatic distances between mimic species and each of the four main model species. *Each point* represents a single model-mimic species pairing. For model abbreviations, see Table 1
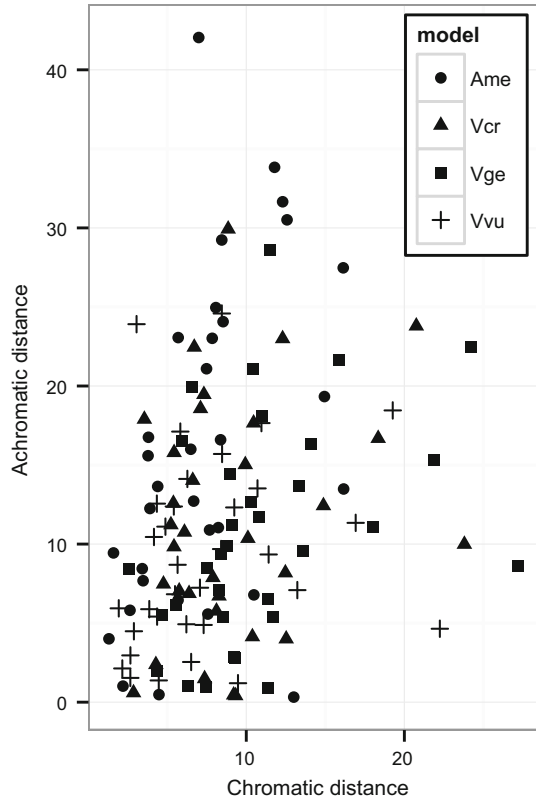
JND values are based. Firstly, predators will rarely have the opportunity to compare two prey items side by side. Temporal separation of the stimuli, as experienced by a predator learning to discriminate between models and mimics, will increase the difficulty of the task (Dyer and Neumeyer 2005).

Secondly, predators may not have the opportunity to view their prey from close range before deciding whether to attack, reducing the visual information available. It is not clear at what typical distance a bird might make its decision. Dlusski (1984) showed that hoverflies would not give flight until a mock predator approached to within 30 cm or less, suggesting that relatively close inspection might be possible on occasion, but he also observed that insectivorous birds could find prey from a distance of 10 m or more. The spatial resolution of the perceived pattern will decline with distance. Passerines can discriminate objects separated by a visual angle of about 1–3 arc min (0.017–0.05°; Donner 1951). This would give a spatial resolution of about 0.2 mm at a distance of 30 cm, which would be enough to perceive the pattern of most hoverflies, but even at a distance of a few metres, very little detail would be visible (2 mm resolution at a distance of 3 m). At that range, rather than perceiving separate patches of colour, the bird would perceive a spectrum that is an average of the two spectra (weighted by area), but it might still be able to learn differences among species based on this colour information.

Thirdly, if the prey is moving, this may make the discrimination more difficult. Notably, motion creates blur which will make borders within the colour pattern less distinct,

Table 1 Achromatic and chromatic distances of each hoverfly species to its closest model

Species	Abbrev.	Achromatic			Chromatic			
		Internal contrast	Closest model	Dist[a]	Closest model	Dist[b]	Patch color	Thorax width
Mimics								
Chrysotoxum arcuatum	Car	41.2	Vvu	1.2	Vge	9.3	C	2.6
Dasysyrphus albostriatus	Dal	55.7	Vcr	10.4	Vvu	8.5	C	2.4
Dasysyrphus tricinctus	Dtr	49.3	Vcr	4.0	Vvu	11.4	C	2.5
Epistrophe grossulariae	Egr	37.5	Vvu	2.5	Ame	3.8	B	3.2
Episyrphus balteatus	Eba	25.9	Ame	4.0	Ame	1.3	C	2.2
Eristalis arbustorum	Ear	29.6	Ame	7.7	Ame	3.5	B	3.2
Eristalis horticola	Eho	35.5	Vvu	4.5	Vvu	2.9	C	3.5
Eristalis interruptus	Eip	32.8	Vvu	7.2	Vcr	5.4	C	3.4
Eristalis pertinax	Epe	31.3	Vvu	8.7	Ame	1.6	C	3.7
Eristalis tenax	Ete	27.4	Ame	5.6	Vcr	3.6	B	4.4
Eupeodes latifasciatus	Ela	52.4	Vcr	7.0	Vge	2.6	C	2.0
Helophilus hybridus	Hhy	45.9	Vcr	0.6	Vvu	1.9	C	3.8
Helophilus pendulus	Hpe	37.9	Vvu	2.1	Vvu	2.2	B	3.0
Leucozona glaucia	Lgl	35.4	Vvu	4.6	Ame	16.2	C	2.6
Melangyna labiatarum	Mla	53.5	Vcr	8.2	Vvu	10.7	C	1.8
Melanostoma scalare	Msc	27.7	Ame	5.8	Ame	2.6	C	1.6
Meliscaeva auricollis	Mau	34.6	Vvu	5.4	Vvu	4.4	C	2.0
Meliscaeva cinctella	Mci	30.3	Ame	8.4	Ame	3.4	C	1.9
Myathropa florea	Mfl	34.1	Vvu	5.9	Vvu	3.9	C	3.8
Parhelophilus versicolor	Pve	43.0	Vge	1.0	Vvu	2.7	C	2.9
Platycheirus albimanus	Pal	28.7	Ame	6.8	Ame	10.5	C	1.8
Platycheirus clypeatus	Pcl	22.9	Ame	1.0	Ame	2.2	B	1.7
Platycheirus occultus	Poc	21.5	Ame	0.3	Ame	13.0	C	1.5
Sericomyia silentis	Ssi	63.9	Vcr	18.6	Vvu	3.1	B	4.5
Sphaerophoria scalare	Ssc	38.5	Vvu	1.5	Vvu	2.7	C	1.6
Syritta pipiens	Spi	22.3	Ame	0.5	Ame	4.5	C	1.6
Syrphus ribesii	Sri	51.1	Vcr	5.8	Vvu	4.9	C	2.8
Syrphus torvus	Sto	44.9	Vcr	0.5	Vvu	7.3	C	2.9
Syrphus vitripennis	Svi	46.8	Vcr	1.5	Vvu	5.5	C	2.4
Volucella inanis	Vin	44.9	Vcr	0.4	Ame	5.7	B	4.8
Volucella pellucens	Vpe	32.9	Vvu	7.1	Ame	8.2	C	4.9
Volucella zonaria	Vzo	38.6	Vvu	1.4	Ame	3.8	B	6.1
Xylota segnis	Xse	15.4	Ame	6.5	Ame	5.7	C	2.6
Models								
Ancistrocerus trifasciatus	Atr	45.3						2.0
Apis mellifera	Ame	21.9						3.6
Ectemnius cavifrons	Eca	65.7						2.9
Ectemnius continuus	Eco	65.9						2.8
Mellinus arvensis	Mar	70.3						2.2
Vespa crabro	Vcr	45.3						5.5

Table 1 continued

Species	Abbrev.	Achromatic			Chromatic			
		Internal contrast	Closest model	Dist[a]	Closest model	Dist[b]	Patch color	Thorax width
Vespula germanica	Vge	44.0						3.6
Vespula vulgaris	Vvu	40.0						3.1

All values are given in units of Just Noticeable Differences

[a] Achromatic distances are calculated as the absolute difference between values of internal pattern contrast (that is, the achromatic distance between coloured and black patches) between the model and mimic

[b] Chromatic distances are the ΔS values between model and mimic for whichever patch type (coloured or black, indicated in the 'patch colour' column) has the larger ΔS

although (at least in humans) cognitive processing can remove much of the blur (Burr 1980).Hoverflies are fast fliers and highly active, but one might expect birds to target them when they are at rest on flowers or vegetation rather than in flight (Dlusski 1984), which would minimise the impact of blur. Motion blur would have a similar effect to the low resolutions described above, in that above a certain level, the pattern would not be visible, and colours of different patches would become merged together. However, a strong colour difference would certainly still be visible under those circumstances.

Importantly, there is considerable variation among species in the levels of mimetic accuracy, with several showing chromatic contrast of less than three JNDs with their nearest model, and others with values of 10 or more. In their natural context, it is likely that the most accurate hoverflies are more or less "perfect" colour mimics. However, contrary to the "eye of the beholder" hypothesis (Cuthill and Bennett 1993), those mimics at the lower end of the accuracy scale should be clearly distinguishable from their models, even if we allow for the difficulties described above. If birds do indeed provide the main selective pressure on hoverfly colours, the observed variation in mimetic accuracy cannot be explained solely by the eye of the beholder hypothesis.

Our data do hint at an alternative explanation for at least some instances of mimetic inaccuracy. The model species that we sampled were all distinguishable in terms of their colours; even *Vespula vulgaris* and *V. germanica*, two very closely related wasps, differ by five JNDs. Models and mimics do not segregate neatly according to their colour (Figures S2 and S3). In contrast to other characteristics such as antenna length, in which models and mimics are consistently separated (Penney et al. 2012), there is no simple rule that could be followed to reliably distinguish hoverflies from wasps on the basis of colour. A predator can therefore adopt one of two strategies: it can learn each species and its colour entirely separately, which would carry a high cognitive burden as well as requiring repeated sampling of potentially dangerous prey (Kikuchi and Sherratt 2015), or it may generalise over a range of colours (Richards-Zawacki et al. 2013; Veselý et al. 2013). In the latter strategy, a large area of colour space would be protected, including many (though perhaps not all) of the hoverfly colours (Figs. S2 and S3), and this would explain the lack of selection for increased mimetic accuracy in those cases.

It is interesting to note that, in the majority of cases, achromatic distances between model and mimic are larger than chromatic distances (Fig. 5 and Table 1). This implies that the chromatic properties of the colour pattern may be under stronger selection from predators than the achromatic properties. The same appears to be true of mimetic

salamanders (Kraemer and Adams 2014), another system in which birds are thought to provide the main selective pressure on colours. Birds may find it difficult to compare achromatic signals that are separated in time and space given changing light conditions (Osorio et al. 1999). In addition, their sensitivity to achromatic contrast declines at small spatial scales (<1° visual angle; Ghim and Hodos 2006), meaning that they may exert little selection for accurate mimicry of luminance properties.

Numerous experiments have demonstrated that colour is an important stimulus for predators attempting to discriminate among prey items (Morrell and Turner 1970; Svádová et al. 2009; Veselý et al. 2013; Kazemi et al. 2014). However, all of these experiments have used stimuli that are well separated in colour space, corresponding to different named colour categories. More behavioural studies are needed to establish predator responses to colour stimuli that differ by more subtle degrees, and to separate the response to achromatic and chromatic properties of the stimulus. Most importantly, future work on inaccurate mimicry must consider the natural history of the predator–prey interactions in order to take account of highly influential variables such as viewing distance and movement.

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